



Community assembly among potential invasive plants in Antarctica shaped by life history characteristics and climate warming

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Abstract Species arrival sequence in new habitats impacts plant community development. This ‘priority-effect’ is documented, but mechanisms by which early arriving plants dominate future communities are less clear, complicating our ability to predict community assembly under future climate warming and assess invasive species threats. This is particularly important for ecosystems that are vulnerable to invasive species, such as those of the Antarctic Peninsula.

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To test how phenological differences and arrival order affect community composition of invasive plants, we simulated maritime Antarctic climate conditions, and a warming scenario. We established monocultures of six species potentially invasive to the Antarctic Peninsula (three forbs and three grasses), which exhibit a range of germination times ranging from 22 and 68 d, and a mixed community of all species. Before entering a simulated winter, half of each monoculture ($n=10$) received the full seed mixture while the other half received seeds of their respective starting species. During the following simulated growing season, we quantified if the community composition was influenced by arrival order and whether species germination and growth responses differed from their monocultures and starting species. Community compositions differed across all starting communities and were typically dominated by the starting species. Phenological differences influenced individual and total biomass and plant height, but faster germinating species did not consistently dominate the final plant community. Forbs and grasses negatively impacted each other's biomass. Warming enhanced priority effects (more negative or positive). Phenological priority has ecologically relevant influences on community assembly, but its effect on plant growth is context dependent in terms of species and temperature conditions. In particular, our data suggest that phenological priority influences plant biomass and size while niche pre-emption affects seed germination. Future trajectories of polar terrestrial plant communities will depend

on the arrival order of colonizing non-native plants and their germination rates.

Keywords Priority effect · Polar ecology · Grasses · Forbs · Phenology · Germination

Introduction

Climate change and human activities are promoting the spread of non-native species into cold biomes (Bennett et al. 2015; Hughes et al. 2020) with potentially large impacts on community composition (Pyšek et al. 2020). Species identity often plays a strong role in shaping community assembly, and the sequence of species arrival (priority) can play a key role in driving community composition (Gleason 1927; Drake 1991). To dominate a community, the first-arriving species needs to grow rapidly in order to consume available resources (niche-pre-emption) or modify the environment (niche-modification) in such a way that later-arriving species are disadvantaged (Drake 1991; Fukami 2015). For plants this requires a shorter germination time than their neighbours, which is a typical characteristic among invasive plants (Luis et al. 2008; Gioria et al. 2016; Gioria and Pyšek 2017; Alexander and Levine 2019; Hess et al. 2019). Communities developing in relatively stable environments with a large species pool are more likely to show priority effects, while highly disturbed environments with smaller species pools are likely to be more deterministic (Chase 2003). In this context, priority effects are unlikely to play a role in polar ecosystems with low native plant diversity, such as those of the Antarctic. However, some non-native species show strong germination and growth responses to warming under Antarctic climate conditions, with potential impacts on community assembly (Molina-Montenegro et al. 2016, 2019; Bokhorst et al. 2021). Species arrival order may therefore, play an important role for future Antarctic terrestrial ecosystems, and established species could determine successive community development. Given the observed and predicted warming rates along the Antarctic Peninsula (Turner et al. 2014; Siegert et al. 2019), and the increasing human activity in this region, the establishment threat of non-native species is high, with potential large impact on native communities through direct competition (Molina-Montenegro et al. 2019; Hughes et al. 2020).

Although, every effort should be made to prevent non-native species establishment in polar regions, untangling underlying mechanisms and impacts will improve our fundamental understanding of polar ecosystems and can help with conservation strategies.

Established non-native plants on sub-Antarctic islands, and some locations along the Antarctic Peninsula, are expanding in range, due to climate change and are negatively impacting native plant communities (Frenot et al. 2005; Upson et al. 2017; Molina-Montenegro et al. 2019). Grasses (e.g., *Poa annua* and *Agrostis capillaris*) and forbs (e.g., *Taraxacum officinale* and *Plantago lanceolata*) are prevalent invasive plant types in (sub-) Antarctic ecosystems (Frenot et al. 2005; Hughes et al. 2020), with large variation in germination timing and represent useful model species to untangle effects of arrival order, germination and climate warming on polar community assembly. During seedling emergence there is little room for direct competition for environmental resources as the seedling depends on the stored resources in the seed. Plants with larger seeds tend to germinate more slowly than those with smaller seeds (Grime et al. 1981), but environmental conditions, including temperature, moisture and light, also affect germination rate and subsequent plant growth (Thompson et al. 1977; Milberg et al. 2000; Rosbakh et al. 2019, 2022). Plants with small seeds and rapid germination may, therefore, dominate the final plant community, but their advantage may be overshadowed by stronger competitors or mediated by environmental variability (Pearson et al. 2002). Once seedlings have emerged they can overshadow later emerging neighbouring seedlings (Ross and Harper 1972), and start using limited soil nutrients and light at the expense of other plants (Hess et al. 2019). Seedling phenology of non-native plants may be part of the puzzle in understanding the future of temperature constrained Antarctic terrestrial ecosystems.

In this experimental study we address three questions: (1) does priority affect community assembly of polar ecosystems with strong abiotic constraints on plant growth? (2) does seedling phenology of non-native species affect community composition? (3) does climate warming affect priority and phenological priority effects? To address these questions, we grew plant communities under simulated Antarctic conditions in climate chambers. By establishing monocultures of six species (none of which are

Table 1 Plant species life history characteristics and experimental design

Species	Plant type		Germination time (days)	Seed mass (mg)
<i>Agrostis capillaris</i>	Grass		47 (\pm 7)	0.04
<i>Deschampsia cespitosa</i>	Grass		41 (\pm 5)	0.2
<i>Taraxacum officinale</i>	Forb		26 (\pm 3)	0.39
<i>Holcus lanatus</i>	Grass		28 (\pm 4)	0.4
<i>Trifolium repens</i>	N-fixing forb		22 (\pm 2)	0.7
<i>Plantago lanceolata</i>	Forb		68 (\pm 10)	1.06
First growing season	Temperature		End of growing season	After winter
	2 °C	7 °C	Seed additions before winter	Response variables
1) Species monocultures	n = 5	n = 5	Initial monoculture seeds	Species emergence
2) Species monocultures	n = 5	n = 5	Mixture of all species	Plant size and biomass
3) Species mixture	n = 5	n = 5	Mixture of all species	Community composition

Summary of mean germination time (see Bokhorst et al. 2021) and seed mass of species used in the priority experimental study. Experimental design consisted of: 1) control plots with species monocultures, 2) monocultures that received seed mixtures to test priority effect, and 3) full mixture communities. All communities were tested under simulated Antarctic conditions at 2 °C or a warming scenario (7 °C). Individual species and community response variables from 2 were compared against response variables from 1 and 3

native to the maritime Antarctic; Table 1) with different seedling germination times during a full growing season, and then adding a seed mixture including all six species at the end of that season, we set out to disadvantage these ‘late-comers’ during the second growing season. We hypothesized that plant communities are affected by priority despite the temperature constraints on plant growth in cold polar environments. The resulting community composition should depend on the relative importance of niche pre-emption by the established species monocultures (through remaining plant parts) and the speed of germination of the late-comers. We hypothesize that species with a shorter germination time will be able to emerge earlier than new shoots of the ‘established’ species at the start of the second season and dominate the plant community by the end of that season. Warming will benefit rapidly germinating species most and dominate among the final plant communities.

Materials and methods

Overall set-up and species selection

To test if priority can play a role for non-native vascular plants under cold Antarctic conditions, we simulated mean growing season soil temperature and light

conditions in temperature controlled climate chambers (see below for experimental conditions). For testing the priority effect, we allowed plants to establish for one growing season in monoculture, followed by adding seed mixtures at the end of summer (Table 1). This approach, across two simulated growing seasons (140 days each) allows testing of new arrivals against a background of established species and avoids artificial staggering of seed arrival within a growing season (e.g. Körner et al. 2008). The experimental design consisted of 5 replicate pots for each species combination and monocultures at both 2 °C and 7 °C (n = 130 plant communities in total). To achieve this, we established monocultures of six non-native plant species (n = 10, each with fifty seeds/species/pot—120 in total) and a full mixed community including all six (n = 5, each with 10 seeds per species—10 in total) during the first season. Seed numbers were chosen to ensure sufficient plant emergence and have equal seed density across experimental units. At the end of that season, half of each monoculture (n = 5) received the same species’ seeds again or a mixture of all six species (n = 5), while the full mixed communities also received all species again. All plant parts developed in the first growing season remained in each experimental pot, as litter or surviving plants, representing the effect of that monoculture on the later arrivals. After a simulated winter (6 months

at $-5\text{ }^{\circ}\text{C}$ in darkness, also acting as cold stratification period), we compared community composition between communities initially started with different species and the full mixed community ($n=6$ initial monocultures + 1 full mixed community), as well as how well individual plant species germinated and grew compared to their monoculture and across the different initial monocultures (Table 1).

To test for potential phenological priority effects we choose species with different germination times. The species included were the nitrogen-fixing forb *Trifolium repens* (22 ± 2 d germination time; all germination data are from Bokhorst et al. 2021), the forb *Taraxacum officinale* (26 ± 3 d), the grasses *Holcus lanatus* (28 ± 4 d), *Deschampsia cespitosa* (41 ± 5 d) and *Agrostis capillaris* (47 ± 7 d) and the forb *Plantago lanceolata* (68 ± 10 d). These species are commonly found growing together in grasslands and ruderal disturbed regions of the Netherlands (Weeda et al. 1994).

All seeds were collected in the Netherlands by the authors or bought from local vendors. Organic material collected beneath an Antarctic moss community was used as the growth substrate (2 cm depth), without any prior history of vascular plant presence (organic carbon content = 48.6%, N = 2.11%, $p=0.48\%$, pH = 4.1). The pots (5 cm diameter pvc tube with plastic bottom containing drainage holes) 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).

Antarctic climate simulation

Simulation of Antarctic soil surface microclimate conditions, representative of sites in the maritime Antarctic (Bokhorst et al. 2008; Convey et al. 2018), was achieved by setting the growth chamber at $2\text{ }^{\circ}\text{C}$ and modulating the diurnal light conditions (photosynthetically active radiation levels), creating realistic soil surface temperatures (mean of $6\text{--}7^{\circ}\text{C}$) during the afternoon as measured in the field (Bokhorst et al. 2007, 2008, 2021). Diurnal light intensity patterns were adjusted every month to simulate the changing light conditions from October to March as measured on Anchorage Island close to the Antarctic Peninsula ($\sim 68^{\circ}\text{S}$). To quantify impacts of climate warming, a

parallel climate chamber was run at $7\text{ }^{\circ}\text{C}$ but all other conditions and numbers of treatments and replicates were kept the same. The $5\text{ }^{\circ}\text{C}$ temperature increase reflects the Shared Socio-economic Pathway (SSP) 5–8.5 global climate warming scenario (Intergovernmental Panel on Climate 2023), which is appropriate given that the northern Antarctic Peninsula region already warmed by $\sim 3\text{ }^{\circ}\text{C}$ in the second half of the Twentieth Century and warming trends of $\sim 0.5\text{ }^{\circ}\text{C}/\text{decade}$ have been reported and are predicted for the remainder of the Twenty-first Century (Turner et al. 2014; Bracegirdle et al. 2019; 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.

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, 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. Similarly, winter temperature can be much lower than the simulated $-5\text{ }^{\circ}\text{C}$, and this experimental approach reflects microclimate conditions underneath sufficient layers of snow to insulate against freezing ambient air conditions. For the objective of this study, to test if priority can affect community assembly under chronically low temperatures ($2\text{ }^{\circ}\text{C}$), mean soil field conditions of sheltered sites were used.

Biological response variables

To test if phenology (phenological priority) affects plant community, we quantified the time to germination of the first seedling for each species in each experimental pot, at the start of the second growing season. Emergence timing was correlated with plant production. At the end of the second growing season, all experimental pots were harvested and we measured for each species then present the plant maximum height, number of plants and total plant dry mass (after 48 h at $70\text{ }^{\circ}\text{C}$). From this we calculated mean plant biomass. Grass seedlings could not be identified to species level and are considered as a unified grass

response variable for pots where grasses were present at harvesting.

Data analyses

To quantify if final plant communities (based on biomass and number of plants per species) were affected by the starting communities we compared species composition using Bray–Curtis distance. To test if plant species germination time and growth (emerged plants, height and biomass) were affected by growing in mixture or monocultures, starting species identity of the mixed community ($n=$ six species) and temperature (2 °C and 7 °C), we used a factorial ANOVA. In addition, to help identify which aspects of each species growth response was affected by priority and temperature, we used factorial ANOVA including starting species identity (mixture communities only $n=65$ in total) and temperature for each species separately.

To test if phenological priority played a role for plant variables in each experimental pot, we quantified how frequently early emerging plants resulted in larger plant variable responses. For this, we calculated the scaled germination time ($GT_{\text{species}}:GT_{\text{pot}}$ mean) for each species that germinated in each pot; expressed as $\text{early} < 1 < \text{late}$ emergence. Then we compared the trends of scaled $(y-\bar{y})/SD$ plant variables (number of plants, plant height, individual biomass and total biomass) across scaled emergence timing within each experimental pot. Where y = the species response variable within an experimental pot, \bar{y} = mean across species within that experimental pot and SD = standard deviation across all species within that pot. A chi-square test was used to identify significant deviations in overall plant response between early and late emerging plants (H_0 : 50:50). For each mixed community that developed from one of the initial monocultures and the full mixed community, we used ANOVA to identify whether species (*P. lanceolata*, *T. officinale*, *T. repens* and grass) differed in their scaled responses to priority and temperature.

To quantify how species-specific plant variables (germination time, plant height and mean plant biomass) were affected by each of the six starting species in each community, we calculated standardized response variables using the formula $(O-E)/E$; where E is the plant species response in its monoculture and O is the observed plant response in a community

initially of a different species or the full mixed community. These calculations were made separately for each temperature treatment. For the grass species we used an expected grass response based on the mean of the respective grass species monocultures. In addition, we calculated the log response ratio for germination timing and biomass production across temperature to identify species response patterns across the different mixed communities.

We used correlation (Pearson) to test for significant relationships between germination time and plant height, individual, total plant biomass and seed mass. In addition, we tested for any evidence of overcrowding or potential shading impacts (e.g., do plants have lower biomass when growing among taller plants or when they have more neighbours?) by correlating plant variables (total number of plants and tallest plants per experimental pot) with plant height, number of plants per species, and individual and total plant biomass. Based on the above tests there was no apparent effect of overcrowding or shading impacts on plant growth, and detailed information is therefore available in the supplementary information.

As species responses were mostly consistent among forbs and grasses respectively, we partly present data on group responses in the results and full detailed species responses are available in the supplementary information. All data were log- or square root-transformed to improve homogeneity of variances. All statistical analyses were performed using R (R-Core-Team 2023).

Results

Community composition response to priority and phenological priority

The initial monoculture identity significantly influenced final community composition at the end of the second summer season (Fig. 1, Tables 1, 2, Table S1). Grasses dominated in terms of biomass and numbers of plants in five out of the seven communities, excepting those initiated as monocultures of *P. lanceolata* and *T. officinale*. Plant size and number of plants did not contribute equally to total biomass for each initial monoculture or the mixed community (Fig. 1c). However, plant dominance in a community was not consistently associated with early emergence as expected.

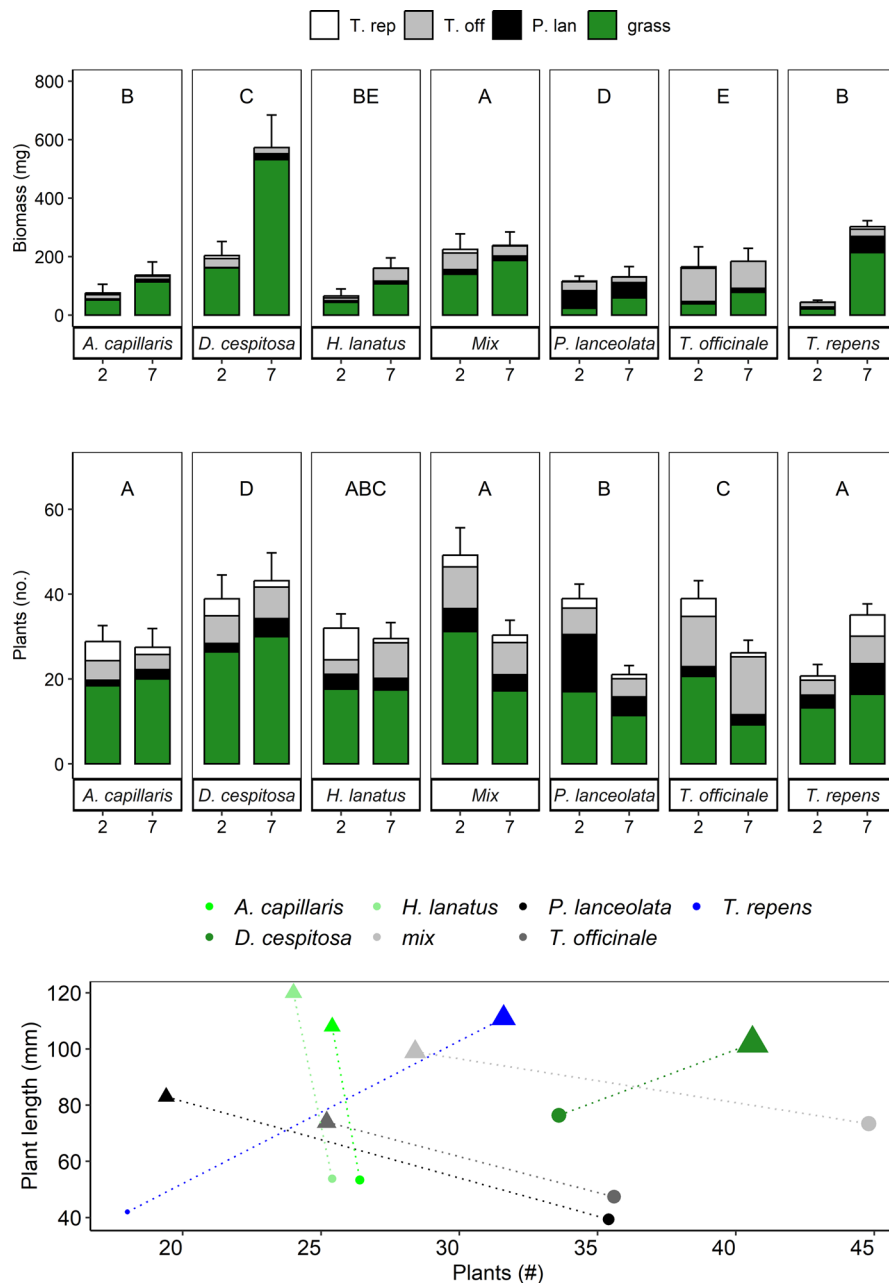


Fig. 1 Temperature and priority effects on plant community composition within mixed communities. Bars show the mean total biomass (A) and number of plants (B) of grasses, *Plantago lanceolata* (*P. lan.*), *Taraxacum officinale* (*T. off.*) and *Trifolium repens* (*T. rep.*) between mixed plant communities under simulated Antarctic conditions (2 °C) and a warming scenario (7 °C) at the end of the second simulated growing season. Each plant community was initiated with a specific monoculture (*Agrostis capillaris*, *Deschampsia cespitosa*, *Holcus lanatus*, *P. lanceolata*, *T. officinale*, or *T. repens*) or all species combined (mix) in the first growing season. At the end of the first

growing season, just before a simulated winter, a seed mix was added. Each bar is the mean of $n=5$ pots. Bars (species) with different capital letters have significantly ($P<0.05$) different community composition based on Bray–Curtis dissimilarity analysis. *Indicate significant differences in numbers of plants between temperature. Error bars represent SE for the whole community. (C) Shifts in numbers of plants and plant size in response to warming (circle=2 °C and triangle=7 °C) across different initial communities; symbol size represents total plant biomass. Please note difference in panel legend

Table 2 ANOVA output (*F* and *P*-values) of the Bray Curtis community comparison of plant biomass and number of plants

	Df	Biomass		No. plants	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Species	6,56	5.3	0.001	4.5	0.002
Temperature	1,56	10.7	0.001	3.5	0.001
Sp×T	6,56	2.1	0.003	1.8	0.017

Overall, early germinating plants produced higher biomass (Figs. 2, S1, Table S2) and resulted in greater number of plants than those that germinated later (Fig. 3a,b), when correcting for within experimental plot variation. Grasses grew taller when emerging earlier than other species within experimental pots, but this phenological priority effect was suppressed for forbs when growing among communities initiated with grasses (Fig. 3c,d). Species biomass was higher for early emerging plants, but limited to intra-specific competition, as the phenological priority effect was suppressed when a species grew in a community initiated by a different species (Fig. S5,6). Larger within-pot differences in germination time between species were associated with higher total plant biomass in communities initiated with forbs at 2 °C, but this pattern was absent among grasses (Fig. S7).

Climate warming and priority

Temperature effects on final community composition were species-dependent for biomass and number of plants (Table 1). Warming nearly always resulted in earlier emergence of plants (Tables 3, 4) but this earlier growth start did not consistently result in greater biomass production (Fig. 4). Warming increased plant biomass 2.5 times among communities initially started by grasses and *T. repens*, but not for the other two forb species and full mixed community (Fig. 1). The number of germinated plants was reduced (38%) among the communities started with *P. lanceolata*, *T. officinale* and the full mixed community with warming, but this was not found for communities initially started with grasses. The number of germinated plants increased by 77% among communities started with *T. repens* under warming (Fig. 1).

Forb plant biomass was suppressed in initial grass monocultures (25%), and this was effect was stronger (50%) with warming (Fig. 5), whereas grass plants

weighed on average 45% less when grown in initial forb monocultures at 2 °C, but weighed more (40%) at 7 °C (Fig. 5). In the full mixed community, grasses were on average heavier than in their monoculture at both 2 °C (39%) and 7 °C (67%), while forbs performed worse. Forb height was reduced (11–20%) when growing among other species compared to their monocultures and warming enhanced this reduction when forbs grew among communities initially of grasses (Fig. 5). Grasses were on average 26% taller compared to their monocultures, except when growing among communities initially of forbs. A detailed description of all species-specific responses is given in the supplementary information.

Discussion

Arriving early creates benefits, even under the cold growing conditions typical of maritime Antarctic terrestrial ecosystems. In this study, the initial species identity in our experimental communities strongly affected the performance of later arrivals and the ultimate community composition, which is in accordance with observed plant growth comparisons across succession gradients (Chapin et al. 1994), and studies where experimental seed sowing was staggered during the growing season (Milbau et al. 2003; Körner et al. 2008; Kardol et al. 2013; Sarneel et al. 2016). However, community composition differences between different initial starting monocultures in this study were not consistently affected by phenological priority or niche pre-emption, instead these differences depend on species life history characteristics related to germination success, plant growth and competition.

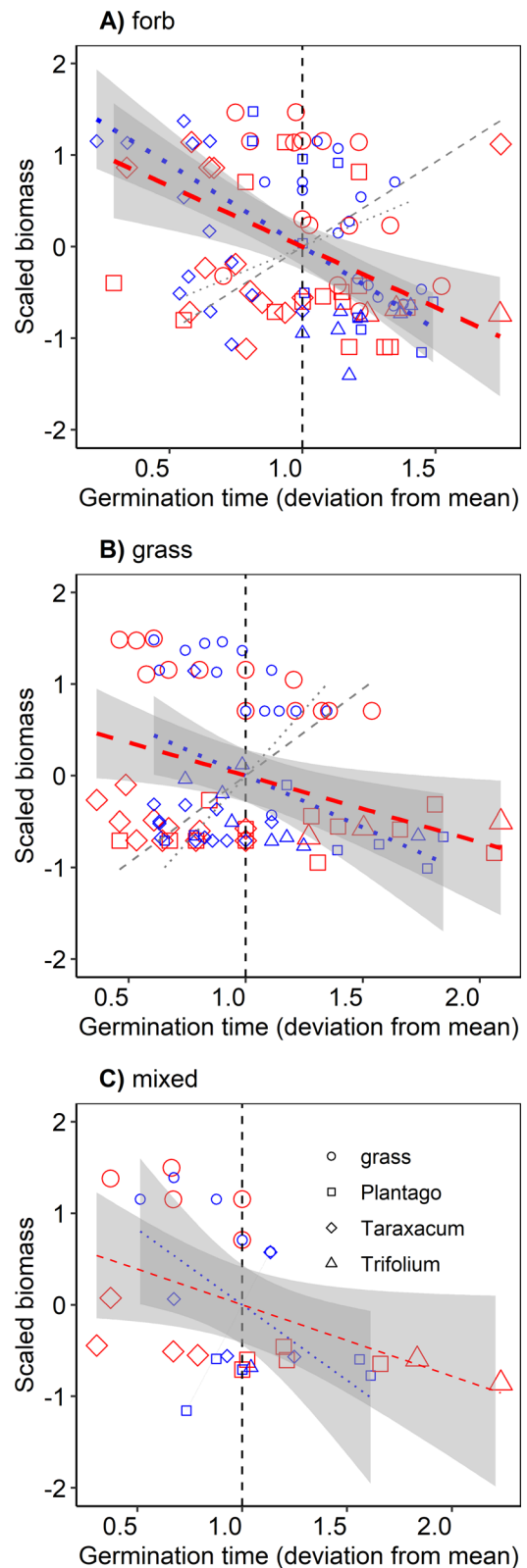
Phenological priority effects

Phenological priority effects appear to play out at different levels within plant communities. Higher biomass was associated with earlier germination within a community, while at the same time, a species biomass dependence on germination timing, consistent with monocultures (Ross and Harper 1972), was greatly inhibited by initial starting species. In a similar manner, the study species generally grew taller after rapid germination, with the exception that grasses outgrew forbs when the initial community consisted of

Fig. 2 Phenological priority effect on individual plant biomass response. Panels show scaled plant biomass compared to early vs. late germination time between mixed communities initiated with different monocultures. **a** forb communities (*Plantago lanceolata*, *Taraxacum officinale*, *Trifolium repens*) **b** grass communities (*Agrostis capillaris*, *Deschampsia cespitosa*, *Holcus lanatus*), and **c** a complete mixture of all six species. Within-pot germination time was standardized by dividing the species time to germination by the mean germination time across all species within each pot. Negative trend lines represent early emerging plants with high biomass, while positive trend lines represent late emergence with high biomass (grey lines). Temperature is indicated by colour, line type and symbol size; 2 °C=blue, dotted and small, 7 °C=red, dashed and large. Line thickness reflects number of observations (Table S2). Negative trends: Forbs $r = -0.608$, $p < 0.001$ ($n = 69$), Grass $r = -0.424$, $p < 0.001$ ($n = 62$)

grasses. Our data suggest that grasses may modify the soil conditions (niche pre-emption) in the first season of establishment in the experiment with the result that forbs germinating in the second season then perform badly. Plant litter of one species can suppress growth of other species by both mechanical obstruction and chemical leachates (Xiong and Nilsson 1999), as shown for grasses on forbs and vice versa (Bosy and Reader 1995; Olson and Wallander 2002). These results are partially inconsistent with those of Alexander and Levine (2019), who showed early germinating plants performed better than later germinating plants, indicating that plant identity also matters.

Although, total number of plants was associated with earlier germination across the whole data set, there were species dependent responses, indicating that not all species can increase their abundance dominance through phenological priority. There was no indication of any causal connection between the germination of one seed and subsequent seeds based on the total number of plants present, as has been reported in some studies of overcrowded plant communities (Bao et al. 2021). The limited responses detected in individual plant biomass in relation to germination timing indicates that plants were restricted in further growth by limiting factors (for rapid germinators) or could quickly reach maximum growth levels (after slow germination). The absence of this pattern in the mixed communities indicates that there was competition for resources. Such competition most likely takes place belowground, mediated by the microbial community or through allelopathic effects (Corbin and D'Antonio 2012), as there was no indication that overcrowding affected the number of plants,



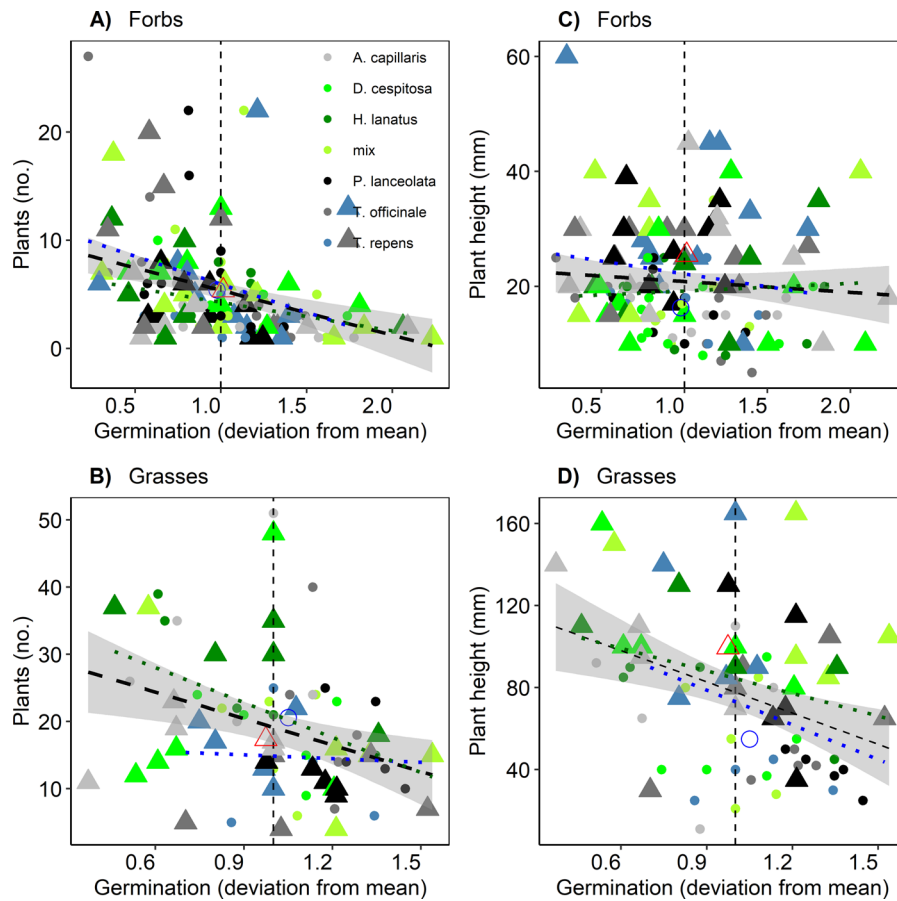


Fig. 3 Phenological priority effect on plant production. Number of emerged plants (**a, b**) and plant height (**c, d**) depended on germination time. Within-pot germination time was standardized by dividing the species time to germination by the mean germination time across all species within each pot. Forb (*Plantago lanceolata*, *Taraxacum officinale*, *Trifolium repens*) and grass (*Agrostis capillaris*, *Deschampsia cespitosa*, *Holcus lanatus*) response variables when growing in communities initiated by different species (see legend panel a). Each data point represents a species response from an experimental pot.

Circles and triangles represent temperature treatments (2 °C and 7 °C respectively). Dashed trend lines represent correlations: No. plants: forbs $r = -0.347$, $p < 0.001$ ($n = 137$); grass $r = -0.340$, $p = 0.004$ ($n = 70$); Plant height: forbs $r = -0.082$, $p = 0.338$ ($n = 137$); grass $r = -0.369$, $p = 0.002$ ($n = 70$). Dotted lines represent correlations among communities initially with forbs (blue) or grasses (green). Note that 'n' is higher than total number of experimental replicates ($n = 70$ mixed communities) because multiple species were obtained from individual experimental pots

their size or biomass as shown for intra-specific competition (Ross and Harper 1972).

Phenological priority effects on community composition may also be expressed through variation in emergence time within a community. Species germination timing differences may result in lower immediate (temporal separation) competition for resources (Schwinning and Kelly 2013; Hood et al. 2021). Within our experimental study, this pattern was present among communities initiated with forbs at 2 °C (Fig. S7). However, it was not observed among the

full-mixed community where there was no initial species dominance, indicating that the influence of phenological priority was present only among the forbs. Grasses appear to be stronger competitors and created more biomass, at individual and total species level (despite 30% lower mean individual plant biomass than forbs; Table S4), irrespective of their relative germination timing within experimental pots, indicating that phenological priority effects are species dependent.

Table 3 ANOVA output (*F* and *P*-values) of the effect of temperature and species initiating the community on mean plant community variables

	df	Germination time		No. Plants		Plant height		Biomass	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Temperature	1,104	31.0	<0.001	0.6	0.606	86.6	<0.001	41.4	<0.001
Mixed	1,104	3.4	0.068	79.9	<0.001	1.5	0.224	41.0	<0.001
Species	6,104	12.4	<0.001	17.0	<0.001	18	<0.001	19.4	<0.001
T×Mix	1,104	1.9	0.171	0.1	0.869	0.2	0.637	0.4	0.510
T×Sp	6,104	1.3	0.271	1.4	0.235	1.6	0.157	3.5	0.004
Mix×Sp	5,104	6.0	<0.001	13.0	<0.001	13.3	<0.001	5.8	<0.001
T×Mix×Sp	5,104	2.2	0.059	1.8	0.123	0.2	0.943	3.1	0.011

Plants were grown under simulated contemporary Antarctic conditions and a +5 °C warming scenario. This analysis includes data from 6 monocultures (n = 5/species/temperature), mixed communities started with a specific monoculture (n = 5/species/temperature) and a full mixed community (n = 10: 5 at 2 °C and 5 at 7 °C)

Table 4 ANOVA output (*F* and *P*-values) of species-specific growth variable comparisons between communities initiated with different monocultures (*Plantago lanceolata*, *Taraxacum officinale*, *Trifolium repens*, *Agrostis capillaris*, *Deschampsia cespitosa*, *Holcus lanatus* or a complete mixture of all six species) under simulated contemporary Antarctic conditions and a +5 °C warming scenario

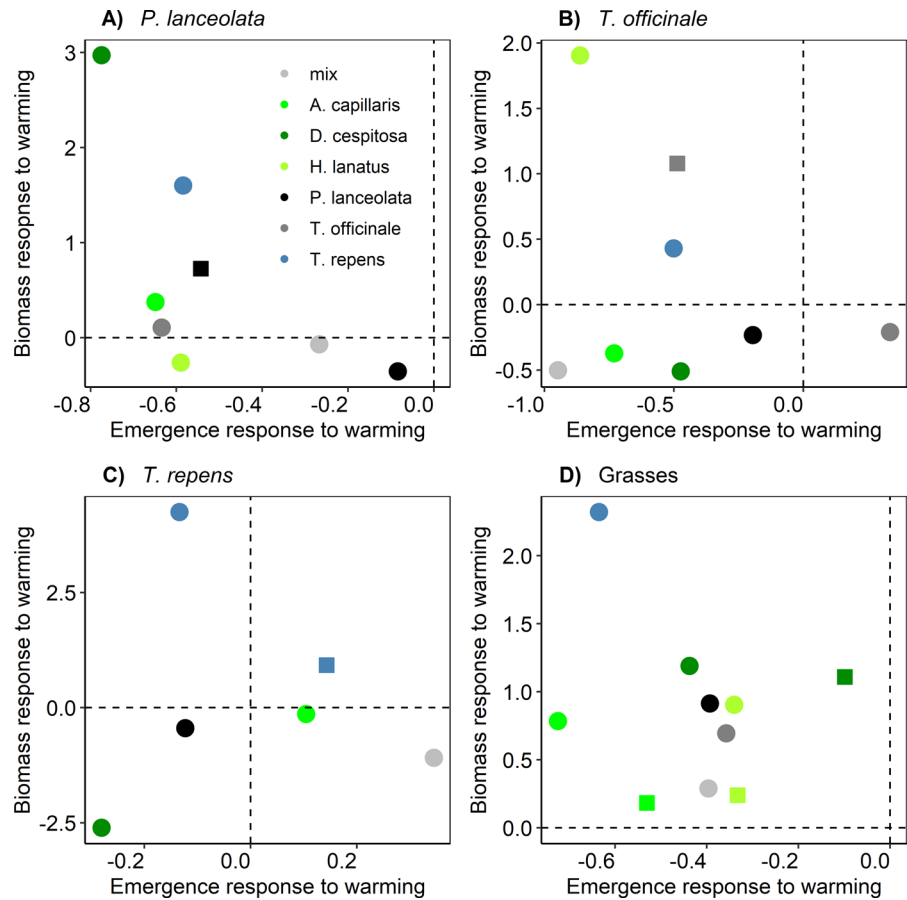
		Temperature		Species		T×Species		
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	
Note that grass responses were not identified to species level and therefore, represent a mixture of <i>A. capillaris</i> , <i>D. cespitosa</i> and <i>H. lanatus</i>	Emergence	<i>T. officinale</i>	38.5	<0.001	2.1	0.069	1.9	0.097
		<i>T. repens</i>	0.7	0.413	6.5	<0.001	2.8	0.031
		<i>P. lanceolata</i>	154.1	<0.001	9.5	<0.001	14.9	<0.001
		grasses	37.8	<0.001	8.7	<0.001	0.6	0.722
	No. plants	<i>T. officinale</i>	0.8	0.368	4.2	0.002	2.0	0.076
		<i>T. repens</i>	15.9	<0.001	0.6	0.712	1.9	0.116
		<i>P. lanceolata</i>	0.1	0.935	3.2	0.012	1.9	0.104
		grasses	2.6	0.111	3.6	0.004	1.6	0.156
	Plant height	<i>T. officinale</i>	21.2	<0.001	3.6	0.005	2.4	0.038
		<i>T. repens</i>	2.1	0.158	2.0	0.098	1.8	0.131
		<i>P. lanceolata</i>	28.5	<0.001	1.5	0.206	0.8	0.604
		grasses	44.9	<0.001	1.8	0.117	1.1	0.401
Biomass	<i>T. officinale</i>	0.3	0.571	4.8	<0.001	2.4	0.038	
	<i>T. repens</i>	11.2	0.002	1.1	0.400	2.1	0.081	
	<i>P. lanceolata</i>	3.9	0.053	3.3	0.010	2.4	0.044	
	grasses	29.2	<0.001	8.3	<0.001	2.6	0.027	

Effect of warming

Warming resulted in more rapid germination, larger plants and higher biomass, as predicted (Milbau et al. 2009; Bokhorst et al. 2021), but not consistently across the different initial community-forming species. Based on our previous study, we anticipated that *H. lanatus*, *T. officinale* and *T. repens* would germinate more rapidly, and benefit more from warming, than *D. cespitosa*, *A. capillaris* and *P. lanceolata* (Bokhorst et al. 2021). However, grasses benefitted

most from warming in terms of growth, but not consistently across all communities, indicating that other mechanisms were involved. The strongest biomass responses to warming were seen in communities initiated with *D. cespitosa* and *T. repens*, primarily driven by taller plant growth and larger numbers of germinated seeds, and in part driven by earlier germination. A similar pattern was observed for communities initiated with *A. capillaris* and *H. lanatus*, but only in terms of taller plants. In contrast, fewer but heavier plants developed under the warming treatment in

Fig. 4 Plant emergence and biomass response to warming. Data points represent the log response ratio of germination time and biomass with warming of the species as described in the panel heading. Circle colours indicate the initial starting community, while squares represent the species response to warming in monoculture. Data points left of the vertical dashed line reflect earlier emergence under warming, while values above the horizontal dashed line indicates higher biomass under warming

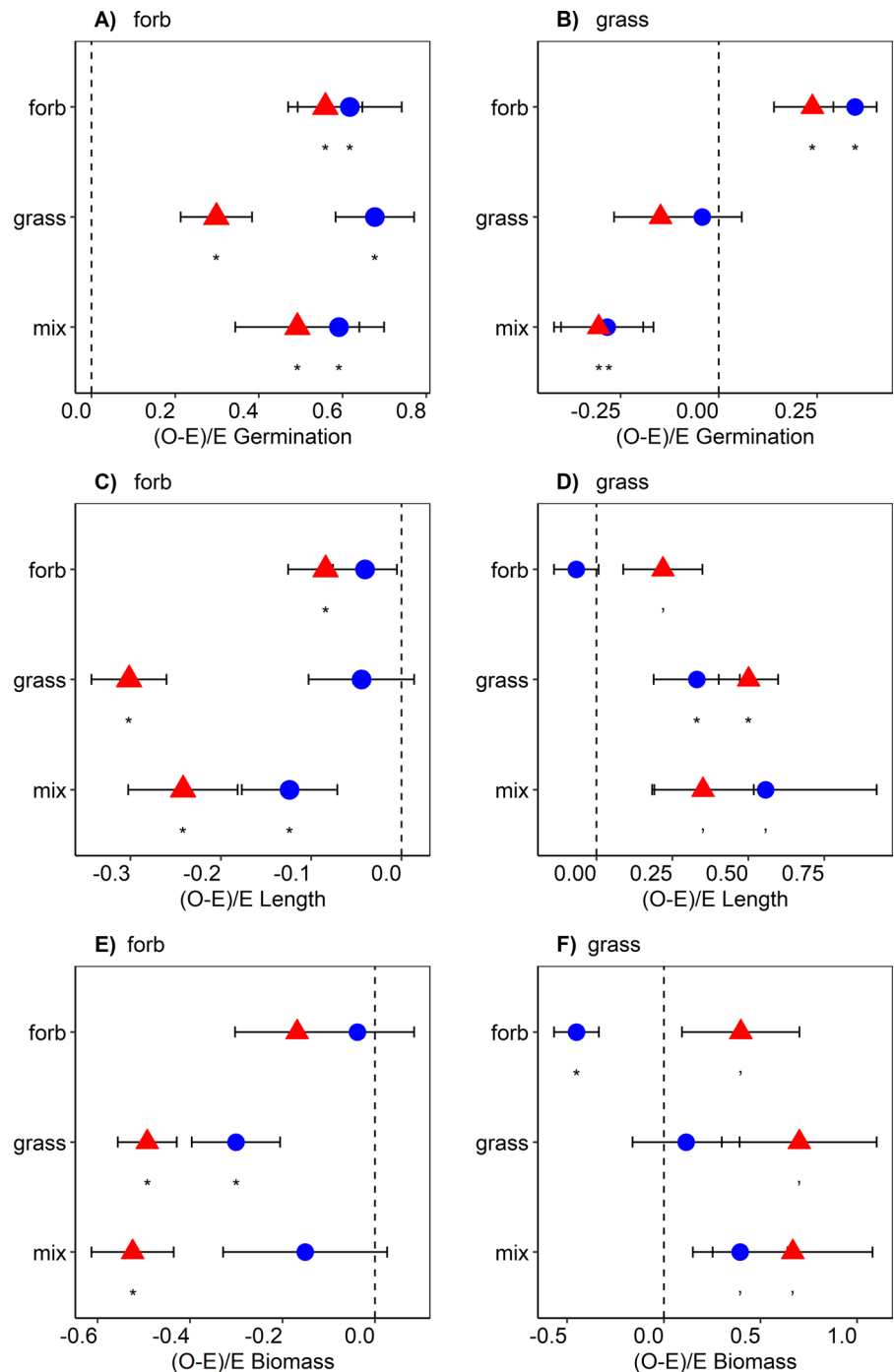


communities initiated with *T. officinale*, *P. lanceolata* and the full mixed community, resulting in no net change in total biomass. By suppressing grass emergence, the forb communities limited plant biomass accumulation under warming. This effect was also present in the full mixed community, indicating that a small number of forb plants were capable of suppressing grass performance (Xiong and Nilsson 1999). Likewise, forbs were hampered in growing taller with warming when the community was initiated with grasses. Warming alleviated some of the negative impact of forbs on the biomass of individual grass plants, resulting in higher mean grass biomass, except when growing among *P. lanceolata*, a species which is known to be a strong light competitor with grasses (van der Toorn and Pons 1988), but did not affect total community biomass. Context-dependent competition is a common phenomenon between forbs and grasses (Akin-Fajiyee et al. 2023), making

it difficult to predict how communities will develop under future warming scenarios.

Grasses have to date been the most successful invasive plant species across sub-Antarctic islands and along the Antarctic Peninsula (Frenot et al. 2005; Molina-Montenegro et al. 2019; Hughes et al. 2020), and based on our findings, will influence the community assembly by limiting forb growth. How this will play out among the moss- and-lichen dominated communities found in Antarctica remains to be seen, but given the competitive effects of vascular plants on cryptogams in Arctic ecosystems (Cornelissen et al. 2001), it seems likely that large changes can be expected at the expense of the native vegetation. Native vascular plants, *D. antarctica* and *C. quitensis*, were not included in this work, but will receive direct competition from non-native vascular plants when they establish. The dense clusters of *D. antarctica* found at some locations along the Antarctic Peninsula (Vera et al. 2013), may hamper

Fig. 5 Priority and warming effect on germination, plant height and biomass. Standardized (observed (O) versus expected (E)) mean plant variables for forbs and grasses across communities with different initial starting community (forb or grass species). A positive value indicates that plant response variables are larger (later germination **A, B** or taller plants **C, D**, greater biomass **E, F**) than found in monocultures at 2 °C (blue circle) and 7 °C (red triangle), while negative values indicate smaller responses compared to monocultures. *: $p < 0.05$; **: $0.05 < p < 0.1$. Values are mean of $n = 15$ replicates (forb and grass) with SE as error bars, and $n = 5$ for mix



the growth of non-native forbs, but competition is likely when other grasses arrive. There is experimental evidence for negative impacts by the non-native grass *Poa annua* on Antarctic vascular plant growth (Cavieres et al. 2018; Molina-Montenegro

et al. 2019), but effects are context dependent, as also found in the current work. The species identity of non-native forbs or grasses is likely to be an important driver of the future community composition that develops, and ecosystem process rates,

under current and future climate warming scenarios in Antarctica.

There was no indication that seed mass affected the germination timing or plant growth of the tested species as anticipated (Grime et al. 1981). This may reflect the low temperature of the experimental conditions used here (Thompson et al. 1977; Milberg et al. 2000; Rosbakh et al. 2022). This study confirms that both niche pre-emption and phenological priority influence plant development through species life history characteristics resulting in the development of contrasting communities. In particular, our data indicate that phenological priority has significant influence on plant biomass while niche pre-emption affects plant germination and plant size. The relative role of these factors in shaping community assembly is however context- and species-dependent, highlighting the complexity of the mechanisms behind priority effects on communities.

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Data availability Will be made available via npdc.nl.

Declarations

Conflict of interest The authors declare that there is no conflict of interest.

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