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RESEARCH

Kelp gull shell middens potentially facilitate root growth of non-native plants in Antarctica

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Abstract

Ecosystem engineering is an important factor influencing species establishment in novel environments. Here we tested how shell middens created by kelp gulls (*Larus dominicanus*) affect the growth of candidate non-native plants under simulated Antarctic conditions. Calcium compounds derived from the shells raised the organic Antarctic substrate pH from 6.0 to 7.3 and resulted in increased plant biomass (21–100%) over a 14-week experimental period compared to plants grown without shell-amended substrate. The increase in biomass was primarily driven by the development of longer and heavier roots. Plant calcium content (mg) doubled under the shell treatment while nitrogen content was unaffected and phosphorous (%) declined by 16–37%, although total accumulated plant phosphorous was unaffected. Our data suggest that, by transferring considerable quantities of marine-derived substrate (shells) into focal locations on land, kelp gulls can potentially act as ecosystem engineers by promoting non-native plant growth in Antarctica. These findings highlight the need for consideration of the potential suitability of marine vertebrate-influenced habitats for non-native plant species growth in remote and pristine environments such as Antarctica.

Keywords Nutrient · Invasion engineer · Polar · Calcium · pH · Phosphorous

Introduction

Facilitation occurs when a species alters the environment in a manner that allows better survival and growth of another species (Callaway 2007; Bronstein 2009). Such interactions can occur within or across trophic levels (Fodrie et al. 2008). One form of facilitation occurs when animal behaviour alters habitat nutrient availability which, in turn, affects population sizes and biodiversity patterns of unrelated species, such as plants and their associated invertebrate communities. This form of facilitation is commonly encountered in coastal regions where birds and marine mammals transfer nutrients from sea to land, particularly in locations where their populations are concentrated such as breeding colonies and haul-out sites, which enhances local populations of plants and invertebrates (Bokhorst et al. 2019; van der Vegt and Bokhorst 2024; Zmudczyńska-Skarbek et al. 2024). Such nutrient hotspots can also benefit plant species that are not native to the locations in question, as reported for sites under nutrient enhancement by penguins, seals, crabs and foxes in different parts of the world (Cocks et al. 1998; Zhu et al. 2014; Gharajehdaghipour et al. 2016; Bokhorst et al. 2022). However, while there is obvious benefit for plant growth from higher nitrogen and phosphorous levels (Aerts and Chapin 2000), the impacts of enhanced micro-nutrient availability, such as calcium (Ca) or magnesium (Mg) (Pandey 2015), have received little research attention. The shells of marine molluscs, for instance, have high calcium content (Barros et al. 2009). Human-created shell middens (such

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as those created by indigenous communities in Baja California) are known to enhance both local plant biodiversity and that of invasive plants (Karalius and Alpert 2010; Vanderplank et al. 2014). Similar facilitation can be predicted in association with other sources of shell deposits, such as deposition of regurgitated shells after foraging which results in the formation of sometimes considerable middens (Wyman 1868; Cadée 1995), as the dissolution of Ca from the shells modifies soil conditions for plant growth (Zheng et al. 2023; Lolas et al. 2024). However, while shell-mediated plant invasions have been reported in eelgrass beds (White and Orr 2011), little or no information exists for undisturbed terrestrial ecosystems. However, many seabird species are known to create such shell deposits in coastal areas (Wright and Kornicker 1962; Cadée 1995) which could, therefore, facilitate plant growth, particularly in ecosystems that are typically deficient in nutrient and mineral sources such as those of the polar regions (Convey et al. 2014).

Calcium is a mineral that is essential for plant physiology and growth (White and Boadley 2003; Jing et al. 2024). It is the third most abundant essential plant nutrient after nitrogen (N) and potassium (K). While Ca is often overabundant in some soils and plant requirements are generally low, deficiency can quickly lead to cell physiological disruptions and even plant death (Hepler 2005). Enhanced soil Ca availability tends to promote plant root elongation and biomass (Emanuelsson 1984; Duan et al. 2022), which would benefit germinating seedlings and newly established plants. Increases in Ca availability also raise substrate pH. For instance, the practice of liming is well known to promote growth of some plants and affect the availability of other nutrients (Haynes 1982; Enesi et al. 2023). Notably, phosphorus (P) availability is affected by soil pH, with P binding to Ca under higher soil pH conditions, thereby becoming less available for plant growth (Penn and Camberato 2019). The consequences of enhanced Ca availability for plant growth are therefore also likely to be mediated by local substrate characteristics.

Establishment of non-native plants is considered one of the greatest threats to the biodiversity and functioning of Antarctic terrestrial ecosystems (Frenot et al. 2005; Hughes et al. 2020), while increased propagule pressure is directly associated with rising levels of human activity (Chown et al. 2012; Huiskes et al. 2014). Non-native species establishment and growth in Antarctica will depend on species ability to cope with the region's typically large environmental variability, not least in soil surface temperature (Convey et al. 2018). It is often micro-scale variability, with temperature hotspots well above the ambient air temperature (Randall et al. 2025), that may allow non-native plants to germinate and grow (Bokhorst et al. 2021). Identifying the local characteristics most suited for non-native plant growth (Molina-Montenegro et al. 2014; Galera et al. 2019; Ballesteros et al. 2022; Bokhorst et al. 2025) may, therefore, facilitate monitoring and mitigation efforts. Antarctic terrestrial ecosystems and vegetation development are generally nutrient-limited (Allen et al. 1967). While higher soil Ca content is often derived from calcareous schists and marble bands (Smith 1978), these are relatively rare in maritime Antarctic regions, where acidic rock types, such as granite, dominate. Thus, in the maritime Antarctic, the region of the continent where non-native species colonisation is highest (Hughes et al. 2025), soils are typically limited in available Ca. In this region, bird activity, such as that of kelp gulls (*Larus dominicanus*) in creating often considerable middens of regurgitated marine mollusc shells (primarily *Nacella concinna*) after foraging (Fig. 1), may facilitate soil development and the growth of both native and non-native plants. Kelp gull activity (and also that of skuas, *Catharacta* spp.), in the form of the accumulation of local plant material within their nests, has also been directly linked with the local dispersal and re-establishment of elements of the native Antarctic terrestrial flora (Parnikoza et al. 2018). Non-native plant growth is most likely in organic substrates across maritime Antarctic environments (Bokhorst et al. 2025), and those regions receive more conservation focus than granite-dominated habitats, but this approach may be too simplistic if shell middens can facilitate plant growth.

The aim of this study was to confirm whether mollusc shells (*N. concinna*) deposited by kelp gulls could facilitate the growth of non-native plants in Antarctic substrates under simulated natural conditions. To address this aim, we quantified seed germination time and subsequent growth of the non-native plants *Taraxacum officinale* (G.H.Weber ex F.H. Wigg.) and *Holcus lanatus* (Linnaeus) under simulated Antarctic summer conditions. These species show rapid population growth in other parts of the world where they have been introduced, and are distributed throughout the southern parts of Chile and on some sub-Antarctic islands (Frenot et al. 2005; McGeoch et al. 2015). Both species are known to be capable of growth on Antarctic substrate under simulated Antarctic climate conditions (Bokhorst et al. 2025). We hypothesised that Ca released from mollusc shells would (1) induce greater non-native plant growth while (2) limiting P-availability and inducing root elongation.

Materials and methods

To test whether non-native plants would benefit from enhanced Ca availability derived from shell middens created by local bird activity, we grew seeds of two plant species not native to Antarctica (*T. officinale* and *H. lanatus*) in non-manipulated or shell-amended substrates. The experiment

Fig. 1 Shell deposit on Anchorage Island (Ryder Bay, south-east Adelaide Island) off the west coast of the Antarctic Peninsula

consisted of 96 microcosm experiments (pots of 4.6 cm diameter and 5 cm height) in which seeds of the two non-native plants (obtained from CruydtHoeck.nl) were grown in Antarctic substrate (2 cm depth) with ($n=8$) and without ($n=8$) addition of mollusc shells (*N. concinna*) under a simulated Antarctic growing season (14 weeks; November – February). The Antarctic growth substrate was obtained during January 2019 from beneath a carpet of the widespread and common moss, *Sanionia uncinata* Hedw., on Anchorage Island (maritime Antarctic, 67.61°S, 68.21°W) and transported frozen (-20 °C) to laboratories in the VU Amsterdam in the Netherlands. Shell material was collected from natural middens on Anchorage Island (Fig. 1). As a further control, we compared growth of the plants in potting soil (Central Park Universal Potting Soil) with ($n=8$) and without ($n=8$) shell (*N. concinna*) addition. To test if non-native plant growth would benefit from Ca addition alone in the absence of shells, we included a further experimental treatment in which $CaCO_3$ was added to experimental pots ($n=8$), again using both Antarctic substrate and potting soil. In total 48 pots were planted with *T. officinale* and 48 with *H. lanatus* seeds across the six experimental treatments.

The shell treatment consisted of 3 g coarsely crushed shells (*N. concinna*) placed on the soil surface (0.2 g/ cm^2). Kelp gull shell middens commonly cover several square meters and contain layers up to tens of cm depth of accumulated shells containing intact and fractured shells (Nolan 1991; Cadée 1999). On Anchorage Island, hand collected samples (25 cm^2 of 2 cm deep, $n=20$) contained on average 42 (SE±4) shells equivalent to 41 (SE±3) g dry mass or ~1.6 g/cm^2 (unpublished data from sampling during January 2018). The 3 g shells per pot used in the experiment therefore represents a low number of shell fragments representative of the edge of a midden or a few shells in isolation. An equivalent amount of $CaCO_3$ was added to the Ca treatment. Considering that a typical mollusc shell contains 95–99% $CaCO_3$ (Barros et al. 2009), there would be 2.85–2.97 g $CaCO_3$ in 3 g crushed shells which, in this study, was rounded to 3 g for the $CaCO_3$ treatment. Shell middens are a well-known and long-lasting feature of gull breeding locations along the Antarctic Peninsula coastline – indeed those on Rothera Point close to the BAS research station are both considerable size and have been present for >30 years (personal observation PC). During the 2025/26 summer, sub-fossil middens were re-exposed by local ice retreat at Rothera that likely date to c. 1000 years ago, given that mosses re-exposed approx. 10 years ago in this retreat have been carbon dated to ~600 years ago (Cannone et al. 2017).

Taraxacum officinale (herb) and *H. lanatus* (grass) were used as representative non-native plant species recognised to have a potential invasion risk in the Antarctic (Frenot et al. 2005). Seeding density was 50 seeds/pot for both species. All pots were watered and subsequently placed in a dark climate chamber at 2 °C (mean growing season soil surface temperature on Anchorage Island) for 2 weeks to allow for cold stratification. Thereafter, the lights in the climate chamber (see regime in appendix) were turned on and plants were watered twice a week over the growing season. A total of 150 mm water was applied over the growing season, which is well within the range of measured precipitation values for sites along the Antarctic Peninsula (Tang et al. 2018). The lights in the climate chamber provided the plants with monthly mean diurnal light conditions mirroring those on Anchorage Island (Bokhorst et al. 2021), ensuring that the light conditions were close to natural conditions. To avoid habituation within the climate chamber, pot positions within containers were randomly repositioned twice a week and the containers were interchanged once a week.

Antarctic climate simulation

The experiment ran for one simulated growing season spanning one Antarctic spring month (November) and the summer months December - February. To simulate natural field conditions, micro-meteorological data (e.g., soil surface conditions) recorded at Anchorage Island (Ryder Bay, Adelaide Island, local to Rothera Research Station) during 2004–2006 were used (Fig. S1). A walk-in cooling chamber (THEBO Horeca, with RIVA Cold refrigeration units, Rivacold srl – Vallefoglia, Italy) was used. The mean air temperature was set to 2 °C and diurnal light intensity was modulated through LED lamps (Hortilight Sunfactor 270; 405 W), horizontally placed 50 cm above the experimental pots.

The light regime of the climate chamber was based on the monthly mean diurnal light conditions recorded on Anchorage Island during one spring month (November) and three summer months (December - February). This light regime was based on photosynthetically active radiation (PAR) levels measured in the field on Anchorage Island (Fig. S2, SKP215 PAR sensors, Campbell Scientific UK). The maximum light levels reached within the climate chamber were approximately 80% of those recorded in the field (field: 1321 μmol/m^2/s). Relative humidity was controlled between 60 and 90%, similar to field conditions, by placing two water baths in the climate chamber. Relative humidity and air temperature were recorded at hourly intervals (HOBO U23 Pro v2, Bourne, MA, USA). The refrigeration units of the climate chamber went through a standard defrost cycle every 6 h, which raised the air temperature to approximately 5.0 °C for 30 min.

We recognize that this experimental simulation of Antarctic soil surface conditions is limited with respect to field climate variability, which also includes freezing and thawing during the growing season (Convey et al. 2018), and therefore, not representative for the whole of the Antarctic Peninsula. However, it does reflect the mean temperature and light conditions vascular plants experience at sheltered sites where the native Antarctic vascular flora persists, and the most likely conditions where non-native plants will establish. The plant response to shell additions in this experimental approach is therefore most relevant for sheltered micro-habitats in the maritime Antarctic where non-natives may establish (Hughes et al. 2025).

Biological responses

From the onset of simulated spring, when the chamber lights were turned on, we noted the number of days until the first seeds germinated in each experimental pot. At the end of the growing season, plants were harvested to quantify the length of the shoot/leaf and longest root, and leaf area (using a canon scanner Lide 110) estimated through ImageJ (Schneider et al. 2012). The dry mass of both the shoot and root were measured following oven drying (48 h at 70 °C). Soil pH was measured for each individual pot using a WTW inoLab® pH 7110 Benchtop Meter. Total plant carbon and nitrogen levels were quantified by dry combustion in an elemental analyser (Flash EA 1112, Thermo Scientific, Rodana, Italy). Total plant Phosphorus (P) and Ca were quantified by digesting plant material (~40 mg) 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 was quantified by spectrophotometry, using the ammonium molybdate method. Ca was quantified via atomic absorption spectrophotometry (AAnalyst 100, PerkinElmer Inc., Waltham, MA, USA) after addition of 1% $LaNO_3$ to break down the phosphate bonds. Total plant accumulated Ca, N and P in each experimental pot was calculated from the % content in each plant sample multiplied by the total plant biomass.

Statistical analyses

A full factorial ANOVA was used to compare the effects of shell and calcium addition, substrate type and plant species on germination time, shoot/root length, root: shoot ratio, shoot/root dry mass, total biomass, leaf area, specific leaf area, soil pH and plant content (% and total content) of Ca, N, P, and C: N and N: P ratios. We checked for homogeneity of variances and normality and applied log transformation where needed. Where the ANOVA outcome was significant, *post hoc* testing (Tukey's HSD, $p<0.05$) was carried out for multiple comparisons. We used correlations to identify if there were consistent patterns between germination time and plant size variables and whether the shell addition affected this. Data analyses and visualisation were carried out in the R environment (R-Core-Team 2023).

Results

Addition of shells or calcium raised the pH of the Antarctic substrate from 6.0 to 7.3 and 7.5, respectively, and increases were also found for the potting soil (Fig. 2). Shell and calcium additions did not affect germination time, which was also not influenced by substrate type (Fig. S3). Earlier germinating plants produced more biomass ($R = -0.28$, $P=0.024$), had longer shoots ($R = -0.43$, $P<0.001$) and roots ($R = -0.47$, $P<0.001$) and produced greater leaf area ($R = -0.33$, $P=0.008$, Fig. S4).

Total plant biomass generated was greater in Antarctic substrate compared to potting soil for *H. lanatus* (125%) and *T. officinale* (249%). Plants produced more biomass (30–100%) when growing in shell-amended Antarctic substrate compared to control treatments, while there were no significant differences in plant biomass between control and calcium-amended substrate (Figs. 3, S5). The greater plant biomass was reflected in significantly longer shoots (14–23%, Fig. S3) and roots (16–69%, Fig. S6), in both Antarctic substrate and potting soil, although biomass differences were primarily driven by greater root biomass (Fig. 3) for both species (*H. lanatus*: 60% and *T. officinale*: 185%), as shoot biomass increased by 4% for *H. lanatus* and 81% for *T. officinale*. No shell effects on plant biomass were apparent in potting soil (Fig. 3). Root: shoot ratio was not affected by shell or calcium additions (Table 1), while leaf area and specific leaf area were impacted by calcium additions only (Table 1, Figs. S7, S8).

Plant calcium levels doubled when grown in shell-amended substrate compared to the control, and increased 7-fold under calcium amendment (Table 2). Plant nitrogen levels (%) were unaffected by shell- or calcium-amendment. However, total nitrogen (mg) accumulated by all plant material was lower under calcium-amendment than in the control. Plant phosphorus (%) was reduced under shell (by16–37%) and calcium (by 42–45%) amendment in the Antarctic substrate (Tables 1 and 2) and, while total plant P (mg) was lowest under calcium amendment, the shell-amended and control plants accumulated equivalent amounts of P. Plant C: N and N: P ratios were unaffected by either shell- or calcium-amendment.

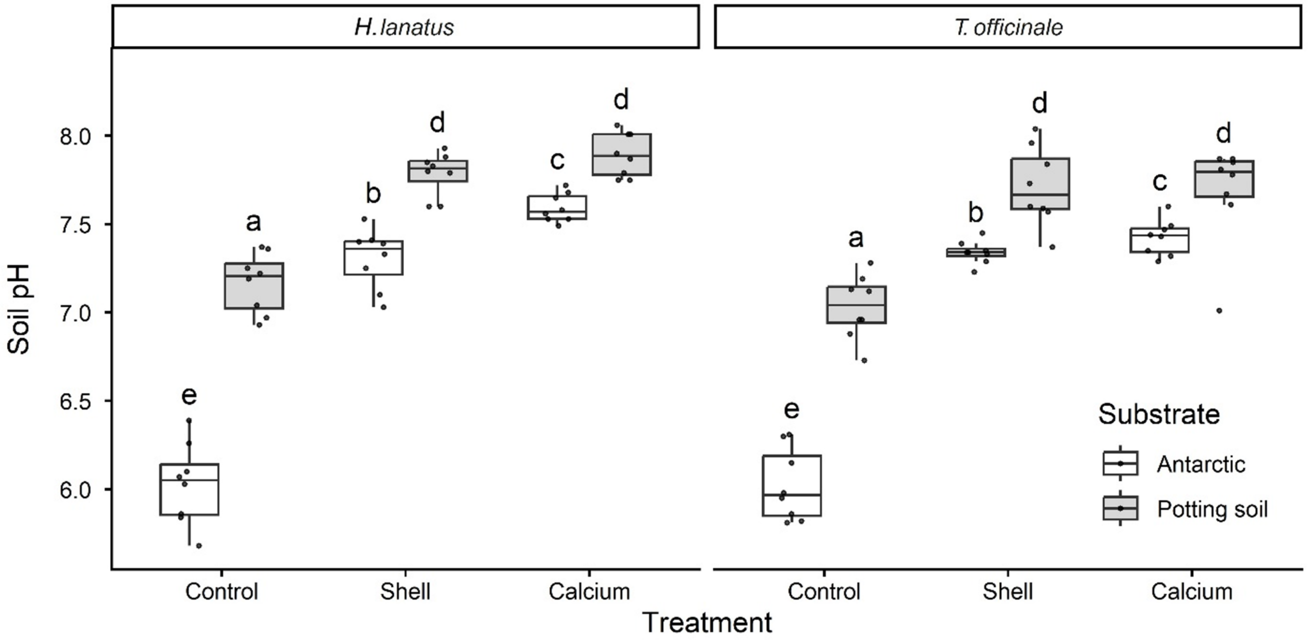

Fig. 2 pH of Antarctic organic substrate and potting soil following shell and calcium carbonate additions. Data from $n=8$ replicate pots for each experimental combination including growth of the potential invasive species, *Holcus lanatus* and *Taraxacum officinale*. The Antarctic substrate was collected from Anchorage Island in Marguerite Bay while potting soil was obtained from a commercial supplier with no further addition of minerals. Boxplots with different letters are significantly different, Tukey HSD, $p<0.05$

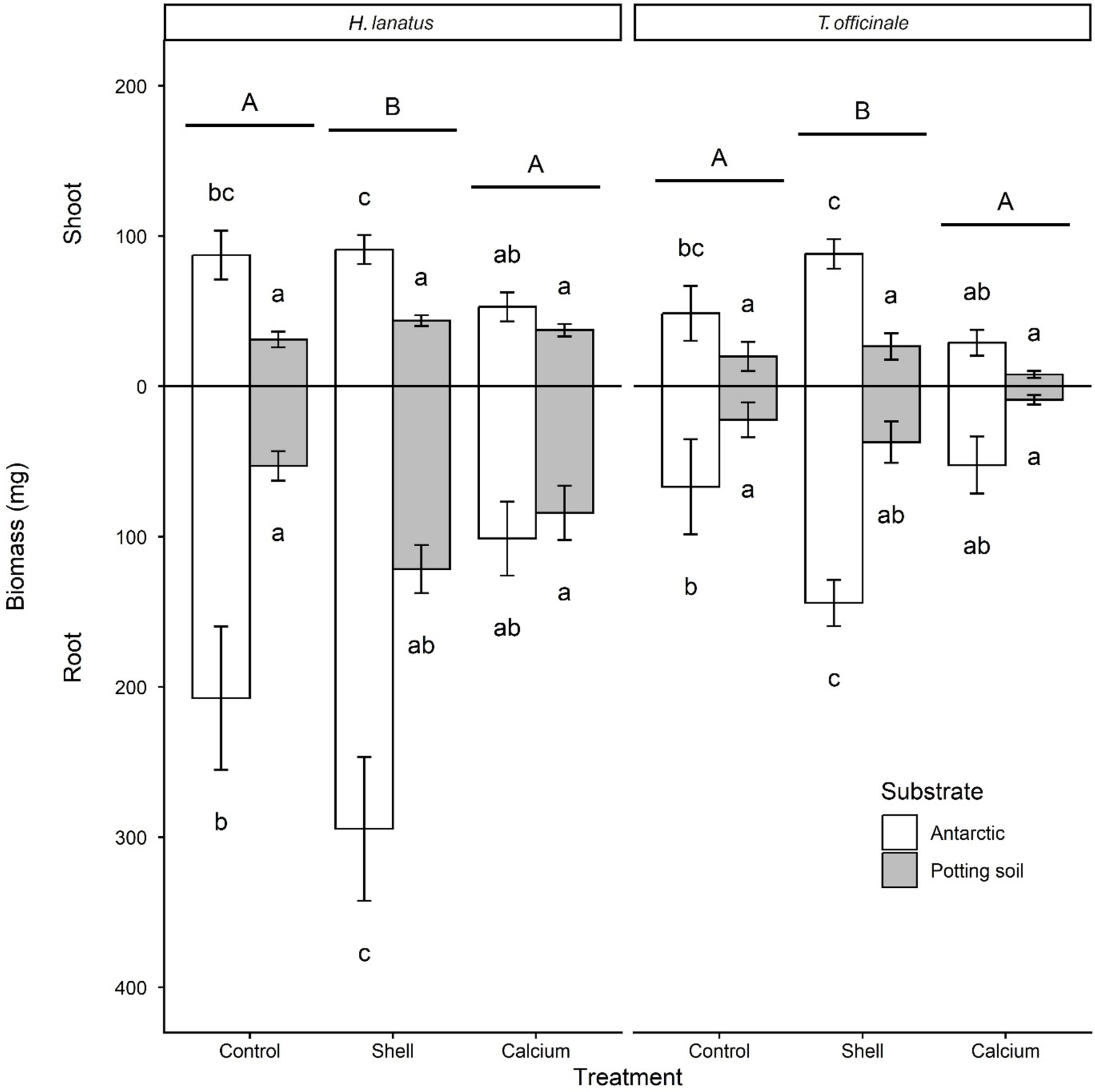

Fig. 3 Shoot and root dry mass of two potential invasive plant species in shell-amended substrate under simulated Antarctic conditions. Mean shoot and root dry mass (mg) of *Holcus lanatus* and *Taraxacum officinale* in Antarctic organic substrate and potting soil with shells or calcium amendment; the control consisted of substrate/soil without any additions. Each bar shows the mean of $n = 8$ replicate pots with the standard error of the mean. Bars with different letters are significantly different (Tukey HSD, $p < 0.05$); capital letters indicate species×treatment effects, with lowercase letters indicating substrate×treatment effects

Discussion

Physical modification of an environment or input of nutrients can greatly affect plant growth. In this study we show that native kelp gulls have the potential to act as an invasion engineer in the maritime Antarctic region through their deposition of mollusc shells, acting in a similar manner to human-created shell middens (Karalius and Alpert 2010; Vanderplank et al. 2014). While transfer of nutrients, such as nitrogen and phosphorus, by animals clearly generates direct benefits for plant growth in the polar regions (Gharajehdaghipour et al. 2016; Zwolicki et al. 2016; Bokhorst et al. 2022; Convey et al. 2024), the data generated in this

Table 1 ANOVA output (F and P-values) testing the effects of shell- and calcium-amendment on potential invasive plant growth responses in Antarctic substrate and potting soil for *Holcus lanatus* and *Taraxacum officinale*. Analysis was based on $n=48$ experimental pots per species. insufficient plant material was available for Ca analysis of *T. officinale*. Sub = substrate, Tre = Treatment, Sp = Species

	Treatment		Substrate		Species		Sub×Sp		Tre×Sub		Tre×Sp		Tre×Sub×Sp	
	$F_{2,84}$	*p*	$F_{1,84}$	*p*	$F_{1,84}$	*p*	$F_{2,84}$	*p*	$F_{2,84}$	*p*	$F_{2,84}$	*p*	$F_{5,84}$	*p*
Soil pH	369.8	<0.001	273.6	<0.001	6.7	0.011	1.8	0.182	46.2	<0.001	0.3	2.375	0.1	0.870
Germination time	0.1	0.926	3.9	0.510	32.0	<0.001	5.4	0.022	2.0	0.141	0.4	0.649	1.2	0.294
Shoot length	8.8	<0.001	41.1	<0.001	229.4	<0.001	11.6	0.001	1.6	0.211	0.6	0.869	0.2	0.832
Root length	20.1	<0.001	10.8	<0.001	67.6	<0.001	0.1	0.768	2.1	0.122	0.5	1.063	0.2	0.824
Total biomass	42.0	<0.001	12.3	<0.001	30.3	<0.001	1.7	0.189	4.6	0.012	0.3	0.727	1.5	0.223
Shoot biomass	9.5	<0.001	44.7	<0.001	12.8	<0.001	0.1	0.822	3.4	0.037	0.6	1.063	1.2	0.297
Root biomass	12.5	<0.001	37.4	<0.001	36.2	<0.001	2.9	0.094	4.7	0.011	0.4	1.707	1.9	0.161
Leaf area	12.9	<0.001	37.5	<0.001	45.7	<0.001	1.6	0.203	4.0	0.022	0.1	3.936	1.6	0.213
Specific leaf area	0.5	0.625	1.6	0.214	5.3	0.024	0.2	0.629	0.9	0.426	0.4	0.679	0.4	0.650
Root: Shoot ratio	1.9	0.156	2.5	0.117	14.2	<0.001	1.2	0.270	0.9	0.416	1.8	0.179	0.3	0.750
Plant Ca (mg/g)	140.1	<0.001	0.6	0.454	-	-	-	-	0.6	0.534	-	-	-	-
Plant Ca (mg)	14.7	<0.001	12.9	<0.001	-	-	-	-	2.6	0.087	-	-	-	-
Plant N (%)	6.5	0.003	49.0	<0.001	21.1	<0.001	1.3	0.267	2.9	0.066	0.3	0.759	0.1	0.794
Plant N (mg)	9.9	<0.001	46.6	<0.001	15.1	<0.001	4.0	0.051	3.5	0.037	3.5	0.037	0.1	0.803
Plant P (%)	22.2	<0.001	90.7	<0.001	42.5	<0.001	12.6	<0.001	9.4	<0.001	2.3	0.106	1.2	0.303
Plant P (mg)	22.1	<0.001	79.2	<0.001	70.5	<0.001	15.1	<0.001	7.5	0.001	3.4	0.038	3.3	0.044
Plant C: N	3.5	0.037	80.6	<0.001	29.2	<0.001	0.9	0.327	4.6	0.015	3.3	0.043	0.9	0.348
Plant N: P	2.2	0.120	31.2	<0.001	35.3	<0.001	0.1	0.907	2.0	0.151	1.4	0.265	1.6	0.207

Table 2 Mineral and nutrient content of potential invasive plants grown in shell- or calcium-amended substrate (Antarctic organic substrate or potting soil) under simulated Antarctic climate conditions. Values are mean of $n = 8$ experimental pots, with SE given in parentheses. '-' indicates that insufficient plant material was available for chemical analysis. Tukey letters indicate significant differences ($p < 0.05$) between treatments and substrate within species. Capital letters indicate consistent treatment effects irrespective of substrate

	Species	H. lanatus			T. officinale		
	Treatment	Control	Shell	Calcium	Control	Shell	Calcium
Ca (mg/g)	Potting	13.0 (1.34) a	25.1 (2.86) b	102.8 (15.4) c		-	-
	Antarctic	14.2 (1.06) a	29.4 (2.6) b	93.6 (12.2) c		-	-
Ca (mg)	Potting	1.1 (0.2)	4.3 (0.8)	14.4 (4.4)		-	-
	Antarctic	4.0 (0.9) A	11.2 (1.7) B	15.6 (4.3) B		-	-
N (%)	Potting	1.13 (0.03) abc	1.14 (0.03) abc	0.96 (0.08) a	0.98 (0.03) ab	1.05 (0.02) abc	-
	Antarctic	1.55 (0.08) d	1.39 (0.02) cd	1.31 (0.06) bcd	1.30 (0.06) bcd	1.15 (0.04) abc	1.15 (0.04) abc
N (mg)	Potting	1.2 (0.1)	1.9 (0.2)	1.1 (0.1)	1.3 (0.2)	1.4 (0.1)	-
	Antarctic	4.9 (0.7) BC	5.4 (0.8) C	1.9 (0.4) A	3.3 (0.5) ABC	2.6 (0.2) AB	1.9 (0.2) A
C: N	Potting	33.9 (1.44) bc	33.8 (1.14) bc	36.1 (2.0) c	39.8 (0.56) c	36.7 (1.28) c	-
	Antarctic	21.9 (1.36) a	25.2 (0.30) a	25.0 (0.96) a	29.3 (1.37) abc	34.1 (1.36) bc	25.8 (1.64) ab
P (%)	Potting	0.26 (0.02) ab	0.28 (0.02) ab	0.21 (0.02) a	0.22 (0.05) ab	0.21 (0.02) ab	0.17 (0.01) a
	Antarctic	0.62 (0.07) d	0.52 (0.02) c	0.34 (0.00) b	0.43 (0.05) d	0.27 (0.02) c	0.25 (0.02) b
P (mg)	Potting	0.27 (0.05) ab	0.44 (0.03) ab	0.24 (0.03) ab	0.14 (0.05) ab	0.17 (0.05) ab	0.04 (0.01) a
	Antarctic	2.00 (0.36) c	2.02 (0.33) c	0.52 (0.14) ab	0.47 (0.17) ab	0.64 (0.10) b	0.21 (0.07) ab
N: P	Potting	4.40 (0.38)	4.25 (0.30)	4.61 (0.19)	6.00 (1.49)	5.21 (0.47)	-
	Antarctic	2.61 (0.24)	2.71 (0.07)	3.88 (0.22)	3.70 (0.17)	4.48 (0.38)	4.43 (0.26)

study demonstrate that increased soil pH and Ca availability also promote greater plant growth.

In line with our hypothesis, plants growing in substrate supplemented with shells produced more biomass compared to other treatments. Calcium-induced growth acceleration is common in plants (White and Boadley 2003), and the lack of even greater growth being achieved in the $CaCO_3$ treatment is consistent with inhibition at higher Ca levels, which is also a common response (White and Boadley 2003). Although both above- and below-ground plant parts showed increases in biomass or size, root elongation and biomass were the strongest responses to the shell amendment. Calcium has been linked to enhanced root elongation (Burström 1952; Emanuelsson 1984; Duan et al. 2022) although, while Ca clearly plays a governing role in various cellular processes, the precise mechanisms by which Ca influences root elongation are unclear (Hepler 2005). Root architecture is governed by nutrient limitations (Ericsson 1995), and the changes in soil pH and Ca availability associated with shell amendment may have affected nutrient availability, such as P, in turn triggering enhanced root growth. Therefore, the enhanced root elongation observed in plants growing with shell amendment may reflect a direct response to higher Ca availability and/or P-limitation, but ultimately result in greater biomass which would enhance plant survival. Marine shell deposits may also result in increased salinity which can, in turn, inhibit plant growth, but no evidence for this was apparent in the current study.

More rapid seed germination was linked with larger final plant size in our experiment and this characteristic was not directly linked to, or affected, by the shell or calcium treatments (Fig. S4). Calcium, through its impact on soil pH, can affect plant growth and this is most clearly observed in the contrast between calcifuge (thriving in acidic conditions) and calcicole (thriving in calcium-rich alkaline conditions) adapted plants (Michalet et al. 2025). Effects of Ca on plant germination determined in experimental studies tend to result in highly context-dependent outcomes (Mulaudzi et al. 2020; Hayes et al. 2023; Akimoto and Ma 2025; Pan et al. 2025). This is also apparent from the pH increase in Antarctic substrate compared to the potting soils, where the latter appears more buffered, probably reflecting differences in the type of organic matter and Ca-binding capacity between the Antarctic substrate and commercial potting soil (Rowley et al. 2018). *Taraxaxum officinale* germination was slower in potting soil compared to the Antarctic substrate which may reflect pH differences (Bokhorst 2025), although exact mechanisms are unclear. The limited germination response to the treatments applied in this study may reflect the ruderal ecology of the study species, as both *H. lanatus* and *T. officinale* occur across a wide range of habitats (Weeda et al. 1994) and can thrive across different soil conditions. Inclusion of calcicole species may have resulted in stronger plant responses to the shell amendments, but currently established non-native plants in Antarctica are ruderal taxa (Frenot et al. 2005; Hughes et al. 2025), so these require the most research attention.

The data obtained did not support our second hypothesis, that shell-amended substrate would promote plant nutrient uptake. Rather, plant P content was reduced under higher Ca (i.e. under both treatments) and most strongly by the $CaCO_3$ treatment. This may indicate that plant-available P was bound by excess Ca in the substrate (Weng et al. 2022). The difference in root biomass achieved in the shell-amended (149 mg ± 54) and $CaCO_3$ (62 mg ± 20) treatments likely reflects a nutrient-deficiency response whereby, in the shell treatment, the plants explore a larger proportion of the substrate by growing more roots (Lambers et al. 2015), while this was inhibited by the much higher Ca content in the $CaCO_3$ treatment. This interpretation is also consistent with the much lower total plant P, which remained equivalent between plants in the shell-amended and control groups but was reduced (50–75%) in the $CaCO_3$ treatment. The $CaCO_3$ treatment also led to an increase in substrate pH which, for the Antarctic substrate, rose from 6.0 to 7.5. The enhanced root growth seen under shell amendment here is consistent with a common trend of root development reported in response to increased soil pH (Meng et al. 2019), although contrasting responses have also been documented (Wang et al. 2020), as well as under P-deficiency (Lambers et al. 2015), so untangling the exact mechanism between Ca, pH and P-availability remains challenging.

Conclusions

Shell middens created by kelp gulls raise the substrate pH and create locally calcium-rich habitats amongst the often barren rocky coastlines of the maritime Antarctic. These calcium hotspots are likely to benefit native plant growth and also that of any non-native plants. While the more organic-rich substrates associated with moss-dominated ecosystems generally provide better habitats for non-native plants in Antarctica (Bokhorst et al. 2025), the current study indicates that habitats that are assumed to be less vulnerable to trampling and designated as human footpaths, such as more barren and rocky coastlines, may still be suitable for plant growth. Plant growth and establishment is, of course, dependent on survival of winter conditions as well as the considerable variation in environmental conditions during an Antarctic growing season (Convey et al. 2018), which could not be simulated in the experimental set-up. Nonetheless, the tested plants performed better when shell additions increased substrate pH and Ca, increasing the likelihood of survival. Kelp gulls in Antarctica, and elsewhere other birds that bring marine mollusc shells onto land may, therefore, act as ecosystem engineers in a similar way as humans have done across various coastlines globally (Karalius and Alpert 2010; Vanderplank et al. 2014).

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Data availability All data from this study is available in the supplementary information files.

Declarations

Ethical approval Not applicable.

Competing interests The authors declare no competing interests.

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