



# Contrasting impacts of non-native isopods and springtails on ecosystem processes under simulated Antarctic climate conditions

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## ABSTRACT

Climate change, coupled with the introduction of non-native organisms, represent major threats to the functioning of ecosystems, especially in species-poor communities such as polar terrestrial ecosystems. In this laboratory study, we quantified the impacts of the non-native springtail *Folsomia candida* and isopod *Porcellio scaber* on seed germination and growth of the non-native grass *Poa pratensis*, and ecosystem respiration. The impacts of invertebrate communities of progressively increasing complexity were assessed, starting with the native springtail *Cryptopygus antarcticus* alone, followed by *C. antarcticus* in combination with *F. candida* or *P. scaber* and, finally, a community including all three species. The impact of these invertebrate communities were studied in a simulation of contemporary Antarctic soil surface conditions (2 °C) and a +5 °C warming scenario over one growing season.

Warming resulted in earlier germination (21 d), 10-fold increased plant biomass, N-content (>5-fold), and higher levels (90%) of ecosystem respiration. Warming also resulted in a 350% increase in *C. antarcticus* abundance.

The presence of the woodlouse *P. scaber* had the strongest impact on the measured soil and plant variables and this impact was largely irrespective of temperature. Impacts included: delay in seedling emergence (4 d), reduced plant emergence (20%), and higher ecosystem respiration (135%). The presence of both *C. antarcticus* and *P. scaber* resulted in 30% higher plant leaf N-content and a reduction in C:N ratio from 21 to 17. The experimental communities containing *F. candida* showed a 37% reduction in plant biomass under warming. The presence of *P. scaber* reduced *C. antarcticus* abundance (94%) but *F. candida* abundance was unaffected.

Our data indicate that non-native invertebrates differ in their ecosystem impacts, with potentially significant consequences for ecosystem functioning and community composition of plants and animals in cold biomes.

## 1. Introduction

Climate warming in combination with increased human activity is expected to increase the risk of non-native species becoming established in colder biomes such as the Antarctic (Bennett et al. 2015; Convey and Peck 2019; Duffy and Lee 2019). Non-native species can introduce novel traits to terrestrial ecosystems that are functionally different to those provided by the native biodiversity, which can lead to changes in key ecosystem process rates (Heemsbergen et al. 2004; Pyšek et al. 2020). Soil communities containing invertebrates with a more diverse set of functional characteristics tend to support increased nutrient mineralization rates and microbial activity, leading to greater plant production

(Partsch et al. 2006; Pieper and Weigmann 2008; Eisenhauer et al. 2011; Coulibaly et al. 2019; Winck et al. 2020). These ecosystem responses are typically more apparent or significant in communities of relatively low species diversity (Zimmer et al. 2005), a common characteristic of polar and particularly Antarctic terrestrial ecosystems (Convey et al. 2014). Invasive earthworms, slugs and midges have already been implicated in increasing soil nutrient availability in polar regions (Smith 2007; Hughes et al. 2013; Blume-Werry et al. 2020; Bartlett et al. in press). Impacts of non-native invertebrates may also affect herbivory and predator-prey interactions (e.g. Lebouvier et al. 2020), with variable impacts on plant production (Bohlen et al. 2004; Lach et al. 2010). As vascular plants are among the most likely groups to invade Antarctic

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terrestrial ecosystems as temperatures keep rising (Duffy et al. 2017; Convey and Peck 2019; Hughes et al. 2020) it is important to understand if there will be synergistic or antagonistic interactions with non-native invertebrates.

Vascular plants have established in Antarctica, particularly in the sub-Antarctic islands but also in the northern maritime Antarctic (Frenot et al. 2005; Hughes et al. 2015), in some cases being successfully eradicated (Pertierra et al. 2013, 2016; Malfasi et al., 2020), and are likely to thrive under continuing warming conditions (Pertierra et al. 2017; Bokhorst et al. 2020). Rapid warming predictions indicate considerable expansion of ice-free areas in the Antarctic Peninsula region by 2100 (Turner et al. 2009; Siegert et al. 2019), thereby creating new habitats for colonization by native and non-native species (Lee et al. 2017; Duffy and Lee 2019). However, nutrient availability also plays a large role in plant productivity, even in the cold and dry environments of Antarctica (Bokhorst et al. 2022). Therefore, activity of organisms that enhance nutrient availability, such as soil invertebrates (Filser 2002; David 2014), may support establishment of non-native plants and the development of their communities in Antarctica. Due to the absence of terrestrial vertebrates (other than the scavenging sheathbill closely associated with marine vertebrate concentrations) and large macrofauna such as earthworms (Russel et al. 2014; Convey 2017), carbon and nutrient cycling rates are slow and are further restricted by low temperatures (Davis 1981; Bokhorst et al. 2007b; Smith 2008). On Signy Island (South Orkney Islands, Maritime Antarctic), the larvae of the non-native chironomid midge *Eretmoptera murphyi* are associated with large increases in soil N-availability (Hughes et al. 2013; Bartlett et al. 2023), indicating that non-native invertebrates can have an important influence on ecosystem process rates that, in turn, influence plant growth when warming and human activity increase their chances of establishment (Hughes et al. 2020).

The impact of invertebrates on ecosystem processes differs depending on their size, feeding activity and mobility (Heemsbergen et al. 2004; de Bello et al. 2010; Lubbers et al. 2020). Earthworms, through their large size and burrowing behaviour, are well known ecosystem engineers and have greatly impacted soil and plant communities in North America (Bohlen et al. 2004). They also affect nutrient mineralization rates in the Arctic at invaded sites (Blume-Werry et al. 2020). However, smaller soil invertebrates, such as springtails and isopods can also impact ecosystem processes, as shown for cold biomes on sub-Antarctic islands (Gabriel et al. 2001; Greenslade and Convey 2012; Lebouvier et al. 2020). Maritime Antarctic springtail communities consist of only a small number of species, often dominated by *Cryptopygus antarcticus*. Their influence on ecosystem process rates is likely to differ from soil-dwelling (euedaphic) species, that are common in soils with a thick organic horizon and have stronger associations with plant roots and soil fungi (Milcu et al. 2006; Coulibaly et al. 2019). Euedaphic springtails tend to be less diverse or abundant at higher latitudes and elevations due to environmental constraints (Bokhorst et al. 2018), but their distributions may shift under climate warming. If such species establish in Antarctic terrestrial ecosystems they may have large impacts on nutrient mineralization rates. Larger invertebrates such as isopods, which have invaded some sub-Antarctic islands, may have large impacts through higher feeding rates and greater faecal production as well as through predation on the native invertebrate community (Slabber and Chown 2002; Jones et al. 2003).

In this laboratory study, we quantified how two non-native invertebrates, that differ morphologically and functionally from the dominant native soil fauna, affect seed germination and growth of a non-native plant (*Poa pratensis*; already established on various sub-Antarctic islands and capable of survival in the maritime Antarctic) and soil CO<sub>2</sub> fluxes under simulated contemporary Antarctic climate conditions and a warming scenario. Representing non-native invertebrates, we selected two common European species, the euedaphic springtail *Folsomia candida* and the woodlouse *Porcellio scaber*. The omnivorous *P. scaber* has already invaded some sub-Antarctic islands where it has led to impacts

on native invertebrates (Slabber and Chown 2002), while *F. candida* has been reported from geothermally heated soil on Deception Island (Greenslade et al. 2012). We hypothesised that: (1) the presence of non-native invertebrates will increase soil nutrient mineralization resulting in higher plant growth and soil CO<sub>2</sub> fluxes, (2) the increase in CO<sub>2</sub> fluxes and plant growth will be greater if both non-native springtail and isopod are present, and (3) application of a realistic warming scenario will increase the impact that non-native invertebrates have on plant growth and soil CO<sub>2</sub> fluxes.

## 2. Materials and methods

### 2.1. Experimental design

To test whether addition of non-native invertebrates (*F. candida* and *P. scaber*) to a community containing the native springtail *Cryptopygus antarcticus* would affect nutrient availability, seed germination and growth of the non-native grass *Poa pratensis*, we conducted a growth chamber experiment, simulating contemporary ambient Antarctic soil surface temperature conditions (2 °C) and a +5 °C warming scenario. We measured carbon fluxes, nutrient leaching, seed germination and plant growth for the duration of one simulated maritime Antarctic summer growing season (83 days).

The native springtail *Cryptopygus antarcticus* (Collembola) was selected as it is one of the most abundant microarthropods in the Maritime Antarctic region and plays an important role in ecosystem processes (Block and Convey 2001). This springtail preferentially feeds on algae and is found in the surface layer of the soil and in moss and algal vegetation (Convey and Smith 1997; Worland and Lukešová 2000; Bokhorst et al. 2007c). The springtails were collected in the field contained in a layer of moss (*Sanionia uncinata*) from Anchorage Island (Ryder Bay, Adelaide Island), transported at 4 °C to the Vrije Universiteit (Amsterdam, Netherlands) where they were stored in a climate chamber at 2 °C. Non-native species were selected based on their risk of being introduced to the Maritime Antarctic as indicated by their current presence on sub-Antarctic islands and reports from heated soils (Slabber and Chown 2002; Greenslade et al. 2012). To test whether invertebrates with likely different impacts on ecosystems compared to the native *C. antarcticus* would influence plant growth and nutrient availability, we selected two species that are not native to the Maritime Antarctic, the springtail *Folsomia candida* and the woodlouse *Porcellio scaber*. *Folsomia candida* is a euedaphic springtail that preferentially feeds on fungal hyphae or grazes on root mycorrhizae (Fountain and Hopkin 2005). Thereby they play an important role in root-associated carbon and nutrient cycling that promotes plant growth (Cragg and Bardgett 2001; Winck et al. 2020; Chauvat and Forey 2021). This species (and euedaphic springtails in general) is currently absent from terrestrial ecosystems of the Maritime Antarctic, with the exception of records as a non-native species in small areas of geothermally active ground and associated vegetation on Deception Island (62°58'S 60°39'W) (Convey et al. 1996; Greenslade and Convey 2012). Although, current environmental conditions may be too harsh for *F. candida* to thrive in Antarctica, this will likely change with future warming, and therefore, we chose this species as a representative of euedaphic springtail species. These springtails were obtained from stock cultures held at the Animal Ecology Department at VU Amsterdam.

*Porcellio scaber* (Isopoda) is an omnivorous detritivore feeding on plant detritus, plant material, faeces, wood, dead animal remains, algae and fungi, thereby contributing to nutrient cycling in soils (Yang et al. 2020). These isopods have a larger body size (180 times larger) than typical springtails and can therefore be expected to have a larger impact on nutrient cycling than springtails (de Bello et al. 2010). In addition, isopods play a key role in litter fragmentation (Abd El-Wakeil 2015) which, in turn, strongly contributes to springtail influence on decomposition process rates (Yang et al. 2012). *Porcellio scaber* is absent from terrestrial ecosystems of the Maritime Antarctic, which contain no

functionally similar or comparably sized invertebrates (Convey et al. 1996; Convey 2017). However, *P. scaber* has been introduced to sub-Antarctic Marion Island (46°54'S, 37°44'E) and is already invasive on cold temperate Gough Island (40°19'S, 9°56'W) (Slabber and Chown 2002; Jones et al. 2003). The woodlice used in this study were collected in Nijmegen (51°49'N, 5°53'E, the Netherlands) under leaf litter and bark. Individuals were stored in the climate chambers at 2 °C until use.

The experimental invertebrate communities included one control, without arthropods, and five different combinations of invertebrate species with increasing community complexity each with eight replicates per temperature level. A full factorial design including all possible species combinations was not used as it is highly unlikely that these non-native invertebrates will survive in habitats where the most dominant native Antarctic species is currently absent. Therefore, we always included the native springtail *Cryptopygus antarcticus*. The communities used comprised: 1) *Cryptopygus antarcticus* (Cant), 20 individuals/pot, 2) *C. antarcticus* + *Folsomia candida* (Cant + Fcan), 20 + 60 individuals/pot, respectively, 3) *C. antarcticus* + *Porcellio scaber* (Cant + Psca), 20 + 2 individuals/pot, respectively, 4) *C. antarcticus* + *F. candida* + *P. scaber* (Cant + Fcan + Psca), 20 + 60 + 2 individuals/pot, respectively and, 5) *C. antarcticus* + *P. scaber* (Cant = Psca), 351 + 2 individuals/pot, respectively. To eliminate any biomass effects on process rates (Heemsbergen et al. 2004), the numbers of individuals were chosen to maintain equal biomass between the native and non-native arthropods. Total abundance used in each pot equals 12,500 ind./m<sup>2</sup> *C. antarcticus*, and 37,500 ind./m<sup>2</sup> for *F. candida*, which, although not peak abundance, is representative for field conditions in the maritime Antarctic and sub-Arctic respectively (Bokhorst et al. 2008, 2018). Species biomass estimates were based on literature for *P. scaber* (12.3 mg), *C. antarcticus* (67 µg) and *F. candida* (21 µg) (Block and Harrison 1995; Caballero et al. 2004; Vilisics et al. 2012). However, due to limitation in numbers available we were able to achieve equal biomass only for Cant + Fcan and Cant = Psca. Woodlouse mortality occurred frequently at the start of the experiment and dead individuals were replaced so as to maintain two living individuals per pot up until the third week of the experiment. We were unable to assess springtail mortality as individuals were too small and hidden beneath the surface and, therefore, no springtail replacements were included.

## 2.2. Simulation of Antarctic microclimate

Full description of experimental setup and microclimate simulation is given by Bokhorst et al. (2021). In short, simulation of the Antarctic soil surface microclimate was performed in growth chambers (THEBO Horeca) with RIVA Cold refrigeration units (Rivacold srl—Vallefoglia, Italy), set to 2 °C or 7 °C. The base temperature (2 °C) is representative of the current mean growing season soil surface temperature as measured at sites along the Antarctic Peninsula (Bokhorst et al. 2008, 2021; Convey et al. 2018). Diurnal variation in substrate temperature (2–11 °C) and light (0–1400 µmol m<sup>2</sup> s<sup>-1</sup>) conditions were adapted every four weeks to mimic the seasonal variation in field microclimate conditions (Bokhorst et al. 2007a, 2008) by using light emitting diode (LED) lamps (Hortilight Sunfactor 270; 405 W). Relative humidity was maintained between 60 and 90%, similar to field conditions, by placing a water bath in the climate chamber. Relative humidity and air temperature were recorded at hourly intervals (HOBO U23 Pro v2, Bourne, MA, USA) in both climate chambers. To quantify impacts of warming on the time required for seed germination, plant growth, nutrient availability and CO<sub>2</sub> flux rates a parallel climate chamber was run at 7 °C. The 5 °C temperature increase reflects the Representative Concentration Pathway (RCP) 8.5 global climate warming scenario (IPCC 2013), which is appropriate given that the northern Antarctic Peninsula region already warmed by ~3 °C in the second half of the Twentieth Century and a warming trend of ~0.5 °C/decade has been reported and is predicted for the remainder of the Twenty-first Century (Turner et al. 2014; Bracegirdle et al., 2019; Siebert et al., 2019).

Organic material (decaying moss; pH 4.1, carbon = 24.0%, nitrogen = 2.1%) for this experiment was collected in January 2018 under moss layers on Anchorage Island (Ryder Bay, south-east Adelaide Island, 67°34'S 68° 07'W) and transported frozen (–20 °C) to laboratories at the Vrije Universiteit Amsterdam. The organic material (±20 g wet mass) was distributed across 96 closed-bottom pots (4.5 cm diameter and 5 cm height) filled to a depth of approximately 3 cm representing the average organic layer depth at Anchorage Island. This decaying moss was chosen as it represents one of the few habitats with high water availability and organic substrate for plant growth along the Antarctic Peninsula in an environment primarily composed of granite boulders and scree. Twenty seeds of *Poa pratensis* (Cruydhoeck.nl) were added to each pot and they were placed in a dark climate chamber at 2 °C for two weeks to allow for cold stratification, during which the pots were kept moist with tap water using a spray bottle. Following stratification, the lights (0–900 µmol m<sup>2</sup> s<sup>-1</sup>) were turned on to begin the onset of the simulated growing season and the pots were divided so that 48 remained at 2 °C and 48 were moved to the warmer chamber set at 7 °C. At that point, invertebrates were added to the experimental pots and a circular mesh cover (20 cm high with 50 µm aperture) was attached to the top of each pot to avoid animals escaping or moving between experimental treatments. All pots were randomly repositioned every week and moved between chambers each month (switching the temperature regime of the chambers at the same time) to avoid any systematic 'chamber effect' throughout the experiment. Pots were watered twice a week over the growing season by carefully removing and replacing the mesh cover for a few seconds and using a bottle top dispenser. Watering resulted in a seasonal precipitation equivalent of 150 mm over the course of the experiment, which is within the range recorded along the Antarctic Peninsula (Tang et al. 2018).

## 2.3. CO<sub>2</sub> flux measurements

CO<sub>2</sub> fluxes in the experimental pots were measured weekly using an infrared gas analyser (IRGA EGM-5 PP-systems) and a continuous gas flow method whereby each individual pot was placed in a closed dark measuring chamber. The core was left to acclimate for 1 min inside the chamber before recording the CO<sub>2</sub> ppm value every 10 s for 2 min. CO<sub>2</sub> fluxes (CO<sub>2</sub> µg/g of organic matter/minute) were calculated using the dry organic matter mass values (after oven-drying at 70 °C for 24 h) from each pot after harvesting at the end of the experiment. Total carbon loss was calculated from the integrated sum of the weekly CO<sub>2</sub> flux measurements.

## 2.4. Nutrient leaching

Concentrations of leachable nutrients (NH<sub>4</sub><sup>+</sup>, NO<sub>3</sub><sup>-</sup> + NO<sub>2</sub><sup>-</sup> and PO<sub>4</sub><sup>3-</sup>) were quantified by adding a surplus of water (40 mL) to each experimental core at the end of the simulated summer season. Holes were pierced at the bottom of each pot and the extractant was collected into a Falcon tube. The leachate was centrifuged at 2000 rpm for 5 min and used to measure NH<sub>4</sub><sup>+</sup>, NO<sub>3</sub><sup>-</sup> + NO<sub>2</sub><sup>-</sup> and PO<sub>4</sub><sup>3-</sup> concentrations using an autoanalyzer (Lachat Quikchem 8000). This approach, although different from standard soil nutrient extraction methods, allows for standardized comparison of leachable nutrients between experimental treatments, and each experimental core resembles a simplified lysimeter (Bender and van der Heijden 2015). The leached nutrients quantified through this method are regarded as an approximation of available nutrients. This non-destructive approach allowed for further work on the plants and soil arthropods in each experimental unit. Ten blanks containing only demineralized water were used alongside the leaching to correct for any contamination in the demineralized water. pH levels were measured using the extractions.

## 2.5. Biotic measurements

To quantify seed germination time, pots were checked twice a week for the first seedling emergence. At the end of the experiment, we counted the total number of seedlings, number of leaves and harvested the above-ground plant biomass, after the nutrient leaching, using tweezers to carefully remove each plant at its base. Biomass was quantified after oven-drying the plant material at 70 °C for 48 h. Total plant N and C were determined by dry combustion with an elemental analyser (Flash EA 1112, Thermo Corporation Italia, Rodana, Italy).

Following the nutrient leaching and plant biomass harvest, live invertebrates were extracted using a Tullgren extractor for 48 h. Mesocosms were placed upside down in the extractor, allowing live animals to move into a receiving vessel containing 70% ethanol. They were then identified and counted under a microscope. The leaching, as described above, lasted less than 1 min and this is unlikely to have induced any mortality among the contained invertebrates. We did not observe any springtails in the leachates, where they would have floated on top, indicating that none were flushed out through the holes.

## 2.6. Statistical analyses

All statistical analyses were carried out in R (R Core Team, 2019). Nutrient and plant data were analyzed using a factorial ANOVA with invertebrate species (*C. antarcticus*, *F. candida* and *P. scaber*) and temperature (2 °C and 7 °C) as fixed factors. However, as *C. antarcticus* was always present, apart from the control as per the experimental design, it was not possible to test all possible interactions. Therefore, we also report Tukey HSD differences ( $P < 0.05$ ) between the six experimental communities (Control, Cant, Cant + Fcan, Cant + Psca, Cant + Fcan + Psca and Cant = Psca) where appropriate. A three-way repeated measures ANOVA was performed to evaluate the effects of invertebrate community composition, warming and time on CO<sub>2</sub> fluxes. Where a significant interaction occurred, a two-way ANOVA and *post hoc* Tukey HSD tests were performed to identify significant differences between treatment communities. To quantify the influence of temperature and invertebrate species on total ecosystem CO<sub>2</sub> efflux we used the relaimpo package (Grömping, 2006). Log or square root transformations were applied on all the dependent variables to reduce the variance of the residuals and to ensure that each model's assumptions were met.

## 3. Results

### 3.1. Temperature and invertebrate effects on leachable nutrients

Leachable soil nutrients were reduced at 7 °C (by 49%, 42% and 94%

for PO<sub>4</sub>, NO<sub>3</sub> + NO<sub>2</sub> and NH<sub>4</sub>, respectively) compared to 2 °C across all treatments (Table S1). The presence of *P. scaber* increased leached NH<sub>4</sub> concentrations four-fold irrespective of temperature, while leached-N (NH<sub>4</sub> and NO<sub>3</sub>) was reduced (>75%) in the treatments containing *F. candida* but only at 2 °C (Tables 1S and 2S). Overall, leached N concentration was highest under the treatment with equal biomass of *P. scaber* and *C. antarcticus* at 2 °C (Table S1). There were no consistent invertebrate effects on leached P concentrations (Table S1). Substrate pH was consistently lower at 7 °C (mean pH 5.8) compared to 2 °C (mean pH 6.0). Lowest pH values (mean pH 5.5 ± 0.15) were found in treatments with equal biomass of *P. scaber* and *C. antarcticus* (Tables S1 and S2).

### 3.2. Temperature and invertebrate effects on seed germination and plant growth

Seed germination was on average 21 days earlier at 7 °C compared to 2 °C (Table 1). The presence of *P. scaber* delayed seedling emergence by 4 days while neither springtail affected germination time (Table 1). Warming led to greater number of seedlings (+3.6 plants per pot compared to 2 °C), irrespective of the invertebrates present, while *P. scaber* reduced seedling numbers by 20% irrespective of temperature (Fig. 1, S1; Tables 1 and 2).

Warming increased plant growth, with three times more leaves, greater total plant height (2.8 times) and higher biomass (1085%) (Table 1, Fig. 1, S1). Plant height was lower at 7 °C when *F. candida* was present (8.4 ± 0.9 cm) compared to warmed plants when this springtail was absent (10.0 ± 0.5 cm) and a similar pattern was found for plant biomass (12.6 ± 2.7 mg vs. 19.9 ± 2.9 mg). There was no consistent effect of *C. antarcticus* or *P. scaber* on plant height or biomass and invertebrates did not affect plant leaf production (Table 1).

Plant nitrogen was lower at 7 °C (1.2 ± 0.07%) compared to 2 °C (3.65 ± 0.15%) across all treatments (Tables 1 and 2). However, due to the higher biomass, total acquired N within plants was nearly five times higher at 7 °C (0.29 ± 0.04 mg) compared to 2 °C (0.06 ± 0.00 mg) (Fig. 1). Presence of *C. antarcticus* enhanced plant N content (2.15 ± 0.24% vs. 2.80 ± 0.16%) and the same pattern was found in the presence of *P. scaber* (2.35 ± 0.15% vs. 3.09 ± 0.23%). Plant C:N ratio was enhanced under warming (25.8 ± 0.9) compared to the ambient conditions (11.6 ± 0.5) across all treatments. The presence of *C. antarcticus* led to reduced C:N values (22.3 ± 2.2 vs. 17.9 ± 1.0) and a similar pattern was observed in the presence of *P. scaber* (20.6 ± 1.3 vs. 16.3 ± 1.3). There were no further significant invertebrate effects in combination with warming on % or total plant N (Tables 1 and 2).

**Table 1**

Seedling emergence, plant growth, N, C:N ratio and ecosystem CO<sub>2</sub> production in response to warming and invertebrate community composition under simulated Antarctic conditions. Invertebrate communities consisted of control (no animals added) and species combination of: *Cryptopygus antarcticus* (Cant), *C. antarcticus* + *Folsomia candida* (Cant + Fcan), *C. antarcticus* + *F. candida* + *Porcellio scaber* (C + F + P) and a treatment where the biomass of *C. antarcticus* matched that of *P. scaber* (Cant = Psca). Mean plant variables are based on 5–8 replicates ± SE as seedlings did not emerge in all experimental pots; Cant + Psca (n = 6), C + F + P (n = 5) and Cant = Psca (n = 6) at 7 °C. \* denotes significant difference between temperature. Communities with the same letters within columns do not differ significantly (Tukey HSD) for the respective variables. ANOVA results are presented in Table S3.

Community	T (°C)	Seedling emergence (days)	Seedlings (no.)	Leaves (no.)	Plant height (cm)	Biomass (mg)	Plant N (%)	Plant C:N	Total CO <sub>2</sub> efflux
Control	2	59.2 (1.5) ab	6.4 (0.6) a	6.6 (0.7) a	3.4 (0.2) ab	1.4 (0.1) ab	3.05 (0.24) a	13.6 (1.2) a	4.5 (0.5) a
	7	36.2 (0.7) *	12.1 (0.5)	26.4 (1.2) *	9.0 (0.3) *	15.0 (1.8) *	1.47 (0.06)*	28.8 (1.2)*	9.1 (0.8)*
Cant	2	58.4 (1.9) ab	6.5 (0.5) a	7.8 (0.9) a	3.7 (0.3) ab	1.5 (0.3) ab	3.13 (0.21) a	12.9 (0.8) a	5.6 (0.6) ab
	7	36.4 (1.4) *	12.4 (1.3)	27.9 (3.5) *	9.1 (0.7) *	16.2 (2.4) *	1.65 (0.18)*	27.4 (2.2)*	9.7 (1.3)*
Cant + Fcan	2	52.9 (2.0) a	8.4 (1.0) a	9.4 (1.0) a	3.8 (0.3) a	1.9 (0.2) a	3.41 (0.20) a	12.0 (0.8) a	5.8 (1.0) ab
	7	36.2 (0.7) *	10.4 (1.3)	24.4 (2.8) *	9.8 (0.9) *	16.6 (3.2) *	1.50 (0.05)*	28.4 (0.9)*	8.8 (1.1)*
Cant + Psca	2	62.0 (2.3) b	6.5 (0.5) a	7.5 (0.8) a	3.0 (0.1) ab	1.0 (0.2) ab	4.05 (0.26) a	9.93 (0.7) a	6.5 (0.6) abc
	7	40.0 (2.4) *	6.9 (2.1)	21.5 (2.6) *	9.6 (1.1) *	14.5 (5.0) *	1.88 (0.25)*	23.2 (3.1)*	15.0 (1.4)*
C + F + P	2	60.0 (2.2) b	6.4 (0.4) a	7.0 (0.7) a	3.6 (0.2) b	1.7 (0.4) b	4.21 (0.52) a	10.7 (1.5) a	7.9 (0.8) bc
	7	38.6 (1.6) *	6.5 (2.9)	20.4 (4.2) *	7.8 (1.2) *	8.6 (4.2) *	2.17 (0.32)*	21.0 (3.3)*	14.1 (1.6)*
Cant = Psca	2	58.1 (2.1) ab	6.8 (0.8) a	7.0 (0.9) a	3.1 (0.2) ab	1.4 (0.4) ab	4.19 (0.30) a	10.1 (1.1) a	8.3 (1.0) c
	7	34.0 (0.8) *	6.3 (1.7)	25.3 (4.1) *	13.2 (1.4) *	36.8 (10.1)	1.85 (0.13)*	23.5 (1.6)*	16.6 (1.5)*



Table 2

ANOVA results (F and P values) of seedling emergence, plant growth, N, C:N ratio and ecosystem respiration under simulated Antarctic soil conditions (2 °C) and a warming scenario (7 °C) (W) in combination with various invertebrate communities. Invertebrate communities consisted of control (no animals added) and species combination of: *Cryptopygus antarcticus*, *C. antarcticus* + *Folsomia candida*, *C. antarcticus* + *F. candida* + *Porcellio scaber* and a treatment where the biomass of *C. antarcticus* matched that of *P. scaber*. Degrees of freedom are 1, 70–86 for each main factor and interaction terms.

	Emergence time		Seedlings		Leaves		Plant height		Biomass		Plant N%		Plant C:N		Total CO <sub>2</sub> efflux	
	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Warming	417.8	<0.001	36.7	<0.001	255.9	<0.001	478.1	<0.001	276.7	<0.001	178.5	<0.001	231.1	<0.001	90.6	<0.001
<i>C. antarcticus</i>	0.0	0.936	1.1	0.304	0.0	0.960	0.2	0.650	0.2	0.670	6.7	0.012	6.6	0.013	14.3	<0.001
<i>F. candida</i>	2.0	0.159	0.1	0.806	0.0	0.868	0.0	0.966	0.0	0.943	0.0	0.892	0.1	0.753	1.8	0.179
<i>P. scaber</i>	6.4	0.014	6.6	0.012	3.8	0.054	0.8	0.362	2.3	0.130	16.8	<0.001	12.2	0.001	29.6	<0.001
WxCan	0.6	0.436	3.3	0.073	2.6	0.109	0.2	0.624	0.0	0.935	1.1	0.299	0.3	0.561	0.1	0.730
WxCan	1.5	0.225	1.1	0.308	1.4	0.244	6.3	0.014	6.6	0.012	0.0	0.988	0.0	0.982	1.6	0.213
WxPsc	0.8	0.373	2.3	0.130	0.1	0.804	2.0	0.159	0.1	0.792	2.5	0.120	2.3	0.133	1.8	0.174
FcanxPsc	1.5	0.224	0.0	0.860	0.6	0.451	1.3	0.250	2.6	0.110	0.1	0.741	0.1	0.742	0.1	0.871
WxCanxPsc	1.1	0.290	2.2	0.138	0.3	0.586	7.3	0.009	2.2	0.140	1.0	0.324	1.4	0.238	0.2	0.646

### 3.3. Temperature and invertebrate effects on CO<sub>2</sub> fluxes and carbon loss

CO<sub>2</sub> fluxes increased over time for pots in the warming treatment but remained stable at 2 °C (Fig. 2a). Total respired carbon was on average 90% greater at 7 °C (14.7 ± 1.6 µg CO<sub>2</sub> g<sup>-1</sup> soil) compared to 2 °C (7.7 ± 0.7 µg CO<sub>2</sub> g<sup>-1</sup> soil) across all treatments. Presence of *C. antarcticus* (+81%) and *P. scaber* (+135%) nearly doubled total CO<sub>2</sub> loss over the course of the experiment, while the treatments containing *F. candida* resulted in reduced (-27%) total CO<sub>2</sub> production (Fig. 2, Table 3). Linear models including temperature and invertebrates with total CO<sub>2</sub> production as response variables explained 70% of the variance, with the largest contribution by *P. scaber* (50%) and warming (33%), while the two springtails both explained less than 10%. There was no consistent correlation between animal biomass and total carbon loss (R = -0.12, P = 0.412, Fig. S3). However, at 2 °C, animal biomass was positively correlated (R = 0.35, P = 0.01) with total carbon loss, while this pattern was not present at 7 °C (Fig. S1).

### 3.4. Effects of temperature and invertebrate community composition on animal abundance

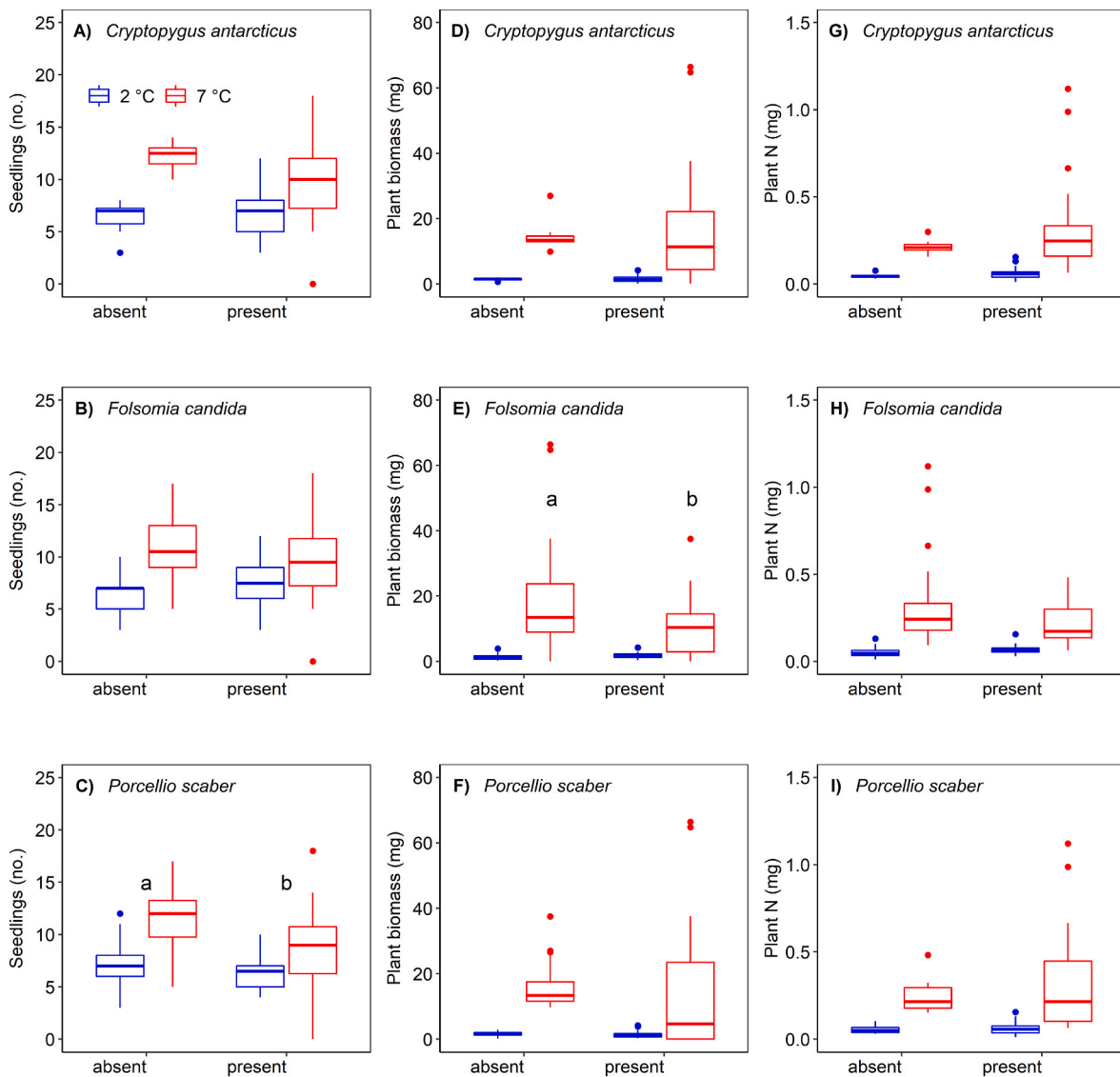
Warming more than tripled the abundance of *C. antarcticus* to 350% above the starting density, while at 2 °C abundance remained constant through the experiment (Fig. S3a; Table S4). Abundance of *F. candida* was reduced to 55% of the initial value at the end of the experiment under warming while very few individuals survived at 2 °C (Fig. S3b). Presence of *P. scaber* was associated with a reduction in abundance of *C. antarcticus* by 94%, but not with that of *F. candida* (Fig. S3).

## 4. Discussion

The introduction of non-native organisms to the Maritime Antarctic may greatly affect the status quo of Antarctic terrestrial ecosystems. Currently, most studies have focused on the biogeographical range and biology of non-native organisms (Frenot et al. 2005; Greenslade and Convey 2012; Baird et al. 2019), but little is known about the effects that they could have on ecosystem process rates and plant feedbacks. In our experiment, the growth of *P. pratensis* and soil processes were primarily affected by the presence of *P. scaber*, while the non-native springtail *F. candida* reduced plant biomass and there was limited impact by the native springtail *C. antarcticus*. There was no evidence for species richness or any complementary effects of having more than one invertebrate species present in relation to the measured variables, as might be expected in these species-poor communities (Zimmer et al. 2005; Partsch et al. 2006; Eisenhauer et al. 2011), indicating that Antarctic environmental constraints may be too strong for such interactions to play a role. Introduction of non-native invertebrates, especially species with larger body size than those currently present in Antarctic terrestrial ecosystems, can greatly influence ecosystem process rates and so alter community composition.

### 4.1. Effects of non-native invertebrates on ecosystem processes

Invertebrate presence lowered soil pH, affected nutrient leaching losses, and enhanced plant nitrogen content. However, plant growth was less affected by these changes than expected. Invertebrate activity typically enhances soil nutrient concentrations, but we were only able to assess this through a modified approach, which likely underestimated total soil nutrient availability. Nevertheless, plant tissue-N was enhanced in the presence of non-native invertebrates, indicating that plants were able to acquire more nutrients due to invertebrate activity. Despite this likelihood of enhanced nutrient availability there was no increase in plant growth. A similar plant response was observed in a study with earthworms in sub-Arctic Sweden (Blume-Werry et al. 2020), indicating that plant growth responses to additional nutrients in cold biomes may either require more time or that other limiting factors are in



**Fig. 1.** Box-and-whisker plot of number of *Poa pratensis* seedlings, total biomass and total nitrogen in response to warming and presence of invertebrate species under simulated Antarctic conditions. Box plots show median values across 2 °C and 7 °C treatments for presence of *Cryptopygus antarcticus* (n = 80), presence of *Folsomia candida* (n = 32) and presence of *Porcellio scaber* (n = 48). Bars with different letters indicate significant differences (Tukey HSD  $P < 0.05$ ) due to the presence of invertebrates. Warming consistently increased plant response variables. ANOVA results are shown in Table 2.

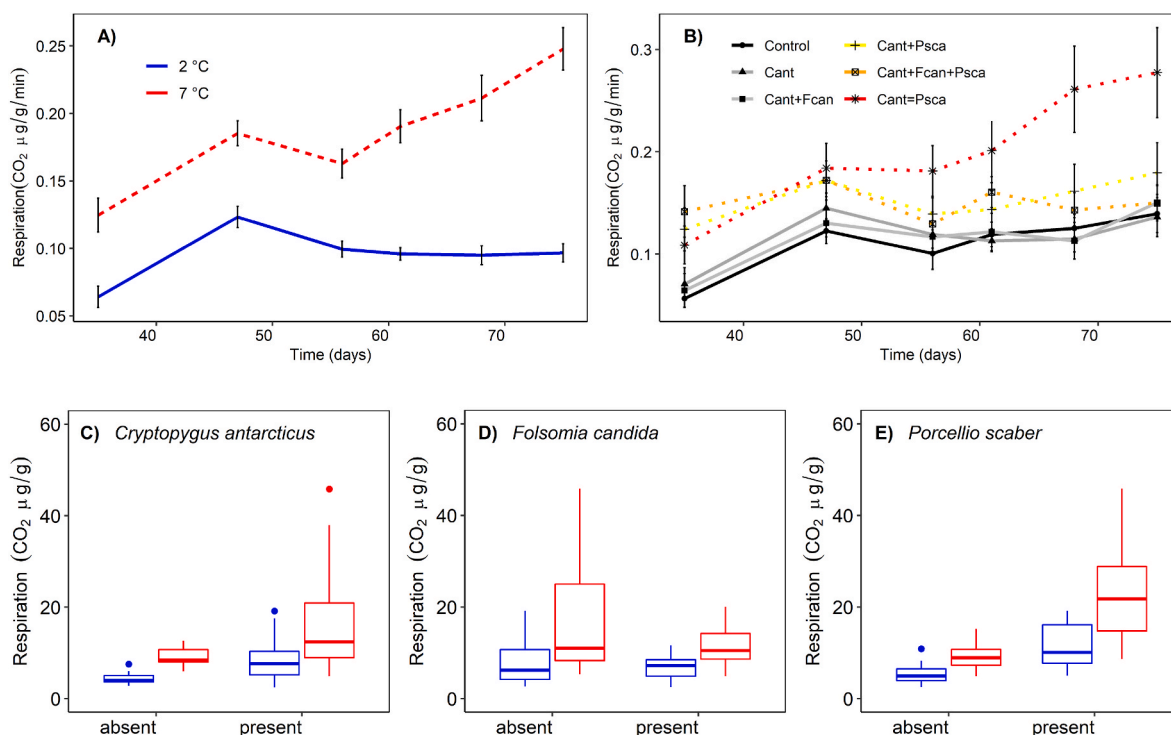
play. Nonetheless, invertebrate presence, and particularly that of *P. scaber*, affected soil processes as has also been observed for the non-native midge *Eretmoptera murphyi* on Signy Island (Hughes et al., 2013; Bartlett et al. 2023). These changes, in turn, can feed back to the soil through enhanced root exudates (Badri and Vivanco 2009) and the production of nutrient-rich litter (Aerts and Chapin 2000), both pathways known to affect soil decomposer communities (Aneja et al. 2006; Fujii and Takeda 2012) and plant growth.

The changes induced by the invertebrates resulted in overall greater  $\text{CO}_2$  production, indicating that the microbial activity was enhanced. This is in accordance with other studies showing enhanced ecosystem respiration rates in the presence of soil invertebrates (Hanlon and Anderson 1979; Heemsbergen et al. 2004). The largest  $\text{CO}_2$  production was measured in the treatments with equal biomass of springtails and woodlice, suggesting that animal respiration would have enhanced  $\text{CO}_2$  fluxes. However, this was not supported by a positive correlation of animal biomass with  $\text{CO}_2$  flux rates (Fig. S3), indicating that invertebrate presence may have resulted in enhanced microbial activity. These findings are consistent with models of Maritime Antarctic ecosystem process rates being microbially driven (Davis 1981). Non-native

detrivores are clearly capable of directly enhancing the Antarctic soil microbial energy pathways, but the build-up of a vascular plant organic litter layer and associated changes in soil decomposer community will likely take many decades.

#### 4.2. Variation between non-native invertebrates

We did not find stronger effects on plant and soil variables when all three invertebrates were present. Instead, *P. scaber*, a morphologically dissimilar and larger non-native invertebrate than any currently found in the Maritime Antarctic, had the greatest impact on ecosystem functions. In contrast, *F. candida* had only small detectable influences, indicating that this euedaphic springtail species does not greatly differ in its influence on ecosystem functions from the native springtail *C. antarcticus*. However, high mortality, assumed by the low recovery rate (Fig. S3), may have occurred early in the experiment and led to limited impacts of *F. candida*. *Folsomia candida* is known to influence soil microbial communities through carbon and nutrient cycles in temperate grasslands (Bakonyi 1989) and has been implicated in increased N-leaching which reduced soil respiration (Frouz et al. 2020).



**Fig. 2.** Soil CO<sub>2</sub> fluxes in response to warming and invertebrate community composition over the duration of a simulated Antarctic growing season. Time represents the number of days since the start of the growing season. **A)** effect of warming on ecosystem CO<sub>2</sub> fluxes. **B)** Effect of invertebrate community composition; control (no animals added) and species combination of: *Cryptopygus antarcticus* (Cant), *C. antarcticus* + *Folsomia candida* (Cant + Fcan), *C. antarcticus* + *F. candida* + *Porcellio scaber* (Cant + Fcan + Pscas) and a community where the biomass of *C. antarcticus* matched that of *P. scaber* (Cant = Pscas). Dotted lines represent communities with woodlice (*P. scaber*) present; values are means based on 8 replicates  $\pm$  SE. Box-and-whisker plot of total respired ecosystem CO<sub>2</sub> at the end of the experiment is presented for each invertebrate species; **C)** *Cryptopygus antarcticus*, **D)** *Folsomia candida* and **E)** *Porcellio scaber*.

**Table 3**

Three-way repeated measures ANOVA results (*F* and *P* values) of soil CO<sub>2</sub> fluxes under simulated Antarctic conditions (2 °C) and a warming scenario (7 °C) (W) in combination with different invertebrate species compositions (Community) over the duration of the growing season (Time, *n* = 6). Invertebrate communities consisted of control (no animals added) and species combination of: *Cryptopygus antarcticus*, *C. antarcticus* + *Folsomia candida*, *C. antarcticus* + *F. candida* + *Porcellio scaber* and a treatment where the biomass of *C. antarcticus* matched that of *P. scaber*. DFn indicates degrees of freedom numerator and DFd indicates denominator.

	DFn	DFd	<i>F</i>	<i>P</i>
Warming (W)	1	7	509.8	<0.001
Community (C)	5	35	13.0	<0.001
Time (t)	5	35	38.1	<0.001
W × C	5	35	1.7	0.169
W × t	5	35	5.4	<0.001
C × t	25	175	2.2	<0.001
W × C × t	25	175	2.3	<0.001

Interestingly, presence of *F. candida* at 2 °C resulted in reduced leaching losses but, with the very low springtail recovery at the end of this part of the experiment, it is unclear for how long their activity was at play here. The low temperatures under which this experiment was carried out may have inhibited *F. candida* activity (Boiteau and MacKinley 2012), and the low recovery indicates that many died, suggesting that *F. candida* is unlikely to establish under current climate conditions in the Maritime Antarctic, other than in exceptional locations such as the geothermally heated soils on Deception Island from which it has previously been recorded (Greenslade and Convey 2012).

The large effect-size of *P. scaber* most likely results from its body size, as this results in higher energy requirements and greater faecal production leading to increased nutrient cycling rates (Kautz and Topp

2000; de Bello et al. 2010; David 2014). However, *P. scaber* negatively impacted the success of *P. pratensis* as they consumed seedlings, thereby delaying emergence time and reducing the total number of seedlings. Similar patterns have been observed with non-native earthworms in deciduous forests (Eisenhauer et al. 2007).

The native springtail *C. antarcticus* had significant impacts on many of the measured variables when present with *P. scaber*, but no significant differences were detected in comparison to the control when it was present alone. It is unlikely that this springtail species does not contribute to ecosystem processes and, rather, this result may be an artifact of the experimental population size. Changes in leaching loss proxy and soil pH were greater in the treatment where the biomass of *C. antarcticus* (220,000 ind./m<sup>2</sup>) matched that of the isopods (Cant = Pscas) compared to that where 20 springtails (12,500 ind./m<sup>2</sup>) were combined with the isopods (Cant + Pscas) per experimental unit. The practical consideration of springtail availability meant that we were unable to include treatments equating to the population densities of several tens or hundreds of thousand individuals per m<sup>2</sup> that are commonly encountered in the natural environment (Bokhorst et al. 2008), but these levels may be required to quantify detectable ecosystem responses.

The low recovery of the native springtail *C. antarcticus* from treatments where *P. scaber* was present suggests that this omnivorous woodlouse may have acted as a predator in this simulated Antarctic environment. Jones et al. (2003) documented a reduction in the abundance of the native terrestrial isopod, *Styloniscus australis*, in lowland habitats of cool temperate Gough Island where *P. scaber* was most abundant, indicating potential effects of competition or possibly predation.

#### 4.3. Impact of non-native invertebrates under climate warming

Warming increased CO<sub>2</sub> fluxes, all plant growth variables and the nutritional status of plant tissue, as anticipated (Bokhorst et al. 2007b, 2021). The greater accumulation of N in total plant biomass under warming indicates that the plants will be able to acquire more soil nutrients as temperatures increase in the Maritime Antarctic. This finding is in line with observed patterns under experimental settings (Cavieres et al. 2018; Bokhorst et al. 2022). In contrast to our third hypothesis, very few effects of interactions between warming and invertebrate communities were detected on plant variables, indicating that the influence of the soil invertebrates on soil process rates was too low to affect plant growth. Only the presence of *F. candida* led to reduced plant biomass (37%) under warming, suggesting that it may have been feeding on the seedling roots in the absence of vascular plant litter and (mycorrhizal) fungi or changing the microbial community (Harris and Boerner 1990; Fountain and Hopkin 2005).

One unanticipated finding was that, in the absence of *P. scaber*, *C. antarcticus* reproduction increased under the warming scenario, with their abundance reaching 350% of that at the start of the experiment. The degree day sums above 0 °C in the experimental pots were 164 and 529 at 2 °C and 7 °C respectively at the time of harvest, indicating that thermal energy requirement for *C. antarcticus* reproduction probably lies within this thermal envelope. This provides useful insight into the thermal requirements for population growth of this slow growing species (Burn 1981; Block and Convey 2001) and indicates that its populations are likely to increase in response to the levels of warming currently experienced and predicted in the Maritime Antarctic.

#### 4.4. Conclusions

Plant growth and soil process rates were strongly enhanced by warming in our experimental treatments but the presence of non-native invertebrates had species-specific effects. The large isopod, *P. scaber*, enhanced plant nutrient status and increased ecosystem CO<sub>2</sub> production. In contrast, the presence of the smaller euedaphic springtail, *F. candida*, reduced plant growth, while little impact on plant nutrient status and CO<sub>2</sub> production was observed. The success of non-native plants in Antarctica is currently inhibited by temperature (Bokhorst et al. 2021) and is likely to increase as regional temperatures continue to increase. However, our data indicate that their establishment and growth can also be affected by the type of invertebrate species that may migrate or co-occur with them in future.

#### 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.2023.109151>.

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