# Nitrogen inputs by marine vertebrates drive abundance and richness in Antarctic terrestrial ecosystems

**Short title:** Penguins promote Antarctic biodiversity

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**Summary**

Biodiversity is threatened by climate change and other human activities [1] but, to assess impacts, we also need to identify the current distribution of species on Earth. Predicting abundance and richness patterns is difficult in many regions, and especially so on the remote Antarctic continent due to periods of snow cover which limit remote sensing, and the small size of the biota present. As the Earth's coldest continent, temperature and water availability have received particular attention in understanding patterns of Antarctic biodiversity [2], whereas nitrogen availability has received less attention [3]. Nitrogen input by birds is a major nutrient source in many regions on Earth [4-7] and input from penguins and seals is associated with increased plant growth [8-10] and soil respiration [11-13] at some Antarctic locations. However, the consequences of increased nitrogen concentrations in Antarctic mosses and lichens for their associated food web has hardly been addressed [14, 15] despite the fact that nutrient status of primary producers can strongly influence the abundance and diversity of higher trophic levels [16, 17]. We show that nitrogen input and $\delta^{15}N$ signatures from marine vertebrates are associated with terrestrial biodiversity hotspots well beyond (>1000 m) their immediate colony borders along the Antarctic Peninsula. Invertebrate abundance and richness was 2-8 times higher under penguin and seal influence. The nitrogen footprint area was correlated with the vertebrate population size. These findings improve our ability to predict biogeographical patterns of Antarctic terrestrial biodiversity through knowledge of the location and size of penguin and seal concentrations.

**Keywords:** Penguin, Elephant seal, Invertebrate, Nitrogen, Polar, Isotope, Cryptogam, Biogeography, Nematode, Moss, Lichen, Springtail, Mite

## Results

*Penguins and seals create nitrogen gradients beyond their colonies*

Penguin colonies (*Pygoscelis adeliae, P. antarctica* and *P. papua*) and seal (*Mirounga leonina*) aggregations created declining gradients of (i) gaseous ammonia ($NH_3$) concentrations in the air, (ii) ammonium ion ($NH_4^+$) concentrations in moss, and (iii) N concentrations in cryptogams (mosses and lichens), well beyond their physical boundaries (Fig. 1, S1, Table 1). Nitrogen availability and cryptogam N was 3-4 times lower in the absence of penguins and seals, and also did not show any correlation with distance to the coast. The cryptogam N patterns also showed declines in $\delta^{15}N$, consistent with declining marine N source influence further inland (Fig. 1). Larger colony sizes of penguins (>10000 breeding pairs) and seal aggregations (>100 individuals) resulted in cryptogam N concentrations being increased at greater distances, creating a larger footprint size (Fig. 1 c-d). The footprint size is here defined as the distance where cryptogam N along penguin- or seal-affected transects equals cryptogam N concentrations in unaffected locations. Intermittent movement of penguins and seals beyond their colonies/aggregations may locally increase cryptogam N, but this effect appears to extend to a maximum of 300 m inland (Fig. 1c). The surface area influenced by nitrogen from penguins and seals ranged between 0.4 and 6.6 $km^2$, representing up to 240 times the colony/aggregation area (Table S1).

*Invertebrate abundance and richness increases with penguin and seal presence*

Moss cover along the study transects was lower in the presence of marine vertebrates (41 %) compared to sites without (54 %) at Signy Island, but was unaffected at the other locations examined. Lichen cover and cryptogam richness along transects were not affected by the

presence of marine vertebrates (Table 1). Ecosystem respiration, measured using an infrared gas analyser attached to a closed chamber over the vegetation, was 2-5 times higher in the presence of penguins at Signy Island (Table 1, Fig. S2). The animals living within the moss and lichen, such as springtails (Collembola), mites (Acari) and roundworms (Nematoda), had 2-8 times higher abundance along transects influenced by penguins and seals at the coast compared to those without that influence (Table 1, Figs. 2, S3). Springtail and mite richness was on average 1.2-2.4 times greater in the presence of penguins and seals in both mosses and lichens (Table 1, Figs. 2, S3). Tardigrade (water bear) abundance was not significantly affected by the presence of penguins or seals.

*Penguin and seal nitrogen traced through the food web*

Microarthropod abundance and richness were positively correlated with cryptogam N (r = 0.82 and 0.47 respectively, both $P < 0.001$) (Fig. 2) but this pattern was not apparent for nematode and tardigrade abundance (Table S3). Ecosystem respiration was positively correlated with cryptogam N (r = 0.73, $P < 0.001$). There were no consistent patterns of microarthropod abundance, richness or ecosystem respiration with cryptogam water content (% water and $\delta^{13}C$), pH or temperature (Table S2), suggesting that N was indeed the primary driver of the observed patterns. This was further confirmed by the strong positive correlations between cryptogam $\delta^{15}N$ and that of the dominant primary consumers, detritivores and even predatory species of the Antarctic terrestrial food web, including springtail species (*Cryptopygus antarcticus*: r = 0.85 – 0.93, *Folsomotoma octooculata*: r = 0.90 – 0.94), oribatid mites (*Alaskozetes antarcticus* r = 0.72 – 0.77 and *Halozetes belgicae* r = 0.86 – 0.98) and predatory nematodes (*Coomansus gerlachei*: r = 0.89 and *Ditylenchus* sp.: r = 0.93) (Fig. S4). In addition there was a strong positive correlation

(r = 0.98) between $\delta^{15}N$ of prey species (*C. antarcticus*) and their predator (the mesostigmatid mite *Gamasellus racovitzai*), indicating that the N from penguins and seals flows from primary producers all the way to the top of the Antarctic terrestrial food web. The Antarctic terrestrial food web is defined here as those organism that live, reproduce and depend on the primary producers on land.

## Discussion

Our study shows that Antarctic terrestrial microarthropod biodiversity, abundance and ecosystem respiration are heavily influenced by N input from marine vertebrates, and that this effect extends well beyond colony/aggregation boundaries. Although impacts of N input by birds and seals on vegetation N concentrations and soil processes have been documented at some Antarctic sites [3, 8, 11, 14, 15, 18, 19] and in particular on sub-Antarctic Marion Island [13, 20], this is the first time that the spatial impact has been systematically quantified across sites with different climate conditions and across the major components of the terrestrial food web along the Antarctic Peninsula. Furthermore, the $\delta^{15}N$ gradients detected in vegetation with distance to colonies [8, 14, 18] were confirmed to be reflected in the major invertebrate groups of the Antarctic terrestrial food web. The data obtained confirm that the link between Antarctic marine and terrestrial biomes can expand kilometers inland [18], strongly influencing terrestrial biodiversity and microbial processes.

### *Predicting spatial biodiversity through marine vertebrate colony size*

Nitrogen input from marine vertebrates can spread many kilometers inland due to the volatilization of ammonia from faecal matter [18, 21], thereby providing an important N source

for Antarctic vegetation. The geographical range of our sampling locations, from the South Orkney Islands (60° S) to Marguerite Bay (67° S), suggests that the N effect is very likely present along the length of the Antarctic Peninsula and Scotia Arc, i.e. the full extent of the maritime Antarctic. Therefore, we compiled a map of the terrestrial nitrogen footprint size of penguin colonies along the Antarctic Peninsula coastline (Fig. 3), using the regression line of Fig. 1c and penguin population data from an online database (http://www.penguinmap.com) [22]. Due to the association between cryptogam N and microarthropod abundance and diversity these footprints are a proxy for high Antarctic terrestrial biodiversity. A similar biodiversity map in principle will be possible to construct using elephant seal aggregations, as their N footprint also increased when more animals were present. However, given the relatively small population sizes included in this study, extrapolation to population sizes of several thousands, as can be found at many sites [23], would be less accurate. Nevertheless, it is now possible to estimate the location and area size of Antarctic terrestrial biodiversity hotspots using the proxy of penguin and seal population data, which are more practicable to quantify through remote sensing than field surveys targeting terrestrial habitats directly would allow for [23, 24].

*Tracing $\delta^{15}N$ through the food web*

Vegetation was limited in the immediate vicinity of penguin and seal aggregations, which is primarily the result of trampling [25], although this is not apparent in the vegetation surveys reported here most likely a result of the focus on vegetated patches for invertebrate sampling. No response of tardigrades (water bears) to vertebrate N input was detected, which is surprising given that the majority feed on vegetation or the contained microbial community [26] and both of these sources were affected. Nematode signatures were correlated with the $\delta^{15}N$ signatures of

the moss they were extracted from (Fig. S4) but there was no consistent correlation with the N content of mosses, indicating that other aspects of the food web (e.g. microbial community, tardigrades, rotifers and smaller nematodes as prey) were affected that supported the higher nematode abundance and may have transferred the $\delta^{15}N$. This is in accordance with their known feeding activity as these nematodes are predators [27]. The same applies for the predatory mites (*G. racovitzai*), which did not have a strong correlation with the cryptogams they were extracted from. Thus, the major elements of Antarctic terrestrial food webs, primary producers, detritivores, grazers and their predators, could be directly linked to the marine-derived $\delta^{15}N$ signature from penguins and seals.

*Influence of nitrogen, water and temperature on Antarctic terrestrial ecosystems*

Understanding and predicting patterns of biota and biodiversity are major challenges in biology. Here we have shown that increased N supply can locally enhance terrestrial microarthropod abundance and biodiversity despite the challenging environmental conditions of the study sites. Water availability and temperature retain a strong influence on patterns of Antarctic biota, especially between habitat types (e.g., high invertebrate abundance in wet moss and low abundance in dry lichens Table 1, Fig. S3) and across large geographical scales [2] but, once these requirements have been met, nutrient availability can shape community assembly and ecosystem processes in Antarctic terrestrial ecosystems.

The relative contributions of temperature, water availability and N on patterns of Antarctic terrestrial biota and biodiversity are hard to quantify. However, climate warming manipulation studies, designed to reduce temperature constraints for biota, generate responses that are orders of magnitude lower [3, 28-30] than those observed between sites with and without

marine vertebrates reported here. This suggests that any changes in the distribution of marine vertebrate colonies and concentrations along the Antarctic Peninsula, as have been observed in recent years [31, 32], may have greater impacts on Antarctic terrestrial ecosystems than temperature increases *per se*.

*Concluding remarks*

Our results have several implications. First, we confirmed that patterns of Antarctic terrestrial biodiversity are locally affected by marine vertebrate colonies and aggregations well beyond their physical boundaries. These terrestrial biodiversity hotspots can now be predicted from knowledge of penguin and seal colony distribution. Second, using data on penguin colony distribution and size we were able to create a terrestrial biodiversity hotspot map for the Antarctic Peninsula coastline. Third, our data confirm that Antarctic terrestrial ecosystems appear to be affected by nutrient availability in the same way as most other ecosystems [33, 34], suggesting that processes regulating community assembly, beyond temperature and water availability [2, 35], also apply on the coldest continent on Earth. Fourth, this study provides strong support for the link between tissue quality of primary producers and abundance and diversity of higher trophic levels, with a particular emphasis on cryptogams as distinct from the vascular plants which form the majority of existing literature [17]. Finally, considering the impact that penguins and seals have on Antarctic terrestrial ecosystems, our data suggest that climate change and anthropologically driven changes in the distribution of penguins and seals [32] will have major implications for local terrestrial biodiversity patterns.

**Author contributions** All authors contributed equally to the design of the work and writing of the manuscript. SB was responsible for conducting the fieldwork, laboratory and statistical analyses.

**Acknowledgments** We are grateful for the logistical support given by the British Antarctic Survey, the Spanish Antarctic program and HMS *Protector* during the fieldwork. We would like to thank all colleagues, field assistants and boating personnel who supported our field campaigns and laboratory work, and provided statistical support; in particular: Richard van Logtestijn, James Weedon, Hans Cornelissen, Stacey Adlard, Mairi Fenton, Ali Massey, Scott Webster, Alistair Docherty, Emily Davey and Inge Bokhorst de Vries. This work was funded by a grant from the Netherlands Polar Programme (NPP-NWO 851.20.016) and by Natural Environment Research Council core funding to the British Antarctic Survey 'Biodiversity, Evolution and Adaptation' team. This manuscript was improved by constructive comments from three anonymous reviewers.

The authors declare no competing interests.

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## Figures

**Figure 1.** Spatial impact of nitrogen input on cryptogam nitrogen concentrations and $\delta^{15}N$ from marine vertebrate concentrations at sites along the Antarctic Peninsula. The nitrogen concentrations were measured along transects at sites near the coast in the presence (closed symbols, dashed line) or absence (open symbols, solid line) of marine vertebrates. (A) nitrogen concentrations of mosses and (B) lichens. The intersection of the solid and dashed line represents the effect size or footprint of vertebrate concentrations as shown in figures C and D. The decline of $\delta^{15}N$ in mosses and lichens (see insets) with distance to the coast illustrates the diminishing impact of nitrogen from the top of the marine food web further inland. Each symbol is the mean of 3-6 replicate sampling points, total number of symbols shown = 61 (38 with and 23 without marine vertebrates) and 68 (40 with and 28 without marine vertebrates) for mosses and lichens, respectively. Footprint size of penguin (C) and elephant seal (D) population sizes on the nitrogen concentration of various cryptogam species along the Antarctic Peninsula and Scotia Arc. Symbol shape as in A and B while colours reflect different cryptogams. The dotted line in panel C shows the extrapolation to data from a penguin colony at Cape Hallet (∗) where lichen nitrogen concentrations declined to 'ambient' levels at approximately 2200 m from the colony (Crittenden et al. 2015), indicating that the regression line in panel C is accurate for larger penguin colonies.

**Figure 2.** Microarthropod species richness and abundance plotted against moss (A) and lichen (B) nitrogen content in the presence (filled symbols, dashed line) or absence (open symbols, solid line) of marine vertebrates along the Antarctic Peninsula in moss (n = 61 data points) and lichen (n = 68 data points) vegetation. Larger symbol sizes represent higher microarthropod abundance (ind./g cryptogam). Each symbol is the mean of 3-6 replicate sampling points. Error bars omitted for

clarity. Symbol types represent different locations: ○ Signy, Δ Byers, □ Rothera. Significant ($P<0.001$) correlation coefficients are shown for the overall richness versus nitrogen (blue solid line).

**Figure 3.** Terrestrial nitrogen footprint size of penguin colonies along the Antarctic Peninsula and Scotia Arc. The red colouring represents the spatial extent (m) of areas with potential high nitrogen input through the presence of penguin colonies and consequently locally high terrestrial invertebrate richness and abundance. The insets show two of the sampling locations of this study: Signy Island (South Orkney Islands 60°43’ S, 45°36’ W), and Byers Peninsula (Livingston Island 62°36’ S, 60°30’ W) and the spatial extent (m) of increased nitrogen of the vegetation.

347 **Figure 1**

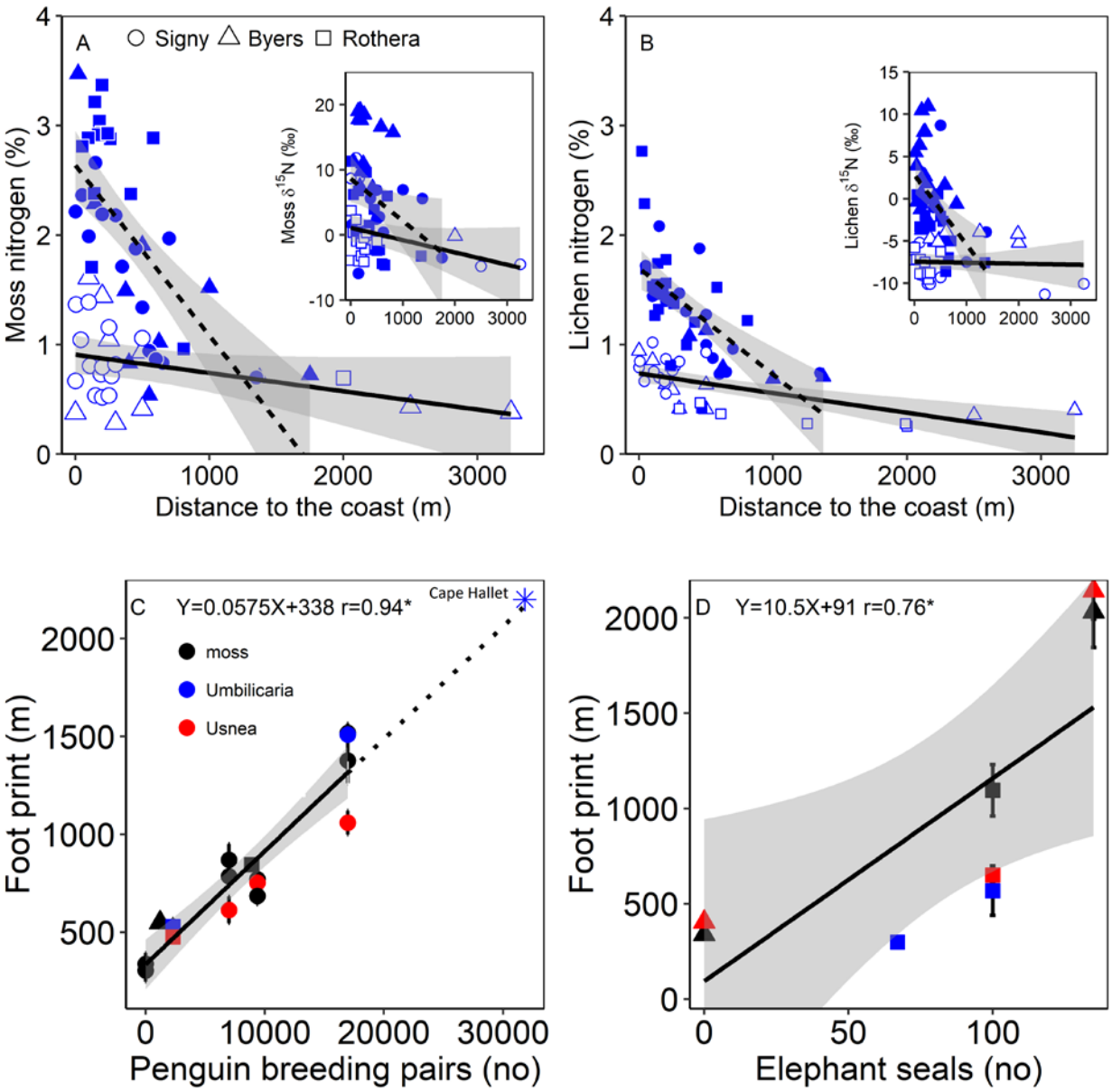


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**Figure 2**

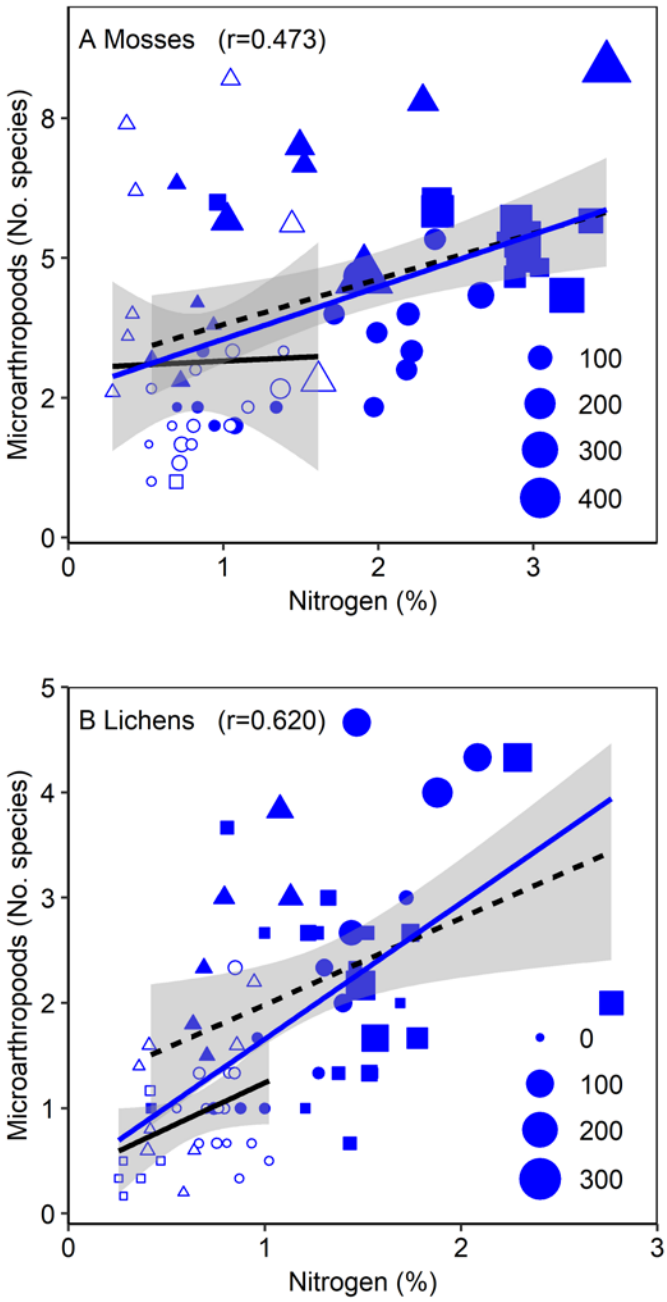
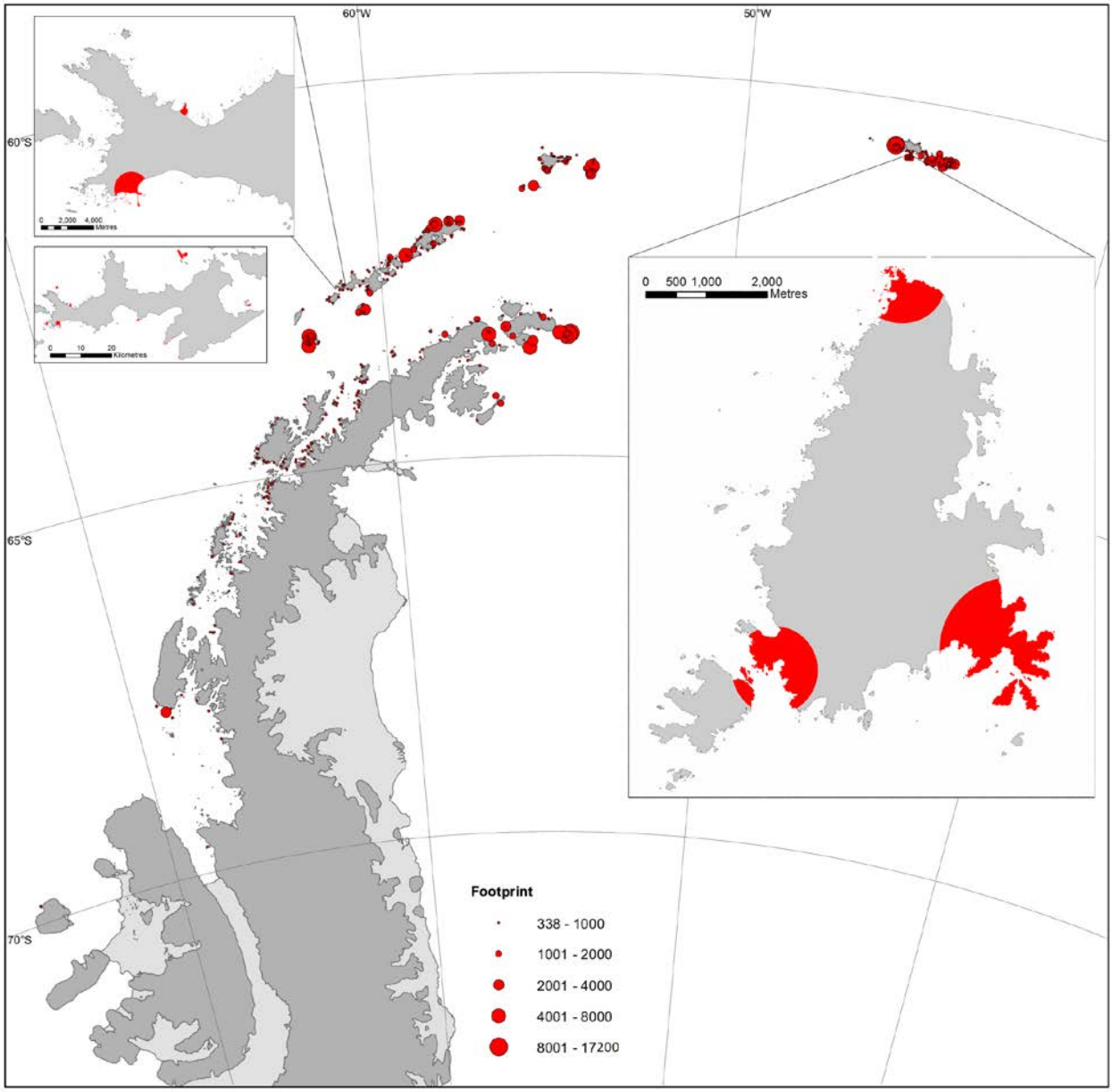

A Mosses (r=0.473)
Microarthropoods (No. species)
Nitrogen (%)
100
200
300
400
B Lichens (r=0.620)
Microarthropoods (No. species)
Nitrogen (%)
0
100
200
300

**Figure 3**


60°W
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65°S
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0 500 1,000 2,000
Metres
Footprint
338 - 1000
1001 - 2000
2001 - 4000
4001 - 8000
8001 - 17200

**Table 1** Mean values of abiotic and biotic variables in moss and lichen communities quantified along transects with distance to the coast at sites in the presence and absence of marine vertebrates (penguins and elephant seals). The total proportion of variance explained as well as the contribution of individual main factors for the invertebrate and $CO_2$ flux, is shown in the last column: Temperature (T), vegetation cover, nitrogen (N) and water content, and pH (moss only) Values in parentheses are SE, *P<0.05, **P<0.01, *** P<0.001

| **Variables** | **Marine vertebrates** | | **Variance explained** |
|---|---|---|---|
| | absent | present | |
| Temperature (°C) | 2.9 (0.8) | 3.7 (0.8) | |
| $NH_3$ (µg $N/m^3$) | 0.13 (0.04) | 0.39 (0.13)*** | |
| $NH_4$ (mg $NH_4$/ml/g) | 0.11 (0.05) | 1.63 (0.84)** | |
| Moss cover (%) | 41.3 (8.4) | 45.9 (8.3)** | |
| Lichen cover (%) | 24.7 (7.4) | 25.8 (6.8) | |
| Cryptogam richness (nr) | 3.0 (0.3) | 3.4 (0.6) | |
| **Moss** | | | |
| N (%) | 0.72 (0.08) | 2.09 (0.23)*** | |
| $\delta^{15}N$ (‰) | 0.72 (1.02) | 6.71 (2.11) | |
| $\delta^{13}C$ (‰) | -25.05 (0.08) | -25.23 (0.21) | |
| Water (%) | 64.1 (4.6) | 68.1 (3.6) | |
| pH | 5.4 (0.3) | 5.4 (0.1) | |
| $CO_2$ flux (mg $CO_2$ $m^2$ $s^{-1}$) | 74.2 (15.0) | 168.0 (55.5)* | 83%: N 36%, cover 35% |
| Microarthropod abundance (ind/g) | 13.1 (4.7) | 125.1 (22.2)** | 75%: N 55% |
| Springtail abundance (ind/g) | 12.1 (4.6) | 100.4 (15.4)' | 72%: N 52% |
| Mite abundance (ind/g) | 1.1 (0.5) | 25.0 (12.6)*** | 69%: N 56%, cover 15%, T 14% |
| Nematode abundance (ind/g) | 43.0 (15.9) | 217.9 (120.7)** | 91%: N 52% |
| Tardigrade abundance (ind/g) | 2.3 (0.8) | 15.3 (5.9) | 37%: |
| Microarthropod richness (nr) | 3.2 (0.6) | 4.7 (0.5)** | 74%: N 57% |
| **Lichen** | | | |
| N (%) | 0.63 (0.08) | 1.32 (0.09)*** | |
| $\delta^{15}N$ (‰) | -6.52 (0.90) | -0.17 (1.60)*** | |
| $\delta^{13}C$ (‰) | -21.94 (0.45) | -22.00 (0.15) | |
| Water (%) | 23.1 (7.1) | 19.7 (3.5) | |
| Microarthropod abundance (ind/g) | 4.9 (3.2) | 36.6 (7.7)*** | 59%: N 72% |
| Springtail abundance (ind/g) | 0.5 (0.3) | 3.5 (1.8)*** | 38%: N 51% |
| Mite abundance (ind/g) | 4.3 (3.3) | 33.1 (8.0)*** | 67%: N 63%, water 20% |
| Nematode abundance (ind/g) | 2.4 (0.6) | 2.5 (1.3) | 38%: |
| Tardigrade abundance (ind/g) | 1.8 (0.7) | 2.4 (1.5) | 52%: |
| Microarthropod richness (nr) | 1.0 (0.1) | 2.3 (0.2)*** | 51%: N 85% |

## Materials and Methods

This study took place at field sites at three locations along the Antarctic Peninsula, all falling between annual thermoclines of -2 °C and -7 °C but having different climates due to cloud cover and precipitation patterns [36]: (1) Signy Island (60° 71'S 45° 59'W; South Orkney Islands) lies on the Scotia Arc north-east of the Antarctic Peninsula and is a small (10 $km^2$) island (Fig. 3). Annual soil temperature is around -2.9 °C, with summer temperatures ranging between 0 and 10 °C, and annual precipitation approximates 400 mm $yr^{-1}$ but varies widely between years [37-40]. (2) Byers Peninsula (62° S 61°'W) is the far western point of Livingston Island (South Shetland Islands) and has an annual temperature of around -2.0 °C with summer temperatures above freezing [41]. Byers Peninsula loses most winter snow by the end of summer, creating a dense network of lakes and drainage streams and hosts some of the highest biological diversity along the Antarctic Peninsula [42]. Precipitation approximates 990 mm $yr^{-1}$ of which a large proportion can be deposited as rain during the summer months [41]. (3) Rothera Research Station (67°34'S 68°07'W) lies in the southern maritime Antarctic region in Marguerite Bay. It has an annual soil temperature of around -3.9 °C with precipitation approximating 500 mm $yr^{-1}$ [40, 43]. Cloud cover is lower than Signy and Byers Peninsula, resulting in much higher radiation levels (+50 %) reaching the soil surface during summer [28]. Sampling at the Rothera location was carried out on nearby islands in Ryder Bay.

At all three locations we established replicate transects (n = 3-6) at multiple sites (n = 2-5) with marine vertebrates either present or absent near the coast; Signy Island and Byers Peninsula had respectively 3 and 2 sites for both presence and absence of marine vertebrates while at Rothera there were 5 sites with and 3 sites without marine vertebrates. Penguin colony densities ranged from 18000-230000 individuals/$km^2$ and seal aggregations between 1200-25000

388 individuals/ $km^2$ (Table S3). Transects extended inland from the coast until reaching glacier
389 edges, another coastline or when vegetation composition did not change visibly (Table S3). We
390 sampled at five points along each transect to quantify nitrogen (N) input and availability, soil
391 temperature, the cryptogam community composition, the invertebrate community living within
392 the cryptogams, ecosystem respiration rates and abiotic variables relevant to invertebrate
393 abundance.

394 *Nitrogen input and abiotic measures*

395 As a measure of N input we quantified airborne ammonia ($NH_3$) concentrations using
396 passive air samplers (RAD 168, Radiello, Padova, Italy) fixed to a pole at 1 m above the ground
397 surface for a duration of 1 week. We were unable to deploy ammonia samplers along each
398 transect due to adverse weather conditions and practical logistic restrictions on visiting some
399 sampling sites more than once. However, ammonia was quantified along transects in the
400 presence and absence of marine vertebrates at all locations. Soil surface temperature was
401 measured at hourly intervals at the bottom of each pole for the same duration as the ammonia
402 samplers were exposed in the field using Hobo-loggers (Hobo UA-001-08, Onset Computer
403 Corp., MA., USA).

404 Moss pH was measured in a 30 ml water solution containing a moss sample (2 g wet
405 mass) collected from each transect sampling point. Afterwards, samples were filtered (Whatman
406 paper filter) and frozen (-20 °C) before being transported to Europe where they were analyzed
407 for ammonium ($NH_4^+$) concentrations using an auto-analyzer (Lachat Quikchem 8000). Water
408 content (%) of sampled cryptogams was quantified by the difference in mass of the samples
409 before microarthropod extraction (see below) and after oven drying at 70 °C. In addition, we
410 quantified $\delta^{13}C$ of each cryptogam sample as this represents a longer-term proxy for cryptogam

411 water content, as $\delta^{13}C$ enrichment indicates wetter growing conditions due to $CO_2$ diffusion
412 limitations [44, 45]. The N concentration and $\delta^{15}N$ signature of each cryptogam sample were
413 quantified by dry combustion in an NC 2500 elemental analyzer (Carlo Erba, Rodana, Italy)
414 coupled with a Delta$^{plus}$ continuous-flow isotope ratio mass spectrometer (Thermo Finnigan,
415 Bremen, Germany). Isotopic values were expressed as:

416 $$\delta^{15}N\ (‰) = (R_{sample} / R_{standard} - 1) \times 1000$$

417 where R is the $^{15}N/^{14}N$ ratio and atmospheric $N_2$ (air) is the standard.

418 *Biotic measurements*

419 The cryptogam species composition was quantified from digital pictures in a quadrat (30
420 cm × 30 cm) at each transect sampling point by measuring the species-specific % cover. At each
421 sampling point we collected lichen (approx. 2-3 g dry mass) and moss samples (5 cm diameter
422 cores) and extracted tardigrades and nematodes, using Berlese funnels, and springtails
423 (Collembola) and mites (Acari), using Tullgren extractors. Because cryptogam growth form can
424 have a large impact on invertebrate abundance [16] we collected the same lichen and moss
425 species along each specific transect, although species did differ between the three locations. For
426 lichens we sampled *Usnea* (predominantly *U. antarctica*) and *Umbilicaria* species (*U. decussata*
427 and *U. antarctica*), although *Umbilicaria* spp. were present at a limited number of transects and
428 locations. Moss samples included different species and families (Table S3). In addition to the
429 mono-species sampling, we sampled the dominant moss species along the Signy Island transects
430 even though this included multiple species within a transect. This multi-species sampling was
431 carried out to test whether the hypothesized invertebrate patterns, in response to the presence of
432 marine vertebrates, would be consistent across changing cryptogam composition. We were
433 unable to perform multi-species sampling at the other two locations.

Extracted tardigrades and nematodes were counted but not further identified except for the largest nematodes in our samples (*Ditylenchus* sp. and *Coomansus gerlachei*) while springtails and mites were identified to species level except for the smaller prostigmatid mites. The $\delta^{15}N$ signature of dominant springtails (*Cryptopygus antarcticus* and *Folsomotoma octooculata*), mites (*Alaskozetes antarcticus*, *Halozetes belgicae*, both Oribatida, and the predatory mesostigmatid mite *Gamasellus racovitzai*) and nematodes (*Ditylenchus* sp. and *Coomansus gerlachei*) was quantified by oven drying multiple individuals per species in tin cups before dry combustion as described as for the cryptogam analyses.

Ecosystem $CO_2$ fluxes in the dominant moss vegetation were measured at each sampling point of each transect except where sufficient moss cover was lacking (all Rothera transects and some of the Byers transects). Measurements were made by placing an opaque grey circular chamber (10 cm diameter × 5 cm height) made from polyvinyl chloride over the vegetation and monitoring the rate of change in headspace $CO_2$ concentration, across nine measurements at 10 s intervals, using an IRGA (EGM-4 PP Systems, Amesbury, MA, USA). To minimize internal chamber air exchange with the external environment, plastic skirts (20 cm wide) were attached to the base of the chamber and weighed down with small pebbles.

*Statistical analyses*

A linear mixed effect model was used to test for the effect of the presence of marine vertebrates, location (Signy, Byers and Rothera) and distance to the coast along the transects as fixed factors, while site was used as a random factor, on the measured abiotic and biotic variables. P-values were obtained by likelihood ratio tests of the full model with the effect in question against the model without the effect in question. Sampling accumulation curves, drawn using iNEXT [46], indicate that species number plateaued and that sampling was sufficient to

457 capture the species richness at sites with and without marine vertebrates (data not shown). To
458 assess the relative importance of environmental variables for the patterns observed in the
459 invertebrate and $CO_2$ flux data, we compared linear models using vegetation cover, water and
460 nitrogen content, temperature and pH using the 'relaimpo' package in R. The footprint size of
461 marine vertebrate colonies and aggregations on measured variables (cryptogam N, invertebrate
462 abundance, richness and $CO_2$ fluxes) was calculated from regression lines through the transect
463 data points with mean values from non-affected sites representing the footprint size limit (Fig. 1).
464 To calculate the footprint area of influence beyond colony borders we used the footprint distance
465 as the radius of a circle with the colony at its center. Because the colonies are located at the coast
466 the circle area influenced by penguins and seals was halved. Colonies were assumed to be
467 circular using the longest distance between edges as the diameter of a circle. Correlation
468 coefficients (Pearson correlation) were calculated for correlations between invertebrate
469 abundance, microarthropod richness, and ecosystem respiration measures with cryptogam
470 characteristics (N, water content, $\delta^{13}C$, temperature and pH). These correlations were based on
471 the transect averages of sampling distance points within each site (i.e. n = 5 for each site). In
472 addition, correlations were made between the $\delta^{15}N$ signature of cryptogams and the $\delta^{15}N$ of the
473 extracted invertebrates, except for the predatory mites which were correlated with their prey,
474 using individual samples collected along all transects. All statistical analyses were carried out
475 using R 3.3.0 [47].
476