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Biological Sciences

The role of substrate characteristics and temperature for potential non-native plant establishment in Maritime Antarctic ecosystems

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Abstract

Polar ecosystems are threatened by non-native plants, and this risk will increase with climate warming. Non-native plant growth depends on Antarctic environmental conditions and substrates, but these influences are poorly quantified. Under laboratory conditions we quantified the growth of *Holcus lanatus*, *Trifolium repens* and *Taraxacum officinale* across nine sub-Antarctic and Maritime Antarctic substrates with varying characteristics. This included, among others, variation in carbon (0.2–27.0%), nitrogen (0.03–2.1%) and phosphorus (0.04–0.54%) contents, under simulated Antarctic conditions (2°C) and a warming scenario. Legacy effects from an established non-native chironomid midge (*Eretmoptera murphyi*) and non-native grasses were included. *H. lanatus* and *T. repens* grew best in organic- and nutrient-rich substrates, while *T. officinale* growth was poorly correlated with substrate characteristics. Warming increased plant size by one to three times, but inconsistently across species and substrates, suggesting that climate change impacts on plant growth will vary across the Maritime Antarctic. A variable response was also observed in the legacy effects of *E. murphyi*, while non-native grasses increased *H. lanatus* and *T. repens* plant size, but not that of *T. officinale*. Plant growth was positively correlated with substrate organic and phosphorus content, and this information was used to trial a novel approach to identifying sites 'at risk' from plant invasions in the Maritime Antarctic.

Keywords: Forb; grass; invasion risk; mapping; policy decision

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Introduction

Climate warming is generating opportunities for non-native species to be introduced *via* human assistance into colder biomes (Chown *et al.* 2012, Hughes *et al.* 2020), with some of these species potentially becoming invasive. Such species may increase local diversity, but they also often modify ecosystem processes to levels that benefit their own population growth at the expense of native species. Due to long-term isolation and the continent's extreme environmental conditions, contemporary Antarctic terrestrial ecosystems have low native diversity compared to areas with milder climates and support only two vascular plant species (Convey *et al.* 2014, Convey & Biersma 2024). However, based on the outcomes of laboratory studies, current soil microclimate conditions can potentially support the germination and growth of a potentially wide range of non-native plants along the Antarctic Peninsula (Duffy *et al.* 2017, Bokhorst *et al.* 2021), and these conditions will improve further under climate warming (Siegert *et al.* 2019). Germination and subsequent growth of plants are, however, also dependent on substrate characteristics (Wenk &

Dawson 2007), but few seed germination studies of non-native plant species have been conducted in Antarctic substrates under relevant microclimatic conditions (Edwards 1979, Bokhorst *et al.* 2021). To assess the potential establishment threat of non-native vascular plants in Antarctica, better understanding is required regarding how this is affected by different Antarctic substrates. This may also enable a better understanding of which locations are most susceptible to the establishment of non-native species.

Antarctic soils are generally poorly developed compared to those found at lower latitudes. Soil formation typically consists of glacial and some aeolian deposits, as well as volcanic ash in some locations, with large variation in sand and clay contents (Simas *et al.* 2015). Sand as a substrate for plant growth is known to negatively affect root development through mechanical resistance and damage (Vine *et al.* 1981), whereas clay/silty soils may be more prone to frost heave (Sheng *et al.* 2013), and high organic content is beneficial for plant growth (Oldfield *et al.* 2020). While Antarctica is predominantly ice-covered, the available substrate type in the ~0.2–0.4% of the continent that is ice-free varies widely, particularly in the Maritime Antarctic, which is the region most likely to be invaded by non-native plants and other groups (Hughes *et al.* 2020). The Maritime Antarctic is also the region of the continent with the most extensive cover of mosses and other cryptogams that create organic-rich substrates (Schaefer *et al.* 2015, Simas *et al.* 2015, Walshaw *et al.* 2024) that could help facilitate

plant establishment and growth in an otherwise rocky and barren landscape. Historical transplant experiments of non-native plants to the Antarctic were relatively successful when planted in low-pH (4.2) organic substrate (Edwards 1979), with similar results obtained when tested under laboratory conditions (Bokhorst *et al.* 2021), but little is known regarding how differences in soil carbon, pH and nutrients affect germination and growth of non-native plants in Antarctica. Climate warming may also release temperature constraints on germination speed and growth (Day *et al.* 2009, Bokhorst *et al.* 2021), allowing plant nutrient use to be more efficient and resulting in greater plant growth (Bokhorst *et al.* 2022). In addition, influential soil characteristics are unlikely to be consistent across different non-native plant species, but understanding of them must form a crucial element of assessing potential invasion threat.

Soil nitrogen and phosphorus promote plant growth, but this nutrient effect can be limited by low temperature (Bokhorst *et al.* 2022). As a result, not all Antarctic substrates with high organic and nutrient contents, such as those found close to bird colonies (Zwolicki *et al.* 2015, Bokhorst *et al.* 2019), may be suitable for non-native plant growth (Liu *et al.* 2018, Kołodziejek 2019). Separately, some substrates may be too young to have developed an organic layer with sufficient nutrients to support plant growth. Although negative impacts by non-native plants on native species have been reported for the sub-Antarctic (Gremmen *et al.* 1998, Frenot *et al.* 2005), non-native plants themselves may benefit from or be hindered by other established non-native organisms (Kuebbing & Nuñez 2016, Martin *et al.* 2023). Species that enhance soil nutrient cycling are likely to accelerate the development of substrate suitability for non-native plants. In this context, the larvae of the non-native midge *Eretmoptera murphyi* Schaeffer, introduced from sub-Antarctic South Georgia, have been linked to large increases in nitrogen availability on Signy Island in the Maritime Antarctic (Hughes *et al.* 2013, Bartlett *et al.* 2023), and this may promote greater non-native plant growth under scenarios of continued temperature increase (Bokhorst *et al.* 2022, Valliere *et al.* 2022). Most sub- and peri-Antarctic islands have already been invaded by multiple vascular plant species (Frenot *et al.* 2005, Upson *et al.* 2017), and their presence could have modified soil conditions to facilitate or hinder the establishment of further species (Perkins *et al.* 2011, Tabassum & Leishman 2016, Bokhorst *et al.* 2024a). Knowledge of such interactions is relevant for understanding non-native species threats, but this topic is currently poorly studied.

Soil characteristics have a strong influence on local plant distribution patterns (Buri *et al.* 2017). Although soils are generally less developed at higher latitudes, there is no clear latitudinal, climate-driven pattern in soil organic matter content or nutrient availability across the Maritime Antarctic (Bockheim *et al.* 2015). Identifying sites of high potential invasion risk is, therefore, less straightforward in comparison to reliance on species distribution models based primarily on temperature (Duffy *et al.* 2017, Bokhorst *et al.* 2021). However, recent soil mapping studies have documented region-specific variation in substrate organic and nutrient contents on islands off the Maritime Antarctic South Shetland Islands archipelago, north-west of the Antarctic Peninsula (Siqueira et al. 2024). If non-native plant growth can respond to variation in substrate characteristics under cold Antarctic climate conditions, these plant growth responses could then be linked to spatial patterns of substrate characteristics and thereby enable the identification of regions most at risk of non-native plant establishment. Such substrate-growth links could have

particular utility at local scales (0.1–1.0 km), as they could make a practical contribution to management at the site/island scale of most known concentrations of botanical diversity in the Maritime Antarctic (e.g. considering the areal extent of most Antarctic Specially Protected Areas (ASPAs) in the region, see Hughes & Convey 2010).

This study addresses multiple questions in the context of assessing non-native species threats for the Maritime Antarctic: 1) does variation in substrate characteristics affect non-native plant germination and growth? 2) Do established non-native species have biotic effects on non-native plant growth under current Maritime Antarctic climate conditions? 3) Does climate warming interact with substrate characteristics and potential biotic effects to influence non-native plant growth? Tested non-native plant species included a grass (*Holcus lanatus* L.) and two forbs (*Taraxacum officinale* Wigg. and the nitrogen-fixing *Trifolium repens* L.), which are recognized high-risk taxa for future Antarctic invasion (Hughes *et al.* 2020) and are capable of growing in high-organic-content substrate types locally present in Antarctica (Bokhorst *et al.* 2021). We hypothesized that: 1) substrates with higher organic matter content would support more plant growth than sandy substrates, 2) warmer temperatures would result in more rapid seed germination and greater growth of all species and 3) already-invaded substrates would support greater plant growth than substrates without non-native species already present. Following up on questions 1 and 3, we then provide a first test of a protocol for identifying sites of potentially high invasion risk by combining substrate-driven plant responses with mapped substrate characteristics on the South Shetland Islands (Siqueira *et al.* 2024).

Materials and methods

Overall design and species selection

The experiment was run for 140 days under simulated Antarctic growing seasons in temperature-controlled climate chambers (see below for experimental conditions). We compared the germination rate and growth of three non-native plants (*H. lanatus*, *T. officinale* and *T. repens*) across nine different substrate types available to us that are commonly found in ice-free areas along the Antarctic Peninsula and Scotia Arc archipelagos (Maritime Antarctic), sub-Antarctic South Georgia and mountain regions of southern South America (Fig. 1a), with a range of soil carbon, nitrogen and phosphorus contents (Table I), under simulated Antarctic growing conditions and a warming scenario (+5°C). Four substrate types were obtained from locations with moss growth (Maritime Antarctic) that had high (> 20%) carbon content, while five substrate types consisted of fine sand/gravel with low (< 20%) carbon content. Substrates were collected at: Navarino Island (Magellanic sub-Antarctic), southern Chile (54.96°S, 67.63°W), South Georgia (sub-Antarctic; native grass community and community invaded by various non-native grasses (Upson *et al.* 2017); 54.28°S, 36.51°W), Signy Island (Maritime Antarctic; beneath *Andreaea* sp. Hedw. moss with and without presence of larvae of the chironomid midge *E. murphyi* (Hughes *et al.* 2013); 60.71°S, 45.59°W), Anchorage Island (Maritime Antarctic; beneath *Sanionia uncinata* Hedw. moss carpet; 67.61°S, 68.21°W), Adelaide Island (Maritime Antarctic; at the base and summit of Stork Peak; 67.52°S, 68.18°W) and Fossil Bluff (Maritime Antarctic; Alexander Island; 71.20°S, 68.17°W; see Fig. 1). Substrates from Adelaide Island and Alexander Island were shipped from the Antarctic frozen (−20°C),
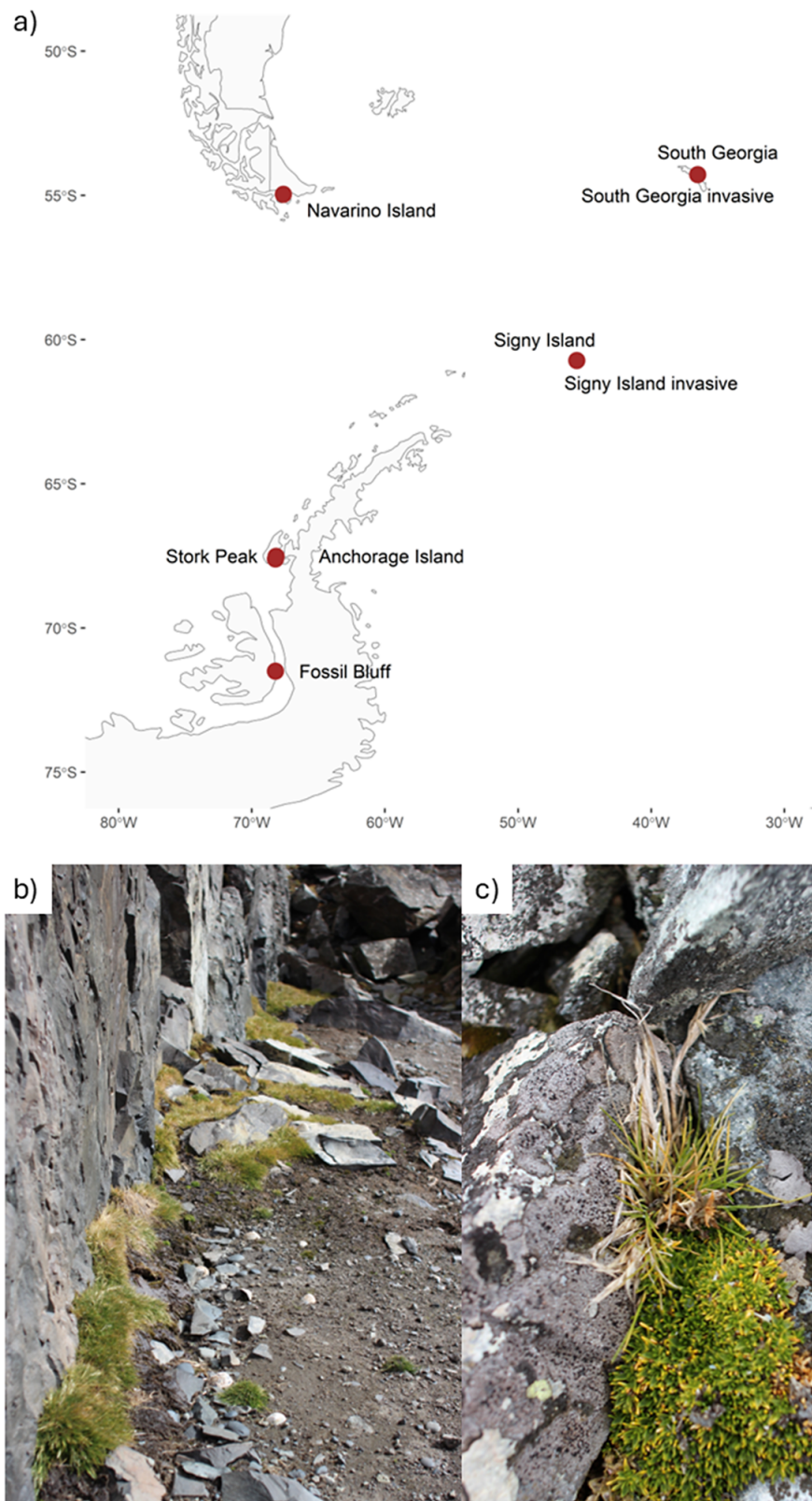
Figure 1. Map of substrate sampling locations from southern South America to the Maritime Antarctic, and *Deschampsia antarctica* typical growth forms at selected sites in the Maritime Antarctic. **a.** Sites where substrates for the non-native growth assays were collected. Note that substrate was collected from the base and summit of Stork Peak (Table I). **b.** *D. antarctica* growth at the base of a north-facing rock face on Byers Peninsula (Livingston Island). **c.** Growth among rubble, in combination with *Colobanthus quitensis*, on Anchorage Island (Ryder Bay, Adelaide Island).

Table I. Substrate characteristics. Substrate pH and nutrient contents used in the invasive species growth experiment. Data are means of n = 5 with SE in parentheses. Superscript letters within columns indicate significant differences between soil types (Tukey's honestly significant difference, P < 0.05). Substrates from South Georgia (SG) and Signy Island (SI) were also sourced from sites with known established invasive species presence. Growth substrate was collected at Navarino Island-Chile (54.96°S, 67.63°W), South Georgia (native grass community and invaded grass community; 54.28°S, 36.51°W), Signy Island (beneath *Andreaea* sp. moss with and without presence of *Eretmoptera murphyi*; 60.71°S, 45.59°W), Anchorage Island (beneath *Sanionia uncinata* moss carpet; 67.61°S, 68.21°W), Adelaide Island (at the base and summit of Stork Peak; 67.52°S, 68.18°W) and Fossil Bluff (Alexander Island; 71.20°S, 68.17°W; see also Fig. 1).

	pH	NH$_4$-N (mg/kg)	NO$_3$-N (mg/kg)	PO$_4$-P (mg/kg)	LOI (%)	C (%)	N (%)	P (%)	C:N ratio	N:P ratio
Chile	5.42 (0.02)[a]	2.56 (0.90)[a]	29.00 (4.15)[a]	0.02 (0.02)[a]	7.73 (0.11)[a]	2.47 (0.04)[a]	0.19 (0.00)[a]	0.08 (0.01)[a]	12.9 (0.07)[a]	2.45 (0.21)[a]
SG	4.48 (0.02)[b]	133.84 (2.76)[b]	484.94 (14.51)[b]	5.00 (0.55)[bc]	51.7 (1.46)[b]	26.90 (0.49)[b]	1.98 (0.03)[c]	0.32 (0.04)[c]	13.6 (0.23)[ab]	6.63 (0.85)[b]
SG - invasive	4.40 (0.05)[b]	21.48 (4.75)[c]	1194.06 (206.70)[c]	2.03 (0.38)[ab]	13.4 (1.40)[c]	6.85 (0.74)[c]	0.46 (0.04)[d]	0.05 (0.01)[ab]	14.7 (0.35)[bc]	10.1 (1.32)[b]
SI	3.86 (0.01)[c]	69.70 (14.78)[d]	1663.64 (34.93)[c]	8.72 (3.02)[c]	47.3 (0.44)[b]	23.90 (0.22)[b]	1.98 (0.02)[c]	0.54 (0.01)[d]	12.1 (0.04)[ad]	3.64 (0.04)[ac]
SI - invasive	4.22 (0.02)[d]	10.98 (0.77)[c]	190.80 (6.56)[d]	2.60 (0.12)[a]	49.8 (2.32)[b]	25.80 (1.19)[b]	1.58 (1.19)[b]	0.19 (0.01)[c]	16.4 (0.41)[c]	8.29 (0.29)[b]
Anchorage Island	4.10 (0.02)[e]	95.38 (3.93)[bd]	339.8 (23.97)[b]	6.82 (0.53)[c]	48.6 (1.75)[b]	24.00 (0.96)[b]	2.11 (0.96)[d]	0.48 (0.01)[cd]	11.4 (0.15)[d]	4.45 (0.08)[bc]
Stork Peak (base)	5.85 (0.02)[f]	0.04 90.02[e]	1.10 (0.03)[e]	0.0 (0.0)[a]	1.75 (0.02)[d]	0.28 (0.00)[d]	0.03 (0.00)[e]	0.05 (0.00)[ab]	8.61 (0.10)[e]	0.62 (0.03)[d]
Stork Peak (top)	6.48 (0.04)[g]	0.14 (1.02)[e]	0.34 (0.02)[e]	0.06 (0.02)[d]	1.85 (0.07)[d]	0.28 (0.01)[d]	0.03 (0.00)[e]	0.04 (0.01)[b]	8.40 (0.13)[e]	0.99 (0.16)[d]
Fossil Bluff	8.36 (0.06)[h]	2.08 (0.57)[a]	0.42 (0.11)[e]	0.24 (0.07)[a]	2.42 (0.18)[d]	0.18 (0.01)[d]	0.04 (0.00)[e]	0.04 (0.01)[b]	5.06 (0.29)[f]	0.90 (0.15)[d]

LOI = loss on ignition.

whereas those from Signy Island, South Georgia and Navarino Island were shipped under cooled (+4°C) conditions. The sampling site on Navarino Island was on the mountain plateau of Cerro Bandera at 600 m above sea level. This site is part of the Magellanic sub-Antarctic region and includes typical Maritime Antarctic fellfield communities of lichens and mosses with mean annual soil temperature of 3.1°C (Bokhorst *et al.* 2024b). Substrate selection was in part opportunistic, driven by the availability of logistical opportunity, and we recognize that this does not encompass all known substrate types found in these regions (Haus *et al.* 2015, Simas *et al.* 2015), but we consider that it includes a large range of typical substrate characteristics.

Ten experimental pots (5 cm diameter PVC tubes with plastic bottoms containing drainage holes) were used per non-native species for each substrate type (10 × 9 substrates × 3 species = 270 experimental pots in total), with half (n = 135) kept at Antarctic temperatures (2°C) and the other half (n = 135) kept under a warming scenario (7°C; see below). Each pot was filled with 2 cm substrate and received 100 seeds of one of the non-native plants. Seeds were cold stratified for 4 weeks in complete darkness at 2°C. The pots were watered twice a week up to an equivalent of 150 mm precipitation per growing season, ensuring that water was non-limiting and within the range of growing season precipitation of the Maritime Antarctic region (Royles *et al.* 2012, Tang *et al.* 2018).

Effect of pre-colonized substrates

To assess the effect of substrates already colonized by non-native and potentially nutrient-releasing invertebrates on non-native plant growth, the study included substrate from Signy Island where larvae of the non-native midge *E. murphyi* Schaeffer have been linked to large increases in nitrogen availability (Hughes *et al.* 2013, Bartlett *et al.* 2023), which may promote greater non-native plant growth under scenarios of continued temperature increase (Bokhorst *et al.* 2022, Valliere *et al.* 2022). Similarly, to assess the possible effect of established non-native plants on later non-native plant arrivals, we included sieved substrate (top 10 cm of soil profile) from South Georgia invaded by various non-native grasses (Upson *et al.* 2017). This element of the study provides a preliminary approach to identifying whether biotic feedbacks between non-native species can affect plant growth under current Maritime Antarctic climate conditions and a realistic climate warming scenario.

Antarctic climate simulation

Simulation of Antarctic soil surface microclimate conditions, representative of sites in the Maritime Antarctic (Convey *et al.* 2018), was achieved by setting the growth chamber (THEBO Horeca, with RIVA Cold refrigeration units, Rivacold srl-Vallefoglia, Italy), at 2°C and modulating the diurnal light conditions (photosynthetically active radiation levels), creating realistic soil surface temperatures (mean of 6–7°C) during the afternoon as measured in the field on Anchorage Island close to the Antarctic Peninsula (~68°S). Diurnal light (photosynthetic active radiation)-intensity patterns were adjusted every month using light-emitting diode (LED) lamps (Hortilight Sunfactor 270; 405 W) to simulate the changing light conditions from October to March as measured on Anchorage Island. Experimental daylength and light intensity increased from October to December, after which it declined again towards March (Fig. S1). To quantify the impacts of climate

warming, a parallel climate chamber was run at 7°C, with all other conditions and numbers of treatments and replicates kept the same. The 5°C temperature increase reflects the Shared Socio-economic Pathway (SSP) 5–8.5 global climate warming scenario (Intergovernmental Panel on Climate Change 2023), which is appropriate given that the northern Antarctic Peninsula region has already warmed by ~3°C in the second half of the twentieth century and warming trends of ~0.5°C/decade have been reported and are predicted for the remainder of the twenty-first century (Siegert *et al.* 2019). To avoid any effects of placement within each chamber, pot positions were randomly repositioned every week and moved between chambers (with chamber temperature adapted) every month to avoid any systematic 'chamber effect' throughout the experiment.

We recognize that this experimental simulation of Antarctic soil surface conditions is limited with respect to aspects of field climate variability, which include abrupt changes in freezing and thawing during the growing season (Convey *et al.* 2018), and therefore is not representative for the whole of the Maritime Antarctic. However, we consider that it does practically reflect the growing season temperature and light conditions that vascular plants experience at sheltered sites, where the native Antarctic vascular flora persists (Fig. 1b,c) and non-native species are most likely to establish.

Biological response variables

At the start of the simulated growing season, we quantified the time to germination of the first seedling for each species in each experimental pot. At the end of the growing season, we measured plant maximum height as a measure of plant production. See Fig. S2 for species-specific correlations between plant height and biomass.

Substrate characteristics

From each bulk substrate (obtained at each location), we sub-sampled five replicates to compare substrate characteristics. Substrate organic matter content was quantified through loss on ignition (LOI) at 550°C, and total carbon and nitrogen levels were quantified by dry combustion in an elemental analyser (Flash EA 1112, Thermo Scientific, Rodana, Italy). Substrate pH (H_2O) was measured in a soil:demi extract (1:6) using a WTW pH meter with Sentix 41 electrode (Inolab Level 2, WTW, Weilheim, Germany). The supernatant was then used to quantify soil extractable nutrients (NH_4-N, NO_3-N and PO_4-P) using an auto-analyser (Lachat Quikchem 8000). Total phosphorus (P) was quantified by digestion in 1 ml of a 1:4 mixture of 37% (v/v) HCl and 65% (v/v) HNO_3, in a closed Teflon cylinder for 6 h at 140°C. Samples were then diluted with 4 ml demineralized water, and total P content was quantified by spectrophotometry, using the ammonium molybdate method.

Data analyses

One-way analysis of variance (ANOVA) was used to compare substrate characteristics (pH, NH_4-N, NO_3-N, PO_4-P, LOI, %C, %N, %P, C:N and N:P). Factorial ANOVA was used to identify how substrate type and temperature (2°C and 7°C) affected germination time and plant height for each of the non-native species. Where significant, *post hoc* testing (Tukey's honestly significant difference (HSD) tests) was performed to compare germination and growth at

2°C and to determine any warming effects for each substrate type. We used correlation (Pearson) to test for significant relationships between germination time and plant height with substrate characteristics ($n = 9$) and between substrate characteristics (Table S1). All data were log- or square root-transformed to improve homogeneity of variances. All statistical analyses were performed using *R* (R Core Team 2023).

There are no consistent overall latitudinal trends in soil characteristics in the Maritime Antarctic; instead, high spatial and local heterogeneity is typical. To visualize the invasive potential of non-native plants, we used data from local-scale, well-sampled and mapped sites of the South Shetland Islands (Siqueira *et al.* 2024). Potential plant invasion was calculated by normalizing (value-min/max-min) the available substrate data variables that overlap with our experimental study (substrate organic and P content) and multiplying this by the correlation coefficient of the plant species' growth response with that substrate variable. In addition, we compared substrate suitability for our grass test species *H. lanatus* at Point Thomas in Admiralty Bay (King George Island), as this is a known location where the non-native grass *Poa annua* L. has established and grows well (Galera *et al.* 2021).

Results

Substrate characteristics

The different substrates showed large ranges of pH (3.9–8.4), soil C (0.2–27%), N (0.03–2.1%) and P (0.04–0.54%) contents and N:P ratio (0.6–9.8; Table I). Substrates from the most southern locations had the lowest soil carbon (0.2%) and nitrogen (0.03%) contents and C:N and N:P ratios but high pH (8.4). Invaded substrates had lower total N and P than non-invaded substrates on both South Georgia and Signy Island but no consistent pattern in leachable nutrients.

Plant growth response

Seed germination was dependent on substrate type and temperature (Tables II & III). Germination took longest on average (±63 days) in high-organic-content substrates from the Maritime Antarctic and was more rapid (±15 days) in low-organic-content substrates from the most southern and northern locations (Fig. 2). *T. officinale* and *H. lanatus* were most responsive to warming, with

Table II. Analysis of variance results of comparisons of effects of temperature (T; 2°C *vs* 7°C), substrate type (S; $n = 9$) and non-native plant species (Sp; *Holcus lanatus*, *Taraxacum officinale* and *Trifolium repens*) on seed germination.

	df	Days until emergence	
		F-value	*P*-value
T	1, 213	339.8	< 0.001
S	8, 213	9.8	< 0.001
Sp	2, 213	186.0	< 0.001
T × S	8, 213	10.0	< 0.001
T × Sp	2, 213	24.2	< 0.001
S × Sp	16, 213	3.6	< 0.001
T × S × Sp	16, 213	1.9	0.026

Table III. Analysis of variance results of substrate type and temperature (2°C *vs* 7°C) effects on seed germination and plant height. *Holcus lanatus*, *Taraxacum officinale* and *Trifolium repens* were grown under simulated Antarctic temperature (2°C) and a warming scenario (7°C) in nine different substrate types.

		Substrate		Temperature		Substrate × temperature	
		F-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value
H. lanatus	Emergence	3.5	0.001	214.0	< 0.001	3.8	< 0.001
T. officinale	Emergence	2.7	0.008	255.9	< 0.001	4.0	< 0.001
T. repens	Emergence	10.6	< 0.001	39.9	< 0.001	4.7	< 0.001
H. lanatus	Plant size	15.6	< 0.001	55.1	< 0.001	2.9	0.005
T. officinale	Plant size	29.9	< 0.001	40.4	< 0.001	7.6	< 0.001
T. repens	Plant size	15.7	< 0.001	97.7	< 0.001	6.0	< 0.001

20 (±2.9) and 15 (±2.4) days advance in germination, respectively, whereas *T. repens* showed a lower response (7 ± 2.7 days) to warming. The acceleration of germination due to warming was very similar irrespective of substrate type (Fig. 2).

Plants were on average ±25% shorter in low-organic-content substrates and larger in high-organic-content substrates, but the latter finding was not consistent across all substrates (Fig. 2). For several substrates warming resulted in very strong growth increases for all three species. Plant size was doubled for *H. lanatus* in Signy Island substrate and invaded substrate from South Georgia (Fig. 2d). *T. officinale* plant size increased with warming and was largest in substrates from Anchorage Island (274%) and Signy Island (137%; Fig. 2e), whereas *T. repens* very strongly increased in size in substrates from Anchorage Island (222%), Signy Island (222%) and South Georgia (139%; Fig. 2f).

Effect of pre-colonized substrates

Germination of *H. lanatus* and *T. officinale* was unaffected by prior non-native species presence, whereas *T. repens* germination was delayed by 16 day (±2 SE) in *E. murphyi*-colonized substrate from Signy Island compared with uncolonized Signy Island substrate. However, these germination responses did not lead to significant plant growth changes between the two substrates (Fig. 2).

Warming doubled *H. lanatus* plant size in grass-invaded substrate from South Georgia, with a smaller (67 %) growth response in non-invaded substrate. However, warming did not affect *H. lanatus* growth in invaded substrate from Signy Island, whereas a growth increase (102%) occurred in non-invaded substrate. Warming induced greater *T. officinale* growth in invaded (132%) and non-invaded (142%) substrates from Signy Island but not in substrates from South Georgia. Conversely, warming induced greater *T. repens* growth (139%) in invaded South Georgia substrate but not in non-invaded substrate, whereas at Signy Island warming resulted in increased growth (221–224%) irrespective of prior non-native species presence.

Substrate characteristics and spatial risk of non-native plant establishment

Plant size of *H. lanatus* and *T. repens* was positively related to substrate organic, C, N and P contents and N:P ratio but negatively related to substrate pH, and these patterns were stronger with warming (Table IV). Conversely, *T. officinale* plant size did not show any significant correlation with substrate characteristics. Substrate mapping predictions in the South Shetland Islands

included various variables, of which C and P content overlapped with the variables explored in our experimental study. Mapped substrate C and P contents were generally low (0–10%), with some higher-content hotspots across selected sites in the South Shetland Islands (Fig. 3). Variation in mapped substrate C and P contents allows, in combination with the plant growth data (Fig. 2 & Table IV), visual identification of potential high-risk establishment sites for the three tested species (Fig. 4). Mapped substrate suitability for the test grass species *H. lanatus* matches with presence of the established non-native grass *P. annua* on King George Island (Fig. S3).

Discussion

All three tested plant species germinated and grew across the wide range of substrate types tested here, which is surprising given the very low organic and nutrient contents of some. However, the species did not grow equally well, and higher-organic-content and higher-nutrient-content substrates (characteristic of already-vegetated areas) supported typically greater growth. These findings suggest that already-vegetated areas, particularly those with moss or vascular plant presence or close to nutrient sources such as penguin colonies (Zwolicki *et al.* 2015, Bokhorst *et al.* 2019), should be of primary concern with regard to invasive plant species threats. Our novel proposed mapping approach provides a means of identifying the distribution of these suitable habitats and, thereby, an additional method for assessing local invasive species threats in the Maritime Antarctic.

The grass *H. lanatus* and the nitrogen-fixing forb *T. repens* grew larger in high-organic-content substrates with greater nutrient availability, consistent with typical responses observed in nutrient fertilization studies and along succession gradients (Chapin *et al.* 1994). In contrast, *T. officinale* grew well irrespective of substrate characteristics, consistent with its ability to grow well across various environments (Molina-Montenegro *et al.* 2013). *T. officinale* showed large growth, especially with warming, when grown in Anchorage Island substrate. Substrates from Signy Island and Anchorage Island (the high-organic-content substrates in this study) did not differ in carbon and nutrient contents, but pH was lower at Signy Island, which can negatively impact growth of *T. officinale* (Buchanan *et al.* 1975). These substrates were obtained from *Andreaea* sp. (Signy) and *S. uncinata* (Anchorage) communities, which are likely to have different associated microbial communities and potentially distinct moss secondary compounds (Commisso *et al.* 2021), which also can affect plant growth (Soudzilovskaia *et al.* 2011, Bokhorst *et al.*
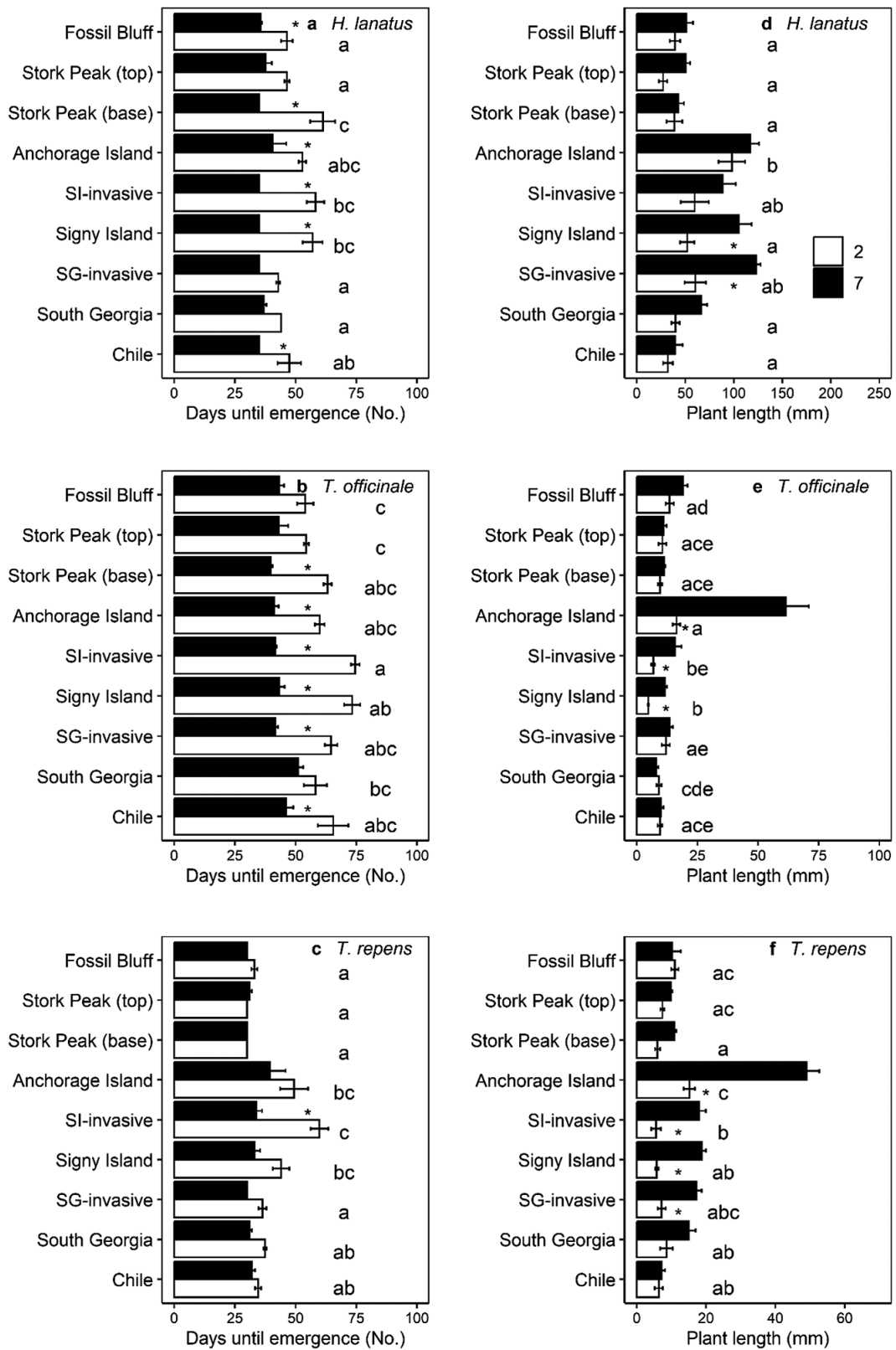
Figure 2. Germination and growth responses of three non-native plant species across nine substrate types and two temperature regimes. Time until germination is shown in panels **a.–c.** and plant sizes at the end of the simulated growing season are shown in panels **d.–f.** Bars are means of n = 5 with SE as error bars (where germination occurred at the same time in some substrates, no variation is apparent). Bars with different letters indicate significant response differences between substrate types at 2°C (open bars), while asterisks denote significant temperature effects (closed bars; 7°C). SG = South Georgia; SI = Signy Island.
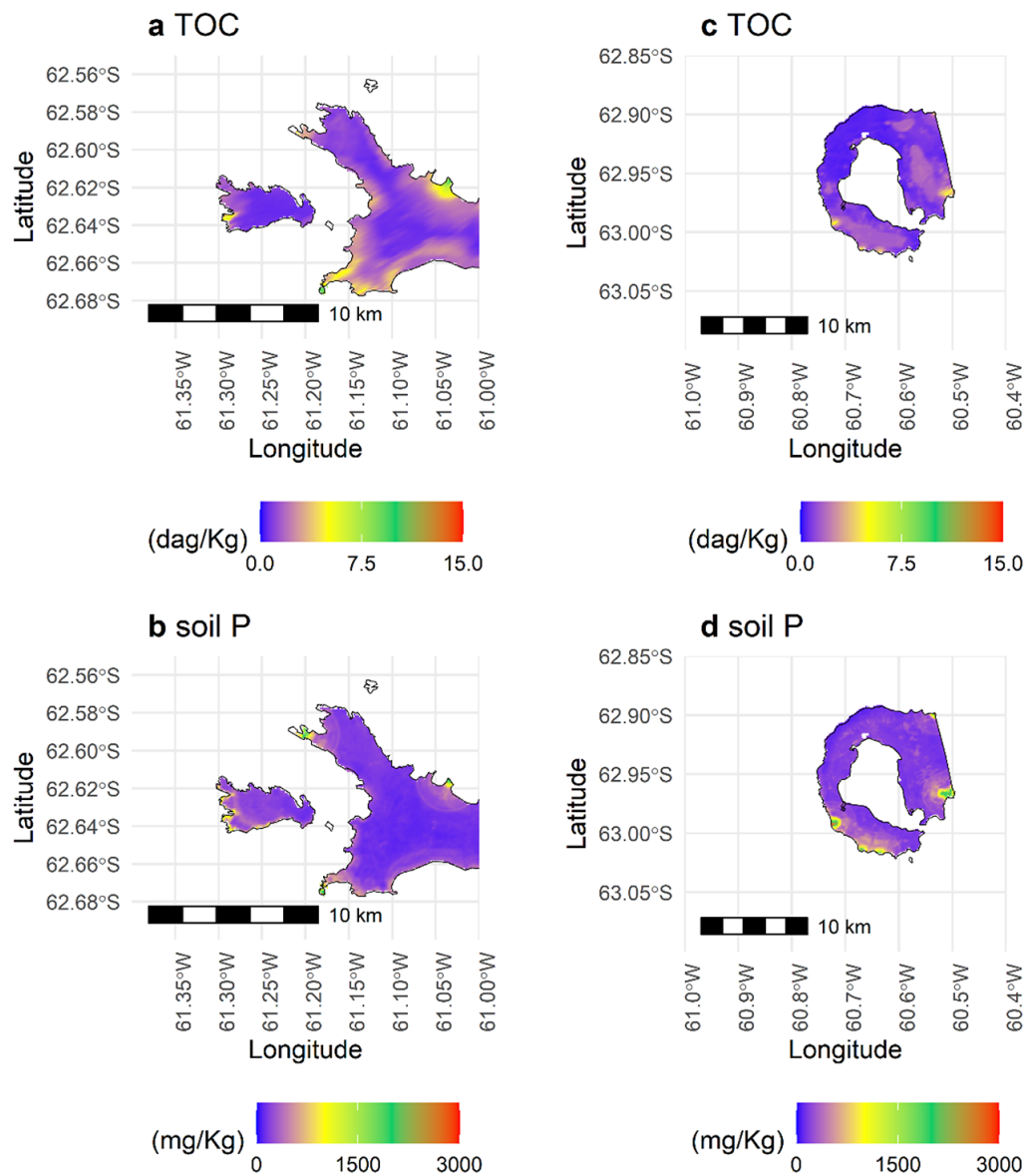
Figure 3. Substrate characteristics on Byers Peninsula (Livingston Island) and Deception Island (South Shetland Islands). Substrate total organic content (TOC; dekagrams (dag)/kg) is mapped for **a.** Byers Peninsula and **b.** Deception Island, and soil phosphorus (P) is mapped in panels **c.** and **d.** Data derived from Siqueira *et al.* (2024).

2022). Overall, the plant responses across the tested substrate types followed expected patterns with regard to organic and nutrient contents, but with differences in detail between the three non-native species.

Plants germinated more rapidly on average under the warming treatment, as expected, which would provide more time for growth during the relatively short Antarctic growing season (Bokhorst *et al.* 2021). However, warming did not consistently result in larger plants, meaning that some substrate characteristics were limiting for further growth, as has also been reported in Arctic regions (Rustad *et al.* 2001). The substrates used in this study were obtained across an environmental gradient covering more than 1800 km (54–71°S) and including large changes in soil and primary producer communities (Convey *et al.* 2014, Convey & Biersma 2024). However, there was no consistently stronger plant growth response to warming from the coldest sampling sites, where

temperature and water are most limiting, or from the warmer locations. Instead, substrates with low N and P contents showed limited growth responses to warming, indicating that, although germination and some growth is possible in these poorly developed substrates that dominate the southern Maritime Antarctic (Haus *et al.* 2015), it is unlikely that extensive vascular plant cover will develop in the foreseeable future, even with considerable warming (> 5°C).

There was no indication that plant growth patterns differed in substrates already invaded by other non-native species. While *H. lanatus* and *T. repens* responses to warming were larger when growing in invaded substrate from South Georgia, they responded less strongly to warming when growing in invaded substrate from Signy Island, possibly indicating that these species benefitted most from indirect effects of other non-native grasses compared to non-native soil fauna. However, we recognize that

Table IV. Correlation coefficients of plant size with substrate characteristics. Bold values represent significant ($P < 0.05$) correlations and italics represent near-significant trends ($P < 0.1$).

	Holcus lanatus		*Taraxacum officinale*		*Trifolium repens*	
	2°C	7°C	2°C	7°C	2°C	7°C
LOI	*0.630*	*0.661*	−0.368	0.257	0.119	**0.716**
C	*0.623*	**0.667**	−0.378	0.235	0.101	**0.709**
N	*0.659*	**0.685**	−0.314	0.318	0.207	**0.770**
P	*0.590*	*0.608*	−0.338	0.359	0.237	**0.728**
C:N	0.405	0.535	−0.394	−0.116	−0.370	0.321
N:P	0.550	**0.729**	−0.114	0.035	−0.102	0.445
pH	*−0.595*	**−0.696**	0.409	−0.092	0.203	*−0.616*
PO$_4$-P	*0.636*	**0.732**	−0.345	0.320	0.209	**0.757**
NH$_4$-N	0.431	0.477	−0.040	0.173	0.415	*0.613*
NO$_3$-N	0.390	**0.723**	−0.482	−0.085	−0.209	0.380

LOI = loss on ignition.

this may also reflect the nature of the substrate, which, at South Georgia, is derived from a vascular plant-dominated system, whereas the Signy Island substrate has a moss origin, and these initial results can be used to guide future studies. Activity of the non-native midge *E. murphyi* on Signy Island has been linked to locally considerably enhanced nitrogen mineralization in a *Polytrichum* moss peat substrate (Hughes *et al.* 2013, Bartlett *et al.* 2023), but this was not apparent in our data from a much shallower *Andreaea* moss carpet (Table I), which may account for the low plant response to warming here. Overall, other non-native species currently established in Antarctica appeared to have little effect on the growth of the tested non-native plant species in this study, differing from reported negative direct impacts in experimental competition experiments between non-native and native plant species in Maritime Antarctica (Molina-Montenegro *et al.* 2012, 2019) and the generally negative influence non-native plants tend to have on each other (Kuebbing & Nuñez 2016). This suggests that the current climate in the region may still be too limiting to allow for soil-mediated species interactions.

The mapping of potential suitable growth sites for non-native vascular plants allows for spatial distinction at a level suitable for management planning at a given location (Fig. 4) and also matches with already-invaded locations on King George Island (Fig. S3). However, this remains a relatively coarse comparison based on substrate characteristic resolution, and therefore its use should be limited to local scales (e.g. < 30 km), as temperature, water availability and light (photoperiod) conditions may override substrate characteristics for plant growth across larger scales. This approach appears to work well for species with relatively strong growth responses to specific substrate characteristics (here substrate C and P), but not for *T. officinale*, which grew equally well across the tested substrates, resulting in low expected growth potential (Fig. 4b). Such an outcome does not imply that *T. officinale* cannot grow at these sites, but it may perform well irrespective of substrate characteristics, indicating that multiple species should be compared for mapping invasive species threats. In addition, vascular plant growth in Antarctica frequently takes place in and around small rock crevices (Fig. 1b,c), which would not be highlighted on a map

of substrate characteristics. The native grass *Deschampsia antarctica* has, for instance, been reported near the edge of the Rotch Dome glacier on Byers Peninsula (Vera *et al.* 2013), in line with its recognized role as a pioneer species (Edwards 1972, Kozeretska *et al.* 2010), while our current mapping indicates low suitability for the non-native grass *H. lanatus* at this location (Fig. 4a). Despite these limitations, the use of substrate characteristics can help in identifying local sites most likely to be invaded by non-native plants.

Most known established Maritime Antarctic and sub-Antarctic non-native species (15 and > 200 documented, respectively) are present near sites with past or present human activities (Frenot *et al.* 2005, Hughes *et al.* 2015, Bazzichetto *et al.* 2021), indicating that the locations of our activities require particular attention, especially where long-term presence or high visit frequencies are probable. A potential hotspot for grass establishment, based on the substrate characteristics, is found near a popular boat landing site and recommended camping site on Deception Island (Fig. 5), and therefore we suggest that the use of these sites needs to be considered in the light of the non-native species threat. Our data show that moss-associated, organic-rich substrates promote plant growth more effectively than more poorly developed substrates. These findings match with findings regarding the facilitation effect of Antarctic mosses on the growth of *D. antarctica* (Casanova-Katny & Cavieres 2012). As a result, we suggest that monitoring for non-native plant presence should focus on the generally richer, moss-dominated habitats that are already present in the Maritime Antarctic. Once established, eradication of non-native plants from the complex matrix of mosses in these communities may be very damaging to the ecosystem (Hughes *et al.* 2015), so capturing these invasive species early on will be crucial. In addition, aggregations of marine vertebrates on land enhance nutrient availability and promote plant growth (Zwolicki *et al.* 2015, Bokhorst *et al.* 2022). Therefore, a combination of mapping soil characteristics and the nitrogen footprint both of larger vertebrate aggregations (Bokhorst *et al.* 2019) and of smaller (even individual) local nesting sites (Parnikoza *et al.* 2018) may provide a pragmatic and practicable approach to identifying sites at the highest risk of being invaded by non-native vascular plants in the Maritime Antarctic, thereby
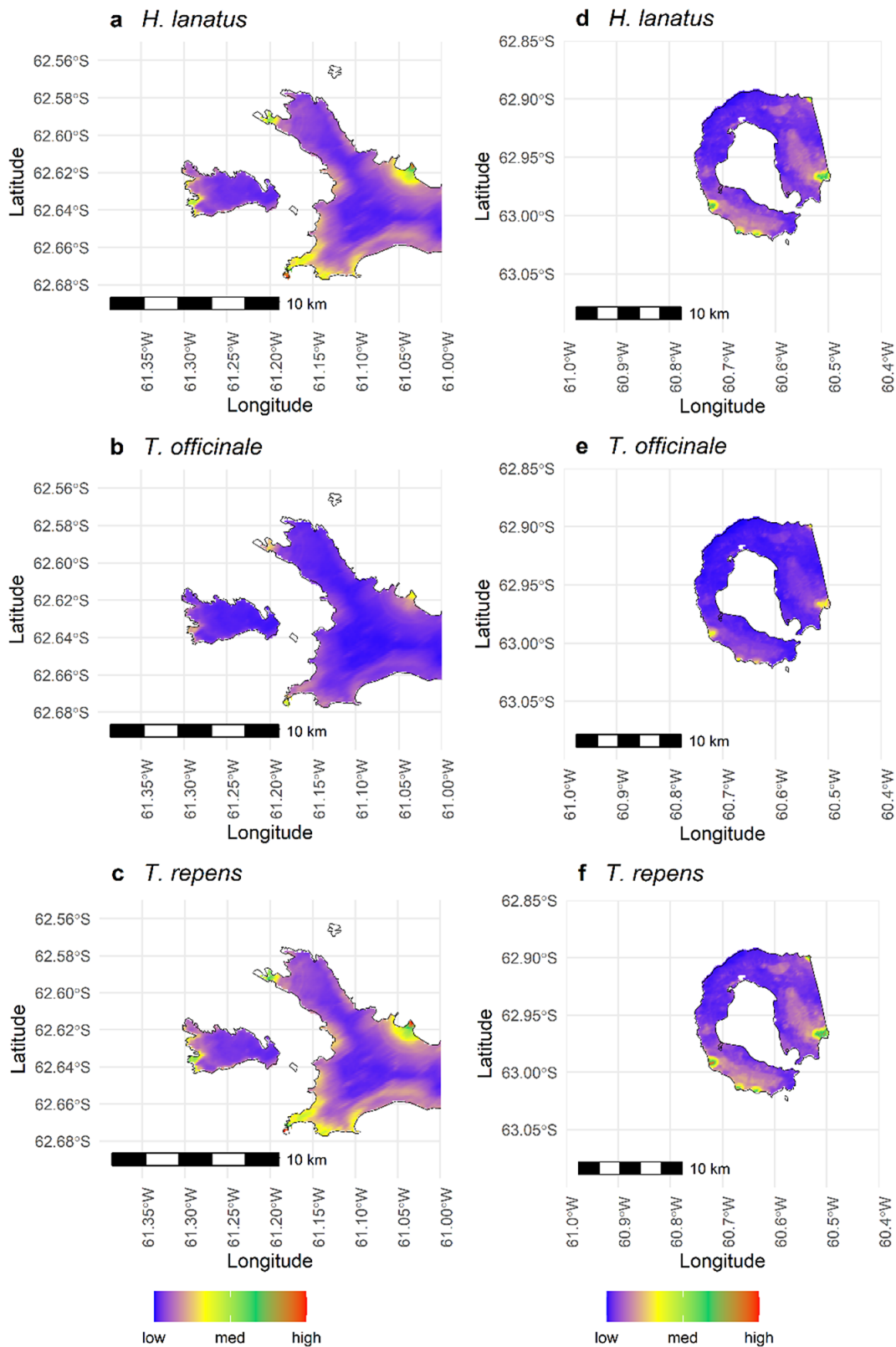
Figure 4. Potential for non-native plant growth across ice-free regions in the South Shetland Islands. Images show the relative growth potential of *Holcus lanatus* (**a.** & **d.**), *Taraxacum officinale* (**b.** & **e.**) and *Trifolium repens* (**c.** & **f.**). Low, medium and high growth potentials are based on the site-specific soil characteristics (organic carbon and soil phosphorus; see Fig. 2) and the growth response across substrates (see Fig. 1 & Table IV).
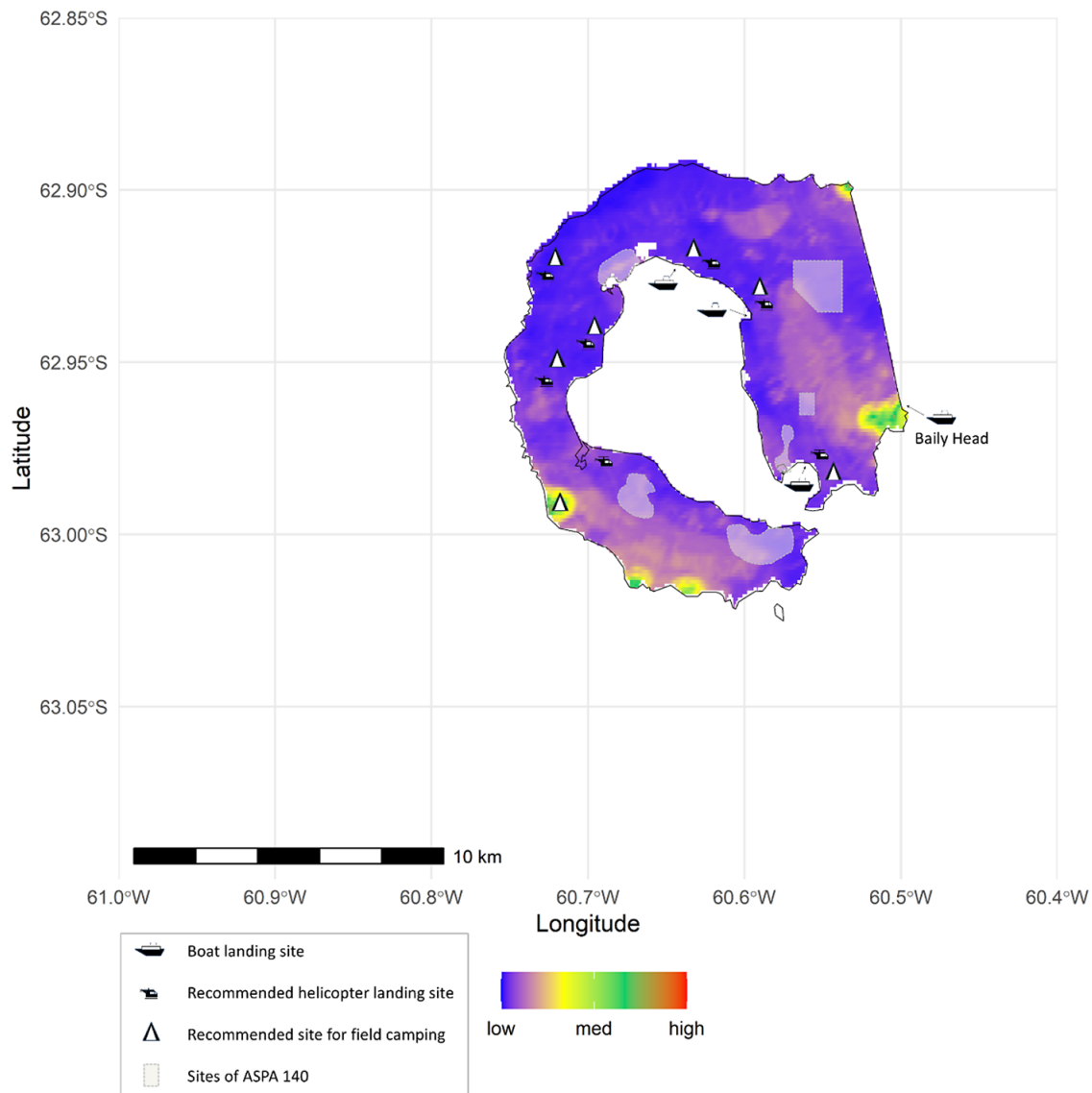
Figure 5. Overlay of potential non-native plant growth with aspects of prominent sub-sites of Antarctic Specially Protected Area (ASPA) 140 Deception Island. Note the high non-native plant growth potential of *Holcus lanatus* near the landing site at Baily Head, which is commonly used for guided tourist visits, and the recommended camping sites at the south-west of the island. Grey shaded regions indicate the defined largest sub-sites of this ASPA (map obtained from APA Database | Antarctic Treaty).

underpinning the planning and selection of key monitoring sites and improving our ability to manage human activities in and impacts on Antarctica.

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