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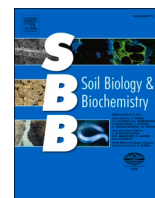
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Ecological consequences of a single introduced species to the Antarctic: terrestrial impacts of the invasive midge *Eretmoptera murphyi* on Signy Island

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ABSTRACT

The nutrient-poor soils of Antarctica are sensitive to change. Recent increases in the number of anthropogenic introductions mean that understanding the impact of non-native species on Antarctic soils is pertinent, and essential for developing future risk assessments and management strategies. Through comparative baseline assessments of vegetation, microbes, soil chemistry, substrate composition and micro-arthropod abundance, this study explored if there are detectable terrestrial ecosystem impacts resulting from the introduction of the chironomid midge *Eretmoptera murphyi* to Signy Island in maritime Antarctica. The key finding was that *E. murphyi* is the likely driver of an increase in inorganic nitrogen availability within the nutrient-poor soils in which it occurs. When compared with the levels of inorganic nitrogen present in soils influenced by native vertebrate wildlife aggregations, the increase in local nitrate availability associated with *E. murphyi* was similar to that caused by deposits from seals and giant petrel colonies. Overall, available nitrate has increased by three- to five-fold in soils colonised by the midge, relative to undisturbed soils. This may ultimately impact rates of decomposition as well as the native plant and micro-arthropod communities of Signy Island.

1. Introduction

The establishment of non-native species is one of the greatest threats to biodiversity globally (Pyšek et al., 2020). With a changing climate likely to assist further species introductions in many regions, as well as increasing anthropogenically-assisted dispersal, establishing the impact of existing invasions is crucial to identifying high-risk species and habitats in the future (Chown et al., 2022; Nielsen and Wall, 2013). Over recent decades there have been a number of introduction events leading to the establishment of non-native invertebrate species in the Antarctic region, particularly in association with human activity (Hughes et al., 2015; Molina-Montenegro et al., 2012). The ecological consequences that result from such introductions remain uncertain, however, with very few detailed studies available to date. In the sub-Antarctic, two predatory carabid beetle species introduced to the island of South Georgia resulted in a significant decline in native detritivores, but an

increase in the body size of one native herbivorous beetle, ultimately leading to negative impacts on local vegetation, demonstrating the potential complexity of the cascading consequences of introductions (Brandjes et al., 1999; Convey et al., 2011; Ernsting et al., 1995). The introduction of one of these two aggressively predatory species early in the Twentieth Century to the sub-Antarctic Kerguelen archipelago has been studied in more detail (reviewed by Lebouvier et al., 2020), highlighting very strong reductions in many native, and in some cases endemic, invertebrate populations, thus warning of a real risk of local extinctions.

The impacts of non-native invertebrates on soil nutrient cycling and soil development remain untested, despite clear evidence from both temperate and sub-Antarctic systems showing the potential for system-wide impacts from just a single species introduction (Addison, 2009; Hänel and Chown, 1998; Smith, 2007). The simple nutrient-poor terrestrial ecosystems of the maritime Antarctic have limited

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biodiversity and are characterised by slow rates of litter turnover (Beyer and Bölter, 2002; Smith, 2007). They are likely to be especially vulnerable to disruption from a non-native detritivore which alters soil nutrient balance, as low nutrient availability has been proposed as an important barrier to the establishment of higher plants in the region (Zwolicki et al., 2015). Within these ecosystems, energy and nutrient cycling are primarily driven by microbes and micro-arthropod detritivores, with any alterations to the nutrient budget having large consequences for ecosystem functioning (Davis, 1981; Koltz et al., 2018). In the future, as climate change increasingly impacts terrestrial ecosystems, it may become harder to separate the impacts of incoming invasive species from those of warming. Thus, regular impact assessments are required over time to better understand how the two factors may interact (Yang and Gratton, 2014).

The polar regions typically host detritivore-dominated terrestrial ecosystems, with most carbon processed from detrital sources, known as 'brown' energy (Koltz et al., 2018). This is especially true in the maritime Antarctic where there is a poor representation of predatory or herbivorous species (Convey, 1996; Hogg et al., 2006), and even more so on the Antarctic continent, where microbes are often at the top of the food chain (Cowan et al., 2010). In more fertile and temperate habitats, soil bacteria are typically greater contributors to mineralising nitrogen than fungi (Naylor et al., 2020). In contrast, fungi are more important in nutrient-poor systems such as those in the polar regions, owing to their ability to break down tougher substrates such as slow-growing mosses, especially in soils lacking arthropods (Wookey et al., 2009), and to metabolise at low water potentials (Whitford, 1989). Microbial abundance therefore has a strong influence on decomposition (Cowan et al., 2010) and microbes are also intimately associated with the gut flora of soil invertebrates, including *E. murphyi* (Bridge and Denton, 2006). Where arthropods such as Collembola and Acari are present, accelerated litter turnover and nutrient release can initially benefit soil bacteria through greater access to organic compounds (Stehouwer, 2004). For example, fragmentation of substrates through invertebrate detritivory releases stored carbon, some of which will be assimilated by invertebrate or microbial decomposers, and some which will be leached away as particulate matter (Wardle and Lavelle, 1997; Wookey et al., 2009). Combined with increased nutrient deposition from excreta, detritivory can alter the C:N ratio, which is closely associated with decomposition rate (Enríquez et al., 1993). However, nitrogen levels in Antarctic soils generally remain low, with nitrogen concentrations of 0.05% recorded in the soils of the Vestfold Hills (Leishman and Wild, 2001), compared with the concentrations of 1–5% that are typical of temperate soils (Bednarek and Tkaczyk, 2002). Higher levels of soil nitrogen in Antarctic substrates are usually only associated with wind-blown guano, with penguins, other seabirds and seals being key contributors to soil nutrients at a local scale throughout the Antarctic region (Ryan and Watkins, 1989; Zhu et al., 2009; Bokhorst et al., 2019). Two species of Chironomidae, *Belgica antarctica* (Jacobs) and *Parochlus steinenii* (Gerke), are the only native higher insects found in the Maritime Antarctic region, along with a third member of the same family, *Eretmoptera murphyi* (Chironomidae, Orthoclaadiinae, Schaeffer, 1914), which has been introduced from its native sub-Antarctic South Georgia to Signy Island (60°S 45°W, Fig. 1) in the South Orkney Islands. Prior to this introduction, Signy Island had no resident insect species (Chown and Convey, 2016). The terrestrial/semi-aquatic larvae of *E. murphyi* are known to contribute to litter turnover on Signy Island (Hughes et al., 2012), but the extent of their role in potentially increasing soil nutrients has not been quantified.

Signy Island hosts typical maritime Antarctic terrestrial ecosystems, dominated by cryptogams – primarily carpet- and turf-forming mosses, lichens and algae. Antarctica's two native vascular plant species, *Deschampsia antarctica* and *Colobanthis quitensis*, also occur on the island, but generally do not form extensive stands (Cannone et al., 2016, 2017, 2022). Signy's brown food web is of limited diversity and, like many maritime Antarctic systems, is dominated by Collembola (most

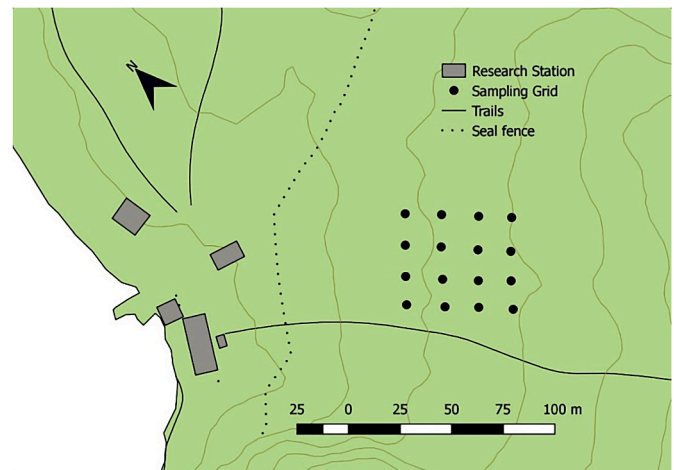


Fig. 1. Map of the 'Backslope' behind Signy Research Station, showing the location of the primary 16 point sampling grid, the seal fence and main footpaths/trails.

commonly *Cryptopygus antarcticus*; Bokhorst et al., 2008; Usher and Booth, 1984), along with Acari (Usher and Booth, 1984), Nematoda, Tardigrada and Rotifera (Maslen and Convey, 2006). Decomposition is restricted by low temperature, the depth of the permafrost active layer, and the lack of significant detritivore activity (Roads et al., 2014). These factors help to create deep moss banks that are some of the best examples of their kind in the Southern Ocean region (Fenton and Smith, 1982), but which could become vulnerable if increased nutrient availability facilitates the establishment of non-native plants (Britton et al., 2018; Royles et al., 2013).

The introduction of the parthenogenetic midge *E. murphyi* to Signy Island, probably in the 1960s, has made it the largest terrestrial animal and the only macro-detritivore present on the island. Since its introduction, which is thought to have been associated with plant transplant experiments from South Georgia and the Falkland Islands (Burn, 1982), the midge has significantly expanded its range to encompass an area of 85,000 m² and is locally highly abundant, far outweighing the biomass of native micro-arthropods where they co-occur (Bartlett et al., 2020; Hughes et al., 2012). Recognising that this detritivore would likely affect litter turnover, Hughes et al. (2012) experimentally assessed its biomass and feeding rate compared with that of the native micro-arthropod community, finding that the midge was likely to increase decomposition rate by almost an order of magnitude. However, no studies have yet examined the impact of *E. murphyi* in the field, or have looked at the range of potential ecological effects resulting from its introduction. Furthermore, few studies have examined terrestrial trophic relationships in the maritime Antarctic, whether involving native or introduced species (Bokhorst and Convey, 2016; Caruso et al., 2013; Convey, 1996). To our knowledge, only one study exists assessing the impact of terrestrial Chironomidae on ecosystem function in the Antarctic region, that of another invasive species in the sub-Antarctic, *Limnophyes minimus* (Hänel and Chown, 1998). Furthermore, all other non-Antarctic studies to date have focused on aquatic chironomid species, usually in a public health context (e.g. Failla et al., 2015).

Soil invertebrates are "underappreciated contributors to global ecosystems through their ecological interactions" (Schmitz et al., 2014). Understanding the manner in which they interact with abiotic variables and affect ecosystem processes is hence a key frontier in ecology. Addressing differences in these responses, for both native and invasive species, is also vital for predicting future change in terrestrial ecosystems. This study examines the possible impacts of *E. murphyi* on Signy Island's terrestrial ecosystems and provides baseline data on interactions between the midge and the soil it inhabits. We hypothesise that the increased detritivory resulting from high abundances of

E. murphyi will have the greatest impacts on plant available soil nitrogen and substrate composition. We investigate whether the presence of the midge may already be impacting the local ecosystem through changes to microbial abundance, micro-arthropod and vegetation communities. We also consider the scale of soil nitrogen changes in relation to existing native wildlife activity (i.e. the terrestrial impacts of marine birds and mammals). This information is required to build greater understanding of Antarctic terrestrial ecosystem functioning and the effects that can result from the introduction of even a single species to such simple communities.

2. Materials and methods

All fieldwork was conducted on Signy Island during the 2016/2017 austral summer. Mixed survey methodologies were chosen in order to meet three aims: 1) to deploy a high-resolution grid to identify the impacts of *E. murphyi* on the ecosystem; 2) to deploy a larger low-resolution grid to survey the local conditions in areas with little to no *E. murphyi* influence; 3) to collect spot samples around marine wildlife concentrations, in order to compare the scale of nitrogen deposition in a 'whole island' context.

2.1. High resolution sampling grid

A sampling grid of 16 points, each 10 m apart, was deployed on the Backslope (unofficial name), located behind the British Antarctic Survey Research Station in Factory Cove, in an area of known *E. murphyi* distribution at high densities (Bartlett et al., 2020) (Fig. 1). The location and scale of this grid was chosen to reflect a gradient of high to zero *E. murphyi* abundance, across a homogeneous area considering slope, aspect and topography. This entire area has been fenced off to prevent seals or penguins accessing and damaging the moss bank habitats (Convey and Hughes, 2022), and therefore limited direct nutrient deposition from other animals is considered to occur at this site; in addition there are no major bird breeding concentrations near the Backslope. Three substrate cores were collected from every grid point with a steel soil corer (\varnothing 2.5 cm, 10 cm length), for analyses of invertebrate abundance, organic substrate composition (i.e. litter (L) depth, organic soil (O) including any peat fraction, mineral soil (A)), inorganic nitrogen, soil organic carbon (SOC), microbial abundance and pH). All cores were returned to Signy Research Station in individual sterile sealed bags. Cores for invertebrate and substrate analysis were processed immediately. Those for microbial analysis were frozen at -20°C , returned to the United Kingdom (UK) by ship (10 weeks) at the same temperature, and then stored at the University of Birmingham until analysis, also at -20°C . Cores used for SOC analysis were also transported back to the UK as above but were kept at $+4^{\circ}\text{C}$. Appendix S1 illustrates an example sampling regime at one grid point.

2.1.1. Invertebrate abundance

To measure *E. murphyi* and native micro-arthropod abundance within the sampling grid, invertebrates were extracted from the collected substrate cores. Individual *E. murphyi* larvae (instars L2–L4), Collembola and Acari were extracted from the cores by washing through stacked sieves (2, 0.5 and 0.25 mm mesh sizes). All invertebrates were then hand-picked from the remaining soil on the 0.25 mm sieve, with the 0.5 mm sieve being checked for any further individuals. Prior to washing, clumps of moss or peat substrate were teased apart with tweezers and checked for any invertebrates before agitation and washing with the rest of the soil core.

Abundances of Acari, Collembola and *E. murphyi* larvae were averaged between the three replicate cores. Densities of animals per square metre were estimated from the product of the number of animals per corer and the corer's surface area (cf. Bartlett et al., 2020; Hughes and Worland, 2010).

2.1.2. Substrate composition

Substrate cores ($n = 3$) were separated out into their constituent elements. Stones and inorganic material (such as metal/building fragments in those plots close to previous/existing infrastructure) were removed, and each substrate type was weighed, dried to constant mass at 60°C and re-weighed. The percentage of each soil horizon in the core was calculated from the subsequent dry mass, after the removal of the vegetation layer. Total substrate depth to the rock/gravel bed was measured *in situ*. This process was repeated three times at each grid point, with the results being averaged to give depth to the nearest 0.5 cm.

2.1.3. Soil chemistry

Available soil inorganic nitrogen ($\text{N}_{\text{inorganic}}$) was captured with cation (CEM) and anion (AEM) ion-exchange membranes (AMI/CMI-7001, Membranes International, Ringwood, USA). Strips of membrane ($10\text{ cm} \times 2.5\text{ cm}$) had a hole punched through the top, with string tied through to aid retrieval. Preparation and elution protocols followed Clark et al. (2011) and Sherrod et al. (2003), respectively, as follows. Prior to installation in the field, the membrane strips were washed with deionised water (dH_2O) to remove impurities and were preconditioned by being saturated overnight in 100 mL of 2M HCl (CEM strips) or being saturated with HCO_3^- by shaking overnight in 100 mL of 1 M NaHCO_3 (AEM strips). Membranes were then rinsed with dH_2O , and CEM strips soaked for a further 12 h in dH_2O . AEM and CEM strips were inserted in pairs into the soil at five points in each of the 16 quadrats, with each pair being placed within 0.5 m of each other (see Appendix S1). Care was taken to ensure that the entire strip was submerged in the substrate, with only strings remaining visible. The strips were left *in situ* for 14 d.

Upon retrieval, membranes were cleaned of substrate with dH_2O , and ions eluted. Membranes were soaked for 3 h on a stirring plate, in either 0.5 M HCl (CEM) or 1 M NaCl (AEM), with 50 mL used per membrane. The AEM/CEM solution for each replicate pair was then transferred into a sterile pre-labelled 50 mL centrifuge tube and frozen at -80°C before being transported back to the UK by ship (10 weeks) at the same temperature and transferred to the University of Birmingham for further storage at -80°C until analysis.

Prior to analysis, the solutions were thawed overnight at room temperature and then analysed immediately with a Skalar Continuous Flow Analyser (Chemistry unit SA3000 and interface SA8505). The Skalar was run on mixed NH_4Cl and NaNO_3 standards (0.2, 0.5, 0.8, 1.2, 3 and 4 mg L^{-1}). The CEM and AEM sample solutions were pooled into one sample vial per replicate pair: 1 mL of each ion solution, with 1 mL of dH_2O were placed into a 3 mL vial. A QC drift analysis (0.5 mg L^{-1} standard) was run every 10 samples to check the accuracy of the results, followed by a wash cycle before auto-sampling resumed sample processing. Reagents used for $\text{NH}_4\text{-N}$ analysis follow Krom (1980), whilst those used for $\text{NO}_3\text{-N}$ analysis follow Gal et al. (2004). Methods for all reagent and standard preparations are given in Appendix S2. Final results were expressed as concentrations (mg L^{-1}), and results were averaged per site to give concentrations of total $\text{N}_{\text{inorganic}}$ per grid point.

2.1.4. Soil organic carbon and C: $\text{N}_{\text{inorganic}}$ ratio calculations

Carbon to inorganic nitrogen ratios (hereafter C: $\text{N}_{\text{inorganic}}$) were used as a proxy for decomposition rates of local substrates (Enríquez et al., 1993). Soil organic carbon (SOC) was calculated through loss on ignition analysis (Heiri et al., 2001). Approximately 5 g of representative soil from each core was placed in a pre-weighed ceramic crucible and oven-dried at 60°C for 24 h. The dried soil was crushed to powder form and reweighed to an accuracy of 1 mg. Powdered soil within the crucible was then heated to 110°C for 5 min to drive water off, before being placed in a muffle furnace at 550°C for 5 h. After the final burn, the crucibles and soil therein were reweighed, and SOC calculated (Eq. 1). An average % SOC was calculated between the three replicate cores. SOC was calculated per gram and multiplied by the dry bulk density (BD) to give SOC g/m^2 .

$$\%SOC = 100 - \left\{ \frac{(Wa - Wc)}{(Wb - Wc)} \right\} \times 100$$

Equation 1. Calculation of soil organic carbon (SOC) as a percentage of soil mass. Where: *Wa* = Weight after burn; *Wc* = crucible weight; *Wb* = weight before burn (Ball, 1964).

2.1.5. Habitat and vegetation survey

Vegetation cover was surveyed using a 1 m² quadrat (Appendix S1) using the classifications in Appendix S3. As *Polytrichum* spp. can outcompete other acrocarpous mosses under increased nutrient conditions (Juutinen et al., 2016), cover by members of this genus was quantified separately from other moss types. Cover represented by different habitat types (fellfield, moss bank, etc.) within each quadrat was also noted as an additional correlate. All cover results are expressed as a percentage of the entire quadrat.

2.1.6. Microbial abundance and soil pH

To establish any relationship between *E. murphyi* and microbial abundance in the soils, culturable microbial abundance in the soil from each grid point was assessed by enumerating colony forming units (CFUs) of fungi and bacteria.

Frozen soil cores were thawed overnight at +15 °C, after which 1 g (fwt) of soil from each was placed in a 15 mL Falcon tube. Sterile water (10 mL) was added to each tube, and the solution vortexed into suspension for 10 min. Dilutions of 10⁻¹ and 10⁻² were made from this suspension and 0.5 mL of each was spread under aseptic conditions onto the surface of 10% tryptic soy agar (TSA) medium. This consisted of 2 g TSA powder (Difco, Becton, Dickinson and co., Sparks, MD, USA) and 6.75 g of bacteriological agar (Oxoid No. 1) in 500 mL of distilled water, poured into single-vented 90 mm diameter Petri dishes. This medium produced both fungal and bacterial growth in trials and was thus used to enumerate culturable members of both microbial groups (Goordial et al., 2016). Three dishes were prepared for each of the three cores from the 16 individual quadrats, resulting in 144 dishes. The dishes were incubated upside-down for 14 d at 9 °C, after which CFUs of bacteria and fungi were counted. The nine counts obtained per quadrat were averaged to obtain a mean value. The pH value of the remaining soil samples was measured by adding approximately the same volume of deionised water to c. 100 g (fwt) soil from each sample to generate slurries and recording pH after 5 min (Hanna HI98130, Hanna Instruments, Leighton Buzzard, UK).

2.2. Local and island-wide soil nitrogen levels

To ascertain background levels of soil N_{inorganic}, several sites from the area local to current *E. murphyi* distribution, but with little to no fly influence, were sampled in addition to the ‘high resolution’ sample grid where there is a known fly presence. A larger grid of 35 points located 100 m apart was deployed over the entire area adjacent to the research station, covering an area of 490,000 m², and incorporating the entire known distribution of *E. murphyi* (cf. Bartlett et al., 2020) (Appendices S4, S5). Randomly selected sites (*n* = 12) were then analysed for soil chemistry using ion-exchange membranes as described previously. Proximity of these sites to seal or penguin activity was noted, along with habitat type and general site characteristics (Appendices S4, S5). One site was lost due to animal interference with the ion-exchange membranes.

In addition to local background data, ion-exchange membranes were also deployed at key wildlife sites and moss banks around Signy Island, in locations similar to *E. murphyi* habitats on the island but where the species is known to be absent. This provided an assessment of the scale of any measured change associated with *E. murphyi* abundance, in relation to the nitrogen deposition typically associated with native marine vertebrate concentrations (e.g. Zhu et al., 2009). Sites were selected to be as close as possible to the wildlife concentrations within

immediate run-off zones, if not directly within the concentrations themselves, whilst still being in vegetated (moss) areas with a substrate profile of gravel, organic soil and litter as per the Backslope (depths variable). Only the site at Elephant Flats, where mineral soils and glacial-fluvial deposits comprised the bulk of the profile, had a substrate composition that differed greatly from that of the Backslope. The protocol followed was as described above, with five pairs of membranes inserted into substrates at each location (see Appendix S1).

2.3. Statistical analyses

Data from the 4 × 4 ‘high resolution’ sampling grid were examined for outliers using Grubbs’ analysis (Grubbs, 1950) with an alpha of 0.05. Outliers were removed (4% of dataset) prior to the use of Spearman’s rank correlations to examine the relationships between *E. murphyi* abundance and all environmental variables. For the nitrogen comparisons across the island, all sites with *E. murphyi* activity (including those in the high-resolution grid) were pooled together (*n* = 18 sites), as were wildlife concentrations (*n* = 7), and control sites from around the island (*n* = 8). Sites from which *E. murphyi* was absent and that were unaffected by seals or penguins were considered as control sites. A Shapiro-Wilk normality test (alpha = 0.05) indicated that the nitrogen concentration data across all sites were not normally distributed, and therefore differences between nitrogen concentrations were explored with either a Mann-Whitney *U* test, or a Kruskal-Wallis test with Dunn-Bonferroni tests for the *post hoc* pairwise comparisons. Analyses were carried out using Prism 7.0.

3. Results

3.1. Terrestrial ecosystem impacts

The Backslope has little mineral soil and is primarily organic matter on a gravel base. *Eretmoptera murphyi* larvae were most abundant at grid plot 1, which had a density of 83807 larvae m⁻², with an average across all 16 grid points of 14867 (±5625 SEM) larvae m⁻². Soil pH value showed very little variation (mean 4.54 ± 0.2). The most significant positive correlations between *E. murphyi* abundance and the measured environmental conditions were with concentrations of N_{inorganic}, and in particular with total nitrogen and nitrate/nitrite concentrations (Fig. 2a and b respectively). Other significant relationships identified included a positive relationship between *E. murphyi* abundance and organic soil as a proportion of the substrate core (Fig. 2f) and a negative relationship between *E. murphyi* abundance and non-*Polytrichum* moss cover (Fig. 2i).

3.2. Local and island-wide soil nitrogen levels

At the local scale, sites at which *E. murphyi* was present had significantly higher levels of total nitrogen compared with control sites (Fig. 3a), because of an increase in NO₃-N concentrations (Fig. 3c). There was no difference in soil NH₄-N concentrations between *E. murphyi* sites and control sites (Fig. 3b). Soils in and around penguin colonies contained the highest concentrations of total N_{inorganic} (Figs. 3d and 4) which was primarily driven by the higher levels of NH₄-N which were between 2.5 and 5 times higher than soils at *E. murphyi*, giant petrel and seal-influenced sites (Figs. 3e and 4c). Consequently, the concentrations of total N_{inorganic} differed significantly between all sites. There were no significant differences detected in NO₃-N concentrations between *E. murphyi*, penguin, giant petrel and seal locations (Fig. 3f).

4. Discussion

The key finding of this study lies in the comparisons of sites now colonised by *E. murphyi* with control and wildlife-influenced sites across Signy Island from which *E. murphyi* is currently absent. These clearly show that the presence of the fly is associated with a three- to five-fold

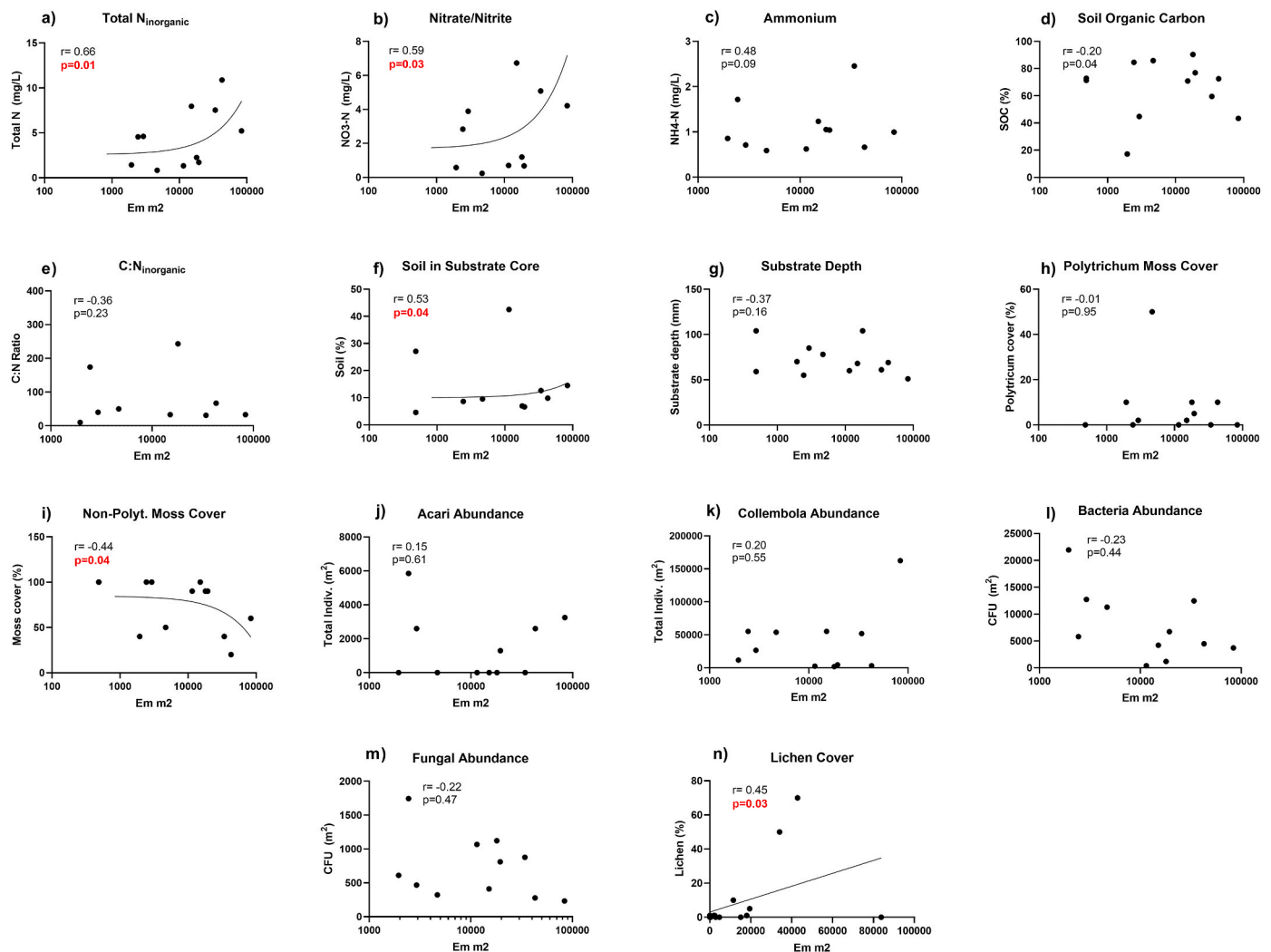


Fig. 2. Correlations between *E. murphyi* abundance (larvae m^{-2}) and surveyed variables from the sampling grid. $N = 16$ sites sampled with $n = 3$ cores from each site assessed for *E. murphyi* larval abundance. Maximum abundance 83,807 larvae m^{-2} . Shown with r and p values from two-tailed Spearman's rank correlations, and semi-log linear regression trend lines. Significant p values are highlighted in bold red. **a)** Total inorganic nitrogen; **b)** NO_3-N ; **c)** NH_4-N ; **d)** % soil organic carbon; **e)** C:N ratio; **f)** % of soil humus in substrate core, **g)** total substrate depth (to bed rock/gravel layer); **h)** % cover of *Polytrichum* moss in the 1 m^2 quadrat; **i)** % cover of other mosses (non-*Polytrichum*) in 1 m^2 ; **j)** total number of individual Acari m^{-2} ; **k)** total number of individual Collembola m^{-2} ; **l)** bacterial colony forming units (CFU) m^{-2} ; **m)** fungal colony forming units m^{-2} ; **n)** % lichen cover in 1 m^2 .

increase in soil inorganic nitrogen availability in the form of available nitrate (NO_3-N) compared to the controls, with concentrations of the ion not significantly different to those found in association with wildlife concentrations (Fig. 3c and f). The presence of the invading midge is also associated with greater organic content in the substrate profile (Fig. 2f), and a decline in non-*Polytrichum* moss species cover (Fig. 2i).

Range expansion of detritivores as a result of climate change at high latitudes could potentially result in accelerated decomposition rates (van Geffen et al., 2011). Hughes et al. (2012) reported that, based on the midge's feeding rate and local population densities, it is capable of increasing litter turnover by almost an order of magnitude compared with all other native micro-arthropods combined at the sites investigated. Another invasive chironomid, *Limnophyes minimus*, introduced to sub-Antarctic Marion Island, is also capable of increasing litter turnover by an order of magnitude over the next most influential species on the island, a native moth, and is now considered to be a keystone species in the terrestrial ecosystems on the island (Klok and Chown, 1997). On Signy Island, we found indications that increased *E. murphyi* abundance may be associated with a deeper organic soil profile (Fig. 2f). This could suggest that, as the midges turn over the litter, they produce a more nutrient-rich substrate in place of the dead moss. However, the depth of

the organic soil profiles may also be a driver of their colonisation, as much as a consequence, and thus further investigations of Antarctic soil development and turnover in association with detritivory are required. These should be integrated with studies of vegetation development and the influences of vertebrate aggregations, as well as regional environmental change influences (Bokhorst et al., 2019; Convey and Peck, 2019).

The scale of nitrogen fertilisation associated with *E. murphyi* presence was similar to that measured in areas influenced by giant petrel colonies and seal wallows but was lower than that associated with penguin colonies (Fig. 3d-f). Ammonium levels in areas colonised by *E. murphyi* were broadly equivalent to those in control sites (Fig. 3b). The lower concentrations of ammonium recorded in soil colonised by *E. murphyi* also indicate that total $N_{inorganic}$ is not a result of wind-dispersed deposition from neighbouring seal or seabird concentrations, which are located ~150–200 m distant in Factory Cove and on Factory Bluffs, respectively. This is exemplified by the low nitrogen levels found in areas directly beneath the Factory Bluffs cliffs, an area closer to both seal and seabird activity (Appendix S5). Dreyer et al. (2015) reported that chironomid adult carcass deposition alone was enough to increase available nitrogen by a very similar factor, in an

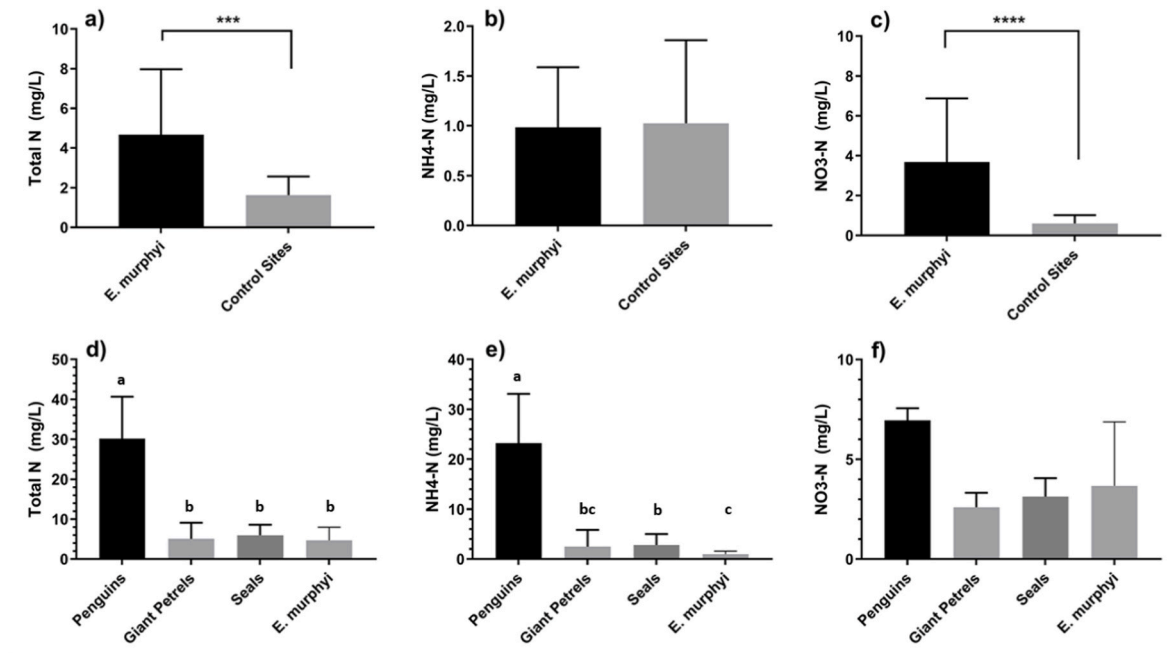


Fig. 3. *Eretmoptera murphyi* influence on available soil inorganic nitrogen measures, compared to control sites (minimal vertebrate and no *E. murphyi* activity) and the major wildlife colonies on Signy I. of penguins, giant petrels and seals (both fur and elephant – data combined). **a-c:** *E. murphyi* vs control sites (non-wildlife), Mann-Whitney U test: Total N, MWU = 101.5, $p < 0.001$; $\text{NH}_4\text{-N}$, MWU = 228.5, $p = 0.8$; $\text{NO}_3\text{-N}$, MWU = 72, $p < 0.001$. **d-f:** Different letters show statistical difference. Soil inorganic nitrogen levels amongst all tested wildlife colonies and sites with known *E. murphyi* activity, Kruskal-Wallis amongst all groups: Total N, $H = 10.5$, $p = 0.01$; $\text{NH}_4\text{-N}$, $H = 19.9$, $p = 0.0002$; $\text{NO}_3\text{-N}$: $H = 7$, $p < 0.001$. Significant relationships within multiple comparisons: Total N, penguin vs; giant petrels $p = 0.04$, seals 0.01 , *E. murphyi* $p < 0.001$; $\text{NH}_4\text{-N}$, penguins vs *E. murphyi* $p = 0.003$, seals vs *E. murphyi* $p = 0.004$; $\text{NO}_3\text{-N}$, no significantly different relationships.

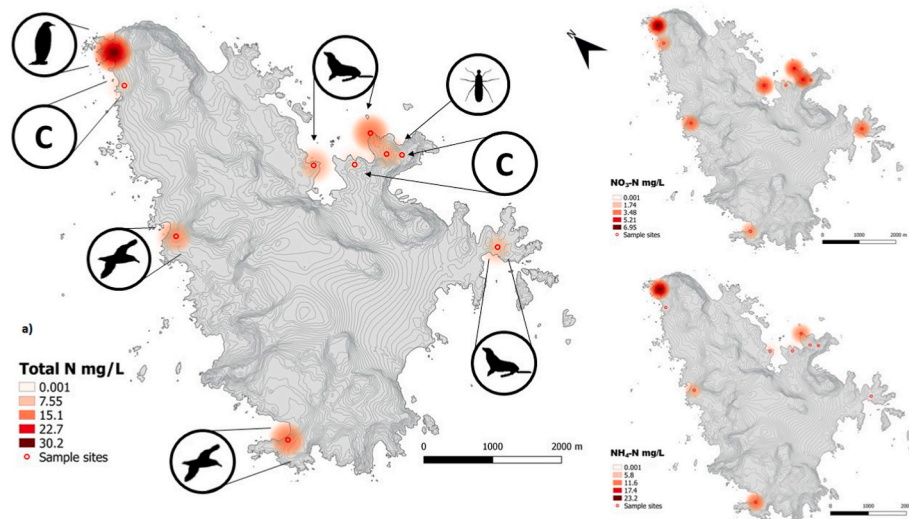


Fig. 4. Map of Signy Island sites sampled: penguin colonies, giant petrel (GP) colonies, seal concentrations, *E. murphyi* location, and habitats with no permanent wildlife or non-native invertebrate activity that are considered as control sites. Soil inorganic nitrogen represented as red ‘clouds’. a) Total nitrogen, b) nitrate ($\text{NO}_3\text{-N}$) c) ammonium ($\text{NH}_4\text{-N}$).

Arctic ecosystem. This led to increased plant biomass and changes in community composition as graminoids slowly took over from dwarf shrubs. In an analogous fashion, the introduction and/or range expansion of earthworms in the Northern Hemisphere, including into the Arctic, is significantly increasing available soil nitrogen, with cascading effects on terrestrial ecosystems, impacting both invertebrates and vegetation (Bohlen et al., 2004; Blume-Werry et al., 2020; Ozawa et al., 2005).

There was a significant negative association between midge abundance and non-*Polytrichum* moss cover (Fig. 2i), but no positive

relationship with *Polytrichum* cover (Fig. 2h). Whilst $\text{NH}_4\text{-N}$ is taken up more rapidly by Signy Island vegetation (Hill et al., 2011), $\text{NO}_3\text{-N}$ is also taken up by plants and soil microbes, and accounts for the majority of $\text{N}_{\text{inorganic}}$ in vegetated sites on Signy. As was seen in Dreyer et al.’s (2015) study, such nitrogen inputs are likely to favour Antarctic graminoids over native cryptogams, with the exception of *Polytrichum* species (Bokhorst et al., 2007; Hill et al., 2011, 2019; Rabert et al., 2017). In the longer term, increased nutrient availability may well favour the establishment of the native grass species *Deschampsia antarctica* (Juutinen et al., 2016; Casanova-Katny and Cavieres, 2012) as

well as any introduced non-native higher plants (Perterra et al., 2016).

Soil bacterial loads were negatively associated with SOC (and subsequently C:N ratio), whilst fungal abundance was positively associated with SOC (Appendix S6). This is a framework that is associated with fungal-dominated food webs and their consumers, Collembola and Acari (Bardgett, 2005), and describes the terrestrial ecosystem of Signy Island well, in addition to other high latitude/altitude soils (Zhang et al., 2017). However, it was not possible within the limits of this study to conduct microbial community analyses based on soil nucleic acids, which may highlight changes at a finer scale involving unculturable microbes. Thus, we recommend further studies to investigate these relationships using DNA or RNA sequencing approaches, with the latter being used to identify active microbes in the soil (Cox et al., 2019).

Chown et al. (2022), reported that densities of three indigenous sub-Antarctic Collembola species were significantly lower on islands that also hosted an invasive Collembola species, in line with the Antarctic Climate-Diversity-Invasion (ACDI) hypothesis (Nielsen and Wall, 2013). The preliminary findings in this study imply that, where the invaders are capable of significantly altering soil chemistry or structure, they could initially positively influence native micro-arthropods, in an analogous fashion to the positive impacts of vertebrate nutrient input identified by Bokhorst et al. (2019). However, increases in soil nitrogen may subsequently benefit later invaders, both invertebrates and plants, to a greater extent than locally adapted indigenous species. Currently, baseline data, including those from this study, are insufficient to identify species-level impacts of invasive species on microarthropod and microbial communities, and can only provide anecdotal support for a positive relationship between Collembola and *E. murphyi*.

We propose that *E. murphyi* and native micro-arthropods aid the

decomposition of vegetation biomass through the fragmentation of detritus, with effects on soil C:N ratio as carbon is released/assimilated, and as nitrogen levels increase through excreta and inputs from dead cells (Fig. 5). It seems likely that additional detritivorous activity from *E. murphyi* introduces high quality biomass with a low C:N ratio into belowground systems (Dreyer et al., 2015). This contrasts with the pre-introduction situation, where deposition from the atmosphere, or vertebrate guano sources that are particularly rich in ammonium, were the only major sources of nitrogen to the system (Bokhorst et al., 2019). The quality and size of the ‘brown’ food web of Signy Island, in terms of the key elements carbon and nitrogen, are major determinants of its function. The addition of *E. murphyi* to this system, therefore, could trigger important changes through the increase in nitrogen input to this low-nutrient environment, in line with the expected impacts of the range expansion of detritivores as a result of climate change at high latitudes (van Geffen et al., 2011, Fig. 5).

5. Conclusions

This study is only the second investigation globally into the effects of a terrestrial chironomid on ecosystem function and is the first to address associated impacts on nitrogen availability. It is also the most comprehensive investigation in the maritime Antarctic of the impacts of a non-native invertebrate on soils. The success of *E. murphyi* on Signy Island has provided an opportunity to consider the impacts of a non-native invertebrate species on these simple, and thus potentially highly vulnerable, Antarctic ecosystems (Fig. 5). We conclude that the species’ introduction has likely increased levels of available $N_{inorganic}$, primarily through changes in NO_3-N concentrations. The scale and form of this

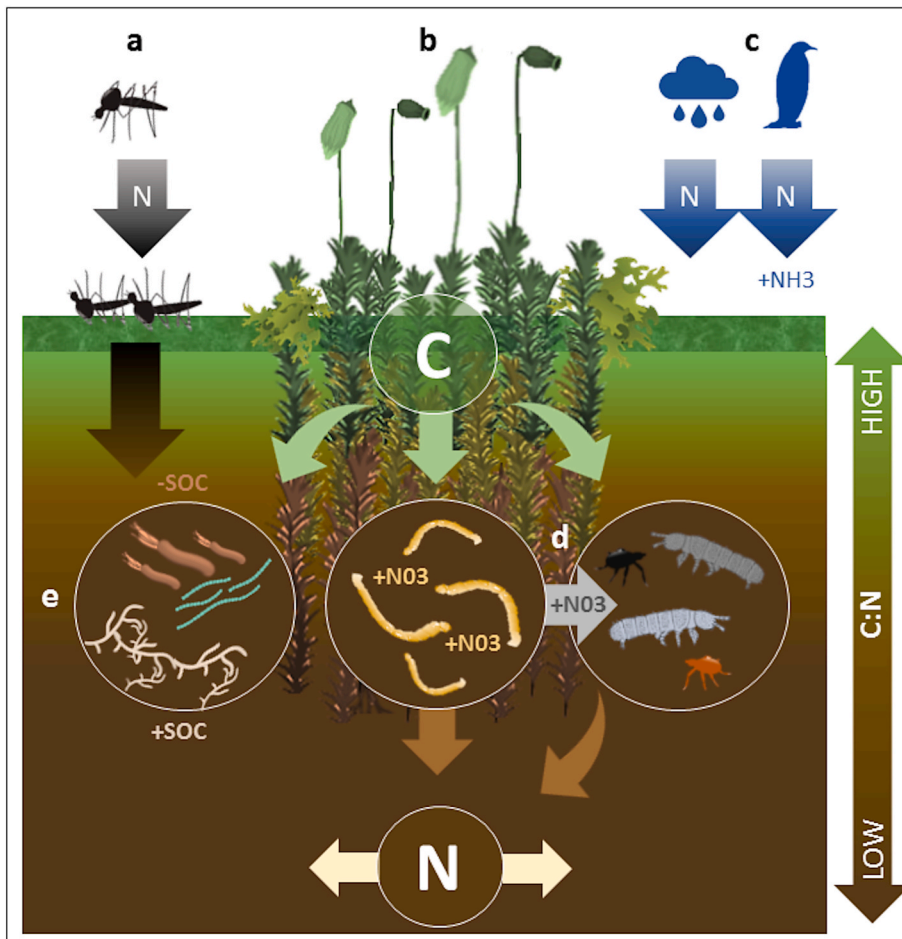


Fig. 5. Schematic of our understanding of terrestrial ecosystem functioning on Signy Island in areas colonised by *E. murphyi*. SOC = soil organic carbon, N = nitrogen, C = carbon. a) Direct nitrogen deposition to the detrital pool through the dead biomass of invertebrates. b) *E. murphyi* and micro-arthropods aid decomposition of the vegetation biomass through fragmentation of the detritus, with effects on the C:N ratio. c) Deposition from atmospheric or ammonium rich guano sources are the only major source of nitrogen to the system. d) C stored in plants is fragmented and either released as particulate matter or assimilated by detritivorous microbes and invertebrates. e) Microbes have differing impacts on SOC, also form part of the diet of *E. murphyi* and Collembola (Bokhorst et al., 2007; Bridge and Denton, 2006) and take up mineralised nutrients through immobilisation. *E. murphyi* is associated with an increase in nitrate levels which may benefit the micro-arthropod community (Bokhorst and Convey, 2016; Gutiérrez-López et al., 2011) and contributes to the nitrogen pool.

increase where *E. murphyi* is present is comparable to the level and type of nitrogen input seen in the vicinity of coastal seal wallows on the island. This provides a strong potential explanation for associated increases in local micro-arthropod abundance which could, in turn, further increase decomposition rates. Over time, increased nitrogen availability has the potential to result in changes in the bryophyte community. Further evaluation of the fate and forms of the nitrogen, as well as the resulting community changes, particularly in terms of moss, micro-arthropod and microbial diversity, is required to fully understand the scale and mechanisms of impacts on the terrestrial community, with Signy Island providing an exemplary model ecosystem for this purpose.

Author contributions

JB, PC and SALH conceived the study. JB designed and conducted the field work and conducted all chemical analyses. JB and KKN conducted the microbial analyses. JB analysed the data and led the writing of the manuscript. All authors contributed to the drafts, data interpretation and final approval for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2023.108965>.

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