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Research Article

Introduced species infiltrate recent stages of succession after glacial retreat on sub-Antarctic South Georgia

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Abstract

Biological invasions are one of the main drivers of global biodiversity decline. At the same time, glacial retreat induced by climate warming is occurring at an alarming rate across the globe, threatening unique taxa and ecosystems. However, we know little about how introduced species contribute to the dynamics of colonisation in newly-deglaciated forelands. To answer this question, detailed inventories of plant and invertebrate communities were undertaken during two summer field seasons in the forelands of three tidewater and three inland glaciers that are retreating on the sub-Antarctic Island of South Georgia. The vascular plant communities present included a large proportion of South Georgia's native flora. As expected, plant richness and cover increased with time since deglaciation along a deglaciation chronosequence. Introduced plants were well represented in the study sites and two species (*Poa annua* and *Cerastium fontanum*) were amongst the earliest and most frequent colonisers of recently-deglaciated areas (occurring on more than 75% of transects surveyed). Introduced arthropods were also present around tidewater glaciers, including an important predatory species (*Merizodus soledadinus*) with known detrimental impacts on native invertebrate communities. Our study provides a rare and detailed picture of developing novel communities along a deglaciation chronosequence in the sub-Antarctic. Introduced species are able to track glacial retreat on South Georgia, indicating that further local colonisation and spread are inevitable as the region's climate continues to warm.

Key words: Biological invasion, *Cerastium fontanum*, chronosequence, climate change, conservation, glacial foreland, glacier-associated communities, *Merizodus soledadinus*, non-native species, *Poa annua*, sub-polar ecosystems

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Introduction

Species introduced through human activities (commonly referred to as introduced, alien, non-native, exotic) are considered invasive when they establish and have negative impacts on native biodiversity and ecosystems (Colautti and MacIsaac 2004). Biological invasions are a key component of global environmental change and represent a major threat to biodiversity across the globe (Pyšek et al. 2020; Roy et al. 2023), especially on islands (Moser et al. 2018), and this threat is likely to grow unless effective biosecurity measures are put in place (Seebens et al. 2021). Sub-polar, polar and mountain biomes are increasingly exposed to the cumulative threat of invasive species and global warming (Thorarinsdottir et al. 2014; Alexander et al. 2016; Rew et al. 2020). Although remote sub-Antarctic islands are expected to be particularly vulnerable, data on introduced species are limited and little is known about future invasion trajectories in the face of climate change (Frenot et al. 2005; Leihy et al. 2023).

In most cold biomes across the globe, glaciers have been rapidly retreating over recent decades (Zemp et al. 2019) and, even in the least extreme scenarios of global warming, the majority of the world's mid- and low latitude glaciers are likely to be lost by 2100 (Rounce et al. 2023). This alarming phenomenon impacts biodiversity across multiple spatial and temporal scales, ranging from the loss of specialised communities in the immediate vicinity of retreating glaciers (Hotaling et al. 2017; Wilkes et al. 2023) to regional impacts on water regimes and sea level (Barnett et al. 2005; Zemp et al. 2019). When glaciers melt, new communities are built and an ecological succession becomes apparent from the filtering gradient of environmental conditions along the deglaciation chronosequence (Ficetola et al. 2021; Pothula and Adams 2022). Some specialised taxa may lose their habitat, while others may benefit from colonisation opportunities provided by the newly-deglaciated areas (Cauvy-Fraunié and Dangles 2019; Bosson et al. 2023). To protect these highly vulnerable ecosystems, it is key to describe and understand the processes of ecological succession following glacial retreat (Jacobsen et al. 2012).

To date, biological invasions in glacier-associated communities have received very little research attention. This is surprising, given that invasive species can fundamentally alter the speed and trajectory of ecological succession in other ecosystems (Kuebbing et al. 2014; Bellingham et al. 2016; Gallego-Tévar et al. 2020). In proglacial streams and fjords, it has been suggested that introduced species may arrive late in the succession process following glacial retreat, but clear evidence for this is lacking (Cauvy-Fraunié and Dangles 2019).

To start to understand interactive effects between biological invasions and glacial retreat, we assessed when and to what extent introduced species infiltrate the early successional sequence of proglacial communities. We surveyed pioneer communities of plants (with a focus on vascular plants and key lichens and bryophytes) and invertebrate species (with a focus on macroinvertebrates and Collembola) colonising glacial forelands around three tidewater and three inland glaciers on the sub-Antarctic Island of South Georgia. South Georgia is an important location to investigate how introduced species enter the sequence of colonisation in newly-deglaciated areas, because it harbours multiple introduced plant and invertebrate species (Frenot et al. 2005; Convey et al. 2010; Black 2022). In parallel, most of South Georgia's glaciers have been rapidly receding for decades and are predicted to continue to do so (Gordon et al. 2008; Cook et al. 2010; Rounce et al. 2023), creating large areas of habitat suitable for colonisation by both native and introduced species.

Materials and methods

Study area

The Island of South Georgia is about 170 km long and up to 40 km wide and is located in the South Atlantic, between 54°S–54°55'S and 35°50'W–38°W, about 1000 km north-east of the Antarctic Peninsula. Despite its geographical isolation and relatively harsh sub-Antarctic climate, South Georgia currently hosts species of plants and invertebrates that were introduced by sealing – and later shore-based whaling – industries between the late 18th and mid-20th centuries (Convey and Lebouvier 2009; Convey et al. 2011; Black 2022) with new introductions occurring up to the present day (Convey et al. 2010; Tichit et al. 2023). Some introduced species have negative impacts on native communities (Ernsting et al. 1995; Houghton et al. 2019) and the island's terrestrial ecosystems may be particularly vulnerable to introductions due to the presence of vacant niches that are readily available to new competitive invasive taxa (Convey and Lebouvier 2009; Houghton et al. 2019). To tackle this issue, the Government of South Georgia & the South Sandwich Islands (GSGSSI) has implemented rigorous biosecurity measures and invasive mammals have been successfully eradicated from the Island (GSGSSI 2013; Martin and Richardson 2019). However, some plant species such as the dandelion *Taraxacum officinale* agg. and the meadowgrass *Poa annua* and invertebrates such as the carabid beetles *Trechisibus antarcticus* and *Merizodus soledadinus* may now be too widespread for any realistic possibility of eradication (GSGSSI 2021).

To assess the ability of established introduced species to colonise deglaciated areas, we surveyed six glacial foreland sites during the austral summer on the north coast of South Georgia (Fig. 1). Three sites, investigated in April 2022, were located in the vicinity of the following tidewater glaciers at low elevation (46 ± 40 m a.s.l.): the Nordenskjöld Glacier between Barff and Greene Peninsulas, the Harker Glacier between Greene and Thatcher Peninsulas and the Lyell Glacier that defines the western limit of Thatcher Peninsula. In January and February 2023, the surroundings of three extant or recently-extinct inland cirque glaciers at higher elevation (378 ± 122 m a.s.l.) were surveyed: Hodges and Col Glaciers on Thatcher Peninsula and an unnamed icecap west of Husvik on Busen Peninsula (locally known as Husvik Glacier). Of these three sites, only Col Glacier currently persists as an ice remnant approximately 30 × 100 m in size. Hodges Glacier rapidly receded after 1970 and was lost in 2008 (Bakke et al. 2021), while Husvik Glacier was lost by the late 1950s ("Map of Falkland Island Dependencies: South Georgia" 1958).

To assess the dynamics of foreland colonisation by terrestrial communities, locations with contrasting times since deglaciation (*tsd*) were sampled at each foreland. For tidewater glaciers, detailed maps of glacial front changes were available (Cook et al. 2010; South Georgia GIS, accessed February 2022), enabling us to sample locations positioned with precision along former glacial fronts with *tsd* between five and 30 years. Depending on site accessibility and logistical constraints associated with fieldwork, we were able to sample one to three replicates uniformly distributed and at least 80 m apart on the retreat line for two to four values of *tsd* at the foreland of each tidewater glacier (Suppl. material 1). As no map or record of deglaciation dynamics was available for the inland glaciers, an area with recent *tsd* was identified closest to the current (Col Glacier) or last known position (Hodges and Husvik Glaciers, "Map of Falkland Island Dependencies: South Georgia" 1958) of the ice remnant (Suppl. material 1). For comparison, a second area with

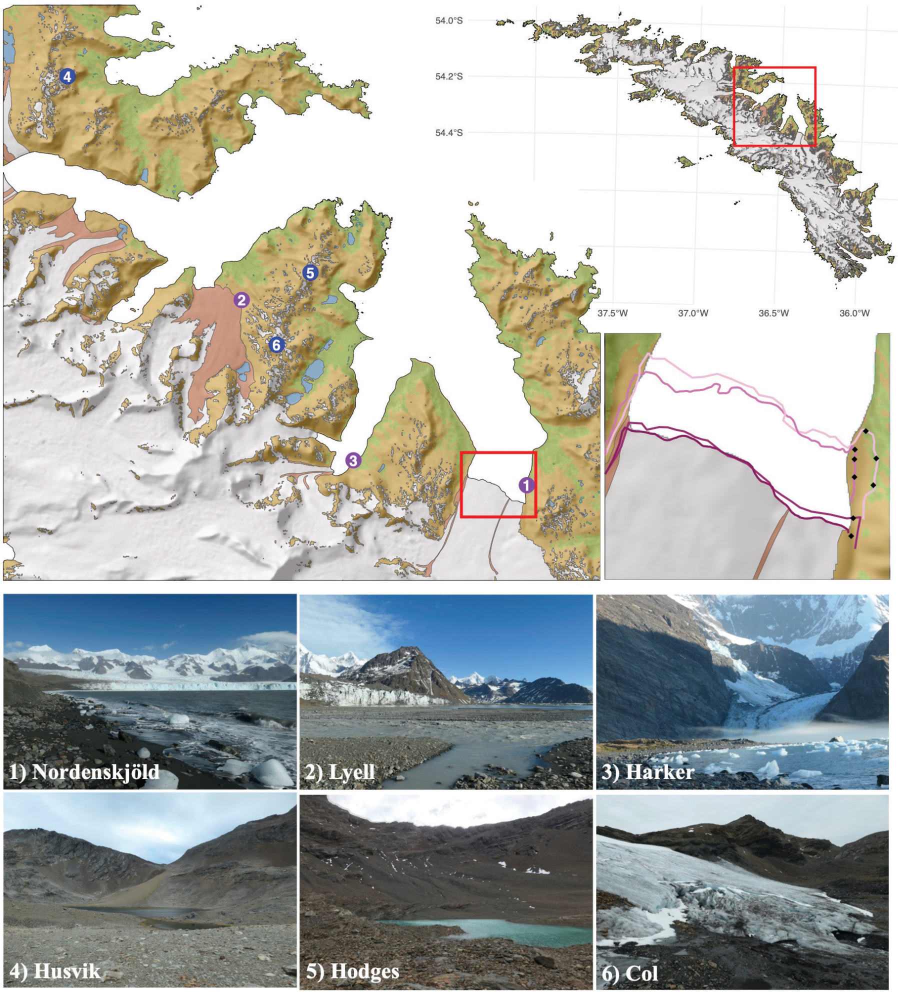

Figure 1. Maps and overview of the six glacier sites on the north coast of South Georgia. Plant and invertebrate communities at three tidewater glacial forelands (1–3 purple) and three inland deglaciated sites (4–6 blue) were surveyed. Centre-right: example of transects (black dots) along former deglaciation fronts (from 1993 to 2017, light to dark purple) in the vicinity of Nordenskjöld Glacier.

older *tsd* was determined at a distance of approximately 200 m in the flow direction of the glacier. The validity of this approach relies on the unverifiable assumption that the retreat rate was similar across the three inland glaciers and over their deglaciation history. For both recent and older *tsd*, three approximately equidistant replicate locations were sampled.

Sampling

At each sampled location, plant communities were surveyed along a 30 m transect. All vascular plants present within six adjacent quadrats (5 × 5 m) either side of the transect line were recorded (yielding 12 records of plant presence/absence per transect), while the cumulative number of bryophyte and lichen morpho-species (photographs provided as Suppl. materials) across two quadrats at opposite ends of the transect was recorded. For the tidewater glacier sites, the cover of plants and lichens was measured through a point-contact sampling procedure using a frame with 10 equidistant pins (length = 50 cm), placed every 2 m along the transect (yielding 15 records of plant cover per transect). The vegetation at inland glacier sites was too sparse to achieve representative point-contact sampling; we therefore used a Braun-Blanquet scale to estimate the cover of plants and lichens in each 5 m quadrat (Suppl. material 2; yielding 12 records of plant cover per transect).

Several invertebrate sampling methodologies were applied in order to achieve the most comprehensive description of the communities present. Ground-dwelling (and secondarily flying) arthropods were sampled using pitfall traps (n = 3) consisting of 250-ml beakers half-filled with a water/washing detergent solution and buried to ground-level at the start, middle and end of each transect. Traps were retrieved after being deployed for approximately 48 h. Macro-invertebrates were extracted from approximately 200 ml of substrate obtained at the same three positions along the transect, using Tullgren extractions for 8 h. Micro-invertebrates were sampled on an opportunistic basis from soaked aliquots of the same substrate. Invertebrates sampled using this non-quantitative method were not included in statistical analyses. Finally, ground-dwelling invertebrates under stones and debris were recorded and sampled during hand searches of 8 min and flying insects were captured using sweep nets along a span of 5 m either side of the transect. All sampled invertebrates were rapidly transferred to ethanol for preservation.

Sample identification

All vascular plants were readily identifiable to species level in the field, based on published description and nomenclature (Burton and Croxall 2012b; POWO 2023) with the exception of the native lesser rush, *Juncus inconspicuus* that was considered to be a synonym of the native greater rush *Juncus scheuchzerioides* Gaudich (Kirschner 2002). Observations of the hybrid between the native greater and lesser burnet *Acaena magellanica* × *tenera* were merged with the data for *A. magellanica*. The introduced species aggregate *Taraxacum officinale* may contain several micro-species and so was reported as *Taraxacum officinale* agg.

While some macroinvertebrates could be identified to species level in the field (Burton and Croxall 2012a), most specimens required detailed assessment of anatomical features under stereo- or light microscopy, with reference to the available literature (Enderlein 1912; Hendel 1937; Gressitt 1970; Convey et al. 1999; Kits 2011). Identification confidence for each taxon was categorised as 'possible', 'probable' or 'certain'. All macro-invertebrates and springtails were identified to species-level. All Sminthuridae were reported as *Sminthurinus jonesi*, since there were no consistent taxonomic features supporting the presence of other species, contrary to what was suggested by Convey et al. (1999). Mites and other micro-invertebrates were categorised into morphotaxa.

Statistical analyses

All statistical analyses were performed in *R* (R Core Team 2022). To assess if the observed presence data reflected the true presence of organisms in the glacial foreland communities (Buddle et al. 2005), we plotted species accumulation curves for each transect with the function *specaccum* from the package '*vegan*' (Oksanen et al. 2007). Visual inspection of these curves indicated if the encounter rate of new species across samples taken was sufficient to compute representative diversity metrics.

To visualise the taxonomic composition of vascular plant communities across *tsd* and glacier site, we performed an ordination on a Jaccard dissimilarity matrix of the presence/absence data at the transect level, using non-metric multidimensional scaling (nMDS) with the function *metaMDS* in '*vegan*' (Oksanen et al. 2007). The score of each species was displayed on the ordination plot.

The presence data were modelled as a function of *tsd* and glacier site through an ordination with the function *cca* from the package '*vegan*' (Oksanen et al. 2007). ANOVA-like permutation tests (n = 999 permutations) for constrained correspondence analysis with the function *anova.cca* were used to test whether community composition was significantly constrained by *tsd*, glacier site and their interaction.

To investigate the effects of deglaciation time on the richness of communities and the presence or cover of species, we employed multivariate models using Bayesian Inference with the package *brms* (Bürkner 2017), treating the glacier site and *tsd* as the main explanatory variables. Tidewater and inland glaciers were modelled separately. As the response of communities may depend on glacier sites, we ran a model with a simple interaction between glacier site and *tsd*. For tidewater glaciers, we ran a model with a quadratic term for *tsd* to reflect non-linear responses, as well as a model with both interaction and quadratic terms. We selected the simplest and most informative model using pairwise comparisons of the expected log pointwise predictive density (ELPD) with function *loo* (Vehtari et al. 2017, Suppl. material 3). The variable *tsd* was a categorical variable for inland glacier sites (recent or old), but continuous and scaled to zero mean and unit variance for tidewater glacier sites. As the availability of mapped former glacial fronts in the period 1993–2018 varied between tidewater glaciers (Cook et al. 2010), the sampling of *tsd* was heterogeneous and not synchronised across glaciers, which prevented the use of a categorical variable to model *tsd*. When the sampling unit (pitfall traps, pin frame or 5 m quadrat) was nested within a transect, transect identity was included as a random effect. Response variables were observed for species richness, plant cover (at species level or higher) and species presence/absence and were modelled using Poisson, zero-inflated binomial and Bernoulli distributions, respectively. Weakly-informative priors determined by a Gaussian distribution (mean $\mu = 0$, standard deviation $\sigma = 10$) were used to model the effects of predictors. Random effects were drawn from a Student's *t*-distribution ($df = 3$, mean $\mu = 0$, standard deviation $\sigma = 10$). Models were run using four chains for 5000 iterations (including 2500 burn-in iterations). Traces of the sampling behaviour of each predictor were scrutinised (Suppl. material 4) and the R-hat convergence diagnostic (Vehtari et al. 2021) was computed (Suppl. material 5) to verify that the models converged towards reliable predictions. A posterior predictive check was used to compare modelled and observed data and evaluate the quality of the models (Suppl. material 4). The significance of each effect being positive or negative was assessed using Bayesian 95% credible intervals (CI_{95}).

Results

Taxonomic inventory

Eighteen native species of vascular plant were found at tidewater glacier sites (Suppl. material 6), representing 78% of the native species known from South Georgia. At inland glaciers, only seven native species were observed (30%). Four introduced species occurred on both types of glacier sites: *Poa pratensis*, *Taraxacum officinale* agg., *Cerastium fontanum* and *Poa annua* (Suppl. materials 7, 8).

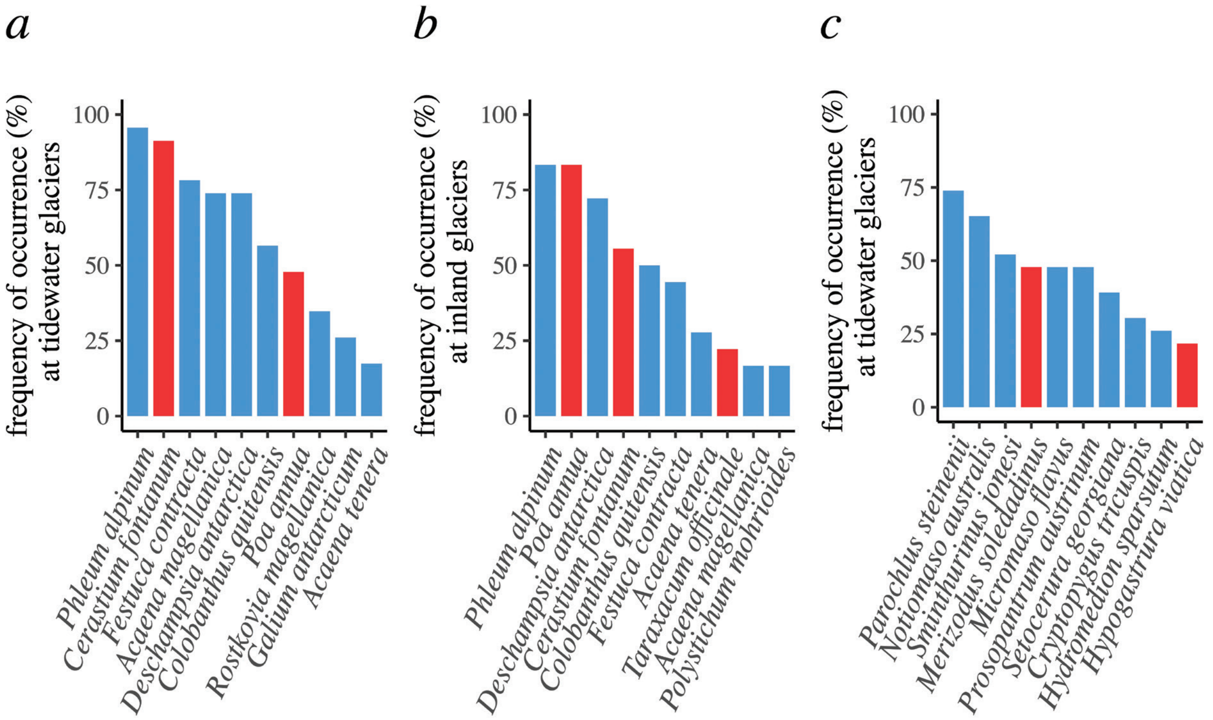

Figure 2. Frequency of occurrence across transects of the 10 most common vascular plants around tidewater glaciers (**a**, n = 21 transects), inland glaciers (**b**, n = 18 transects) and most frequent invertebrates around tidewater glaciers (**c**, n = 21 transects). Introduced species are highlighted in red.

At tidewater glaciers, *C. fontanum* was the second and *P. annua* was the seventh most frequent species (Fig. 2a). On forelands of inland glaciers, *P. annua* was the second, *C. fontanum* the fourth and *T. officinale* agg. the eighth most frequent species (Fig. 2b).

Sixteen native species of terrestrial invertebrates were identified with high confidence at tidewater glacier sites (Suppl. material 6), representing 48% of the native species on South Georgia. At inland glacier sites, only five native species were present, representing 15% of known native species. Five introduced species were found at the tidewater glacier sites and none at the inland sites (Suppl. material 7): *Merizodus soledadinus* (Coleoptera), *Hypogastrura viatica* (Collembola), *Apterothrips secticornis* (Thysanoptera), *Mycomya* sp. (Diptera) and *Trichocera regelationis* (Diptera). *Merizodus soledadinus* and *H. viatica* were the fourth and tenth most frequent invertebrate species, respectively, at tidewater glacier sites (Fig. 2c).

Sampling quality

Accumulation curves of vascular plant species were close to saturation for most of the sampled transects (n = 39, Suppl. material 9), indicating that samples were largely representative of the communities present. However, accumulation curves of invertebrate species did not reach a plateau or were not possible to produce when transects were the smallest replication unit. In the following analyses, we thus calculated diversity metrics only for plants, for which an assumption of near-complete detection was reasonable. We investigated drivers of presence for a subset of the ten most frequently encountered invertebrate species, assuming that detection – though likely incomplete – remained equally probable across sampling sites.

Community-wide effects of time since deglaciation and glacier site

The structure of vascular plant communities was significantly constrained by *tsd*, glacier site and marginally by their interaction in forelands of both tidewater and inland glaciers (Table 1, Fig. 3).

Around tidewater glaciers, the number of bryophyte morpho-species increased linearly with *tsd*, while the number of vascular plant species initially increased and then reached a plateau (Fig. 4, Suppl. material 5). Bryophytes seemed to be more abundant at intermediate *tsd* and there was no clear effect of *tsd* on the cover of vascular plants, but the cover of lichens was higher in areas exposed for longer (Suppl. materials 5, 10). Compared to Harker Glacier, Lyell Glacier hosted a lower number of vascular plant species and a higher number of bryophyte morphospecies, while Nordenskӧld Glacier was associated with a higher cover of bryophytes (Suppl. materials 5, 10).

Table 1. Summary of results from ANOVA-like permutation tests (n = 999 permutations) for constrained correspondence testing whether community composition was significantly constrained by *tsd*, glacier site and their interaction.

	Tidewater glaciers			**Inland glaciers**		
Variable	*F*	*df*	*p*	*F*	*df*	*p*
Time since deglaciation (*tsd*)	3.23	1	0.001	3.45	1	0.007
Glacier site	3.06	2	0.001	4.86	2	0.001
Interaction *tsd*: Glacier site	1.41	2	0.068	2.28	1	0.046

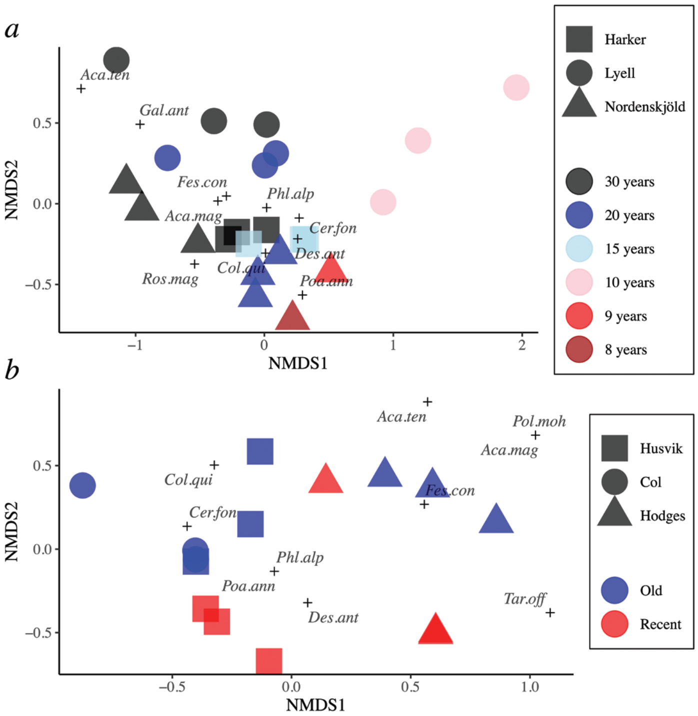

Figure 3. Taxonomic composition of vascular plant communities across time since deglaciation (*tsd* in years) at tidewater (**a**) and inland (**b**) glacier sites. The two first components of a non-metric multidimensional scaling (NMDS) from an ordination on the presence data at the transect level are mapped. Each circle, rectangle or triangle corresponds to a transect from a given site and deglaciation time (black to red). Small crosses represent the score of the ten most frequent species on the ordination plots.

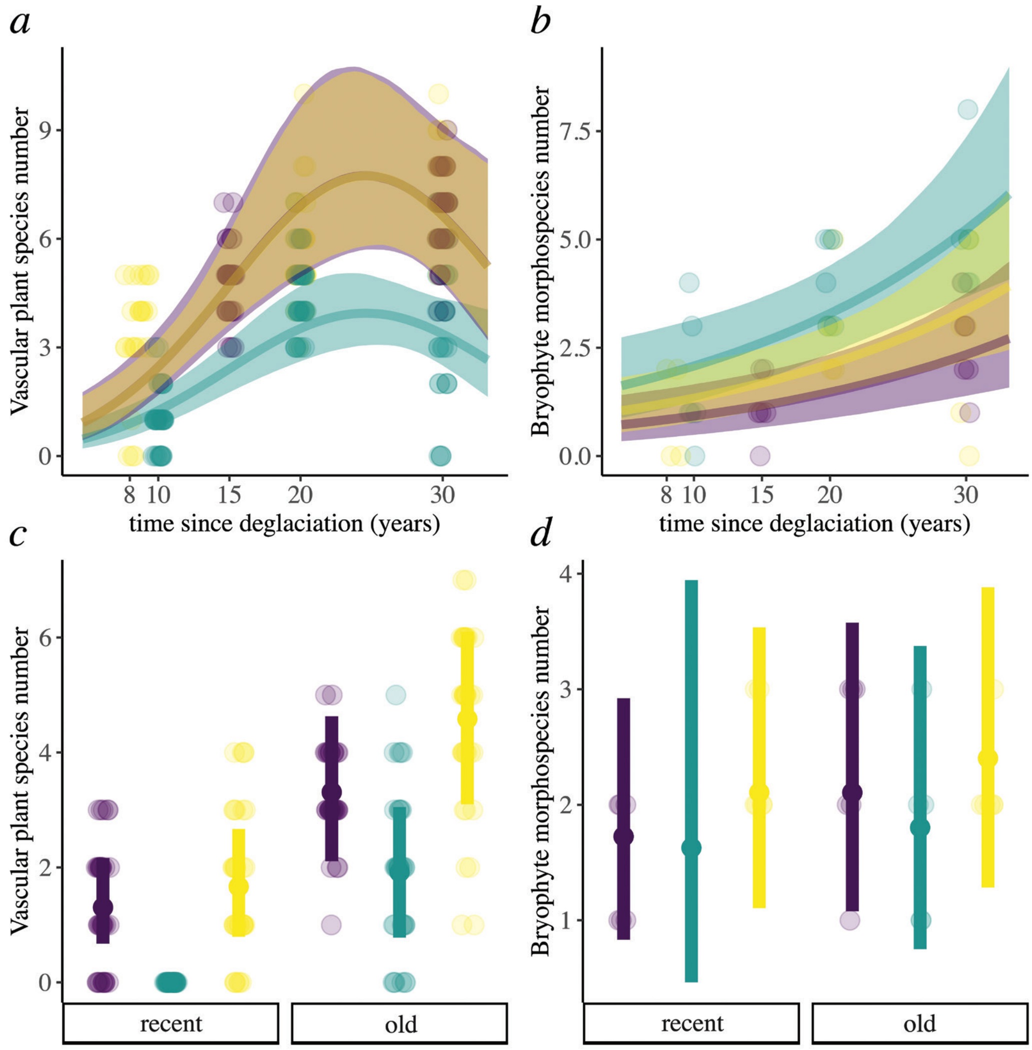

Figure 4. Effect of time since deglaciation (*tsd* in years) on the number of vascular plant species and bryophyte morpho-species at tidewater (**a, b**) and inland (**c, d**) glacier sites modelled with Bayesian Inference. Transparent points represent the original data. Lines (**a, b**) or points (**c, d**) are the estimated mean effects of *tsd*. Purple, turquoise and yellow areas (**a, b**, Harker: purple, Lyell: turquoise, Nordenskjöld: yellow) or intervals (**c, d**, Husvik: purple, Col: turquoise, Hodges: yellow) represent the Bayesian 95% credible intervals, respectively.

At inland glacier sites, there were significantly more vascular plant species in older than in recently-deglaciated areas (Fig. 4, Suppl. material 5), as well as a higher cover of vascular plants and bryophytes (Suppl. materials 5, 10). Compared to Husvik Glacier, Col Glacier hosted a lower number of vascular plant species and reduced cover of vascular plants and of bryophytes (Suppl. materials 5, 10). Hodges Glacier did not differ from Husvik Glacier in terms of community-level metrics.

Species-level effects of time since deglaciation and glacier site

At tidewater glacier sites, the introduced *Cerastium fontanum* and *Poa annua* were most likely to occur across a broad range of intermediate *tsd* (Fig. 5a, Suppl. materials 5, 10), which was also the case for the native species *Deschampsia antarctica* and *Colobanthus quitensis*. The probability of occurrence of the native *Phleum alpinum* initially increased and then reached a plateau with increasing *tsd*. The native *Festuca contracta*, *Acaena tenera*, *A. magellanica*, *Rostkovia magellanica* and

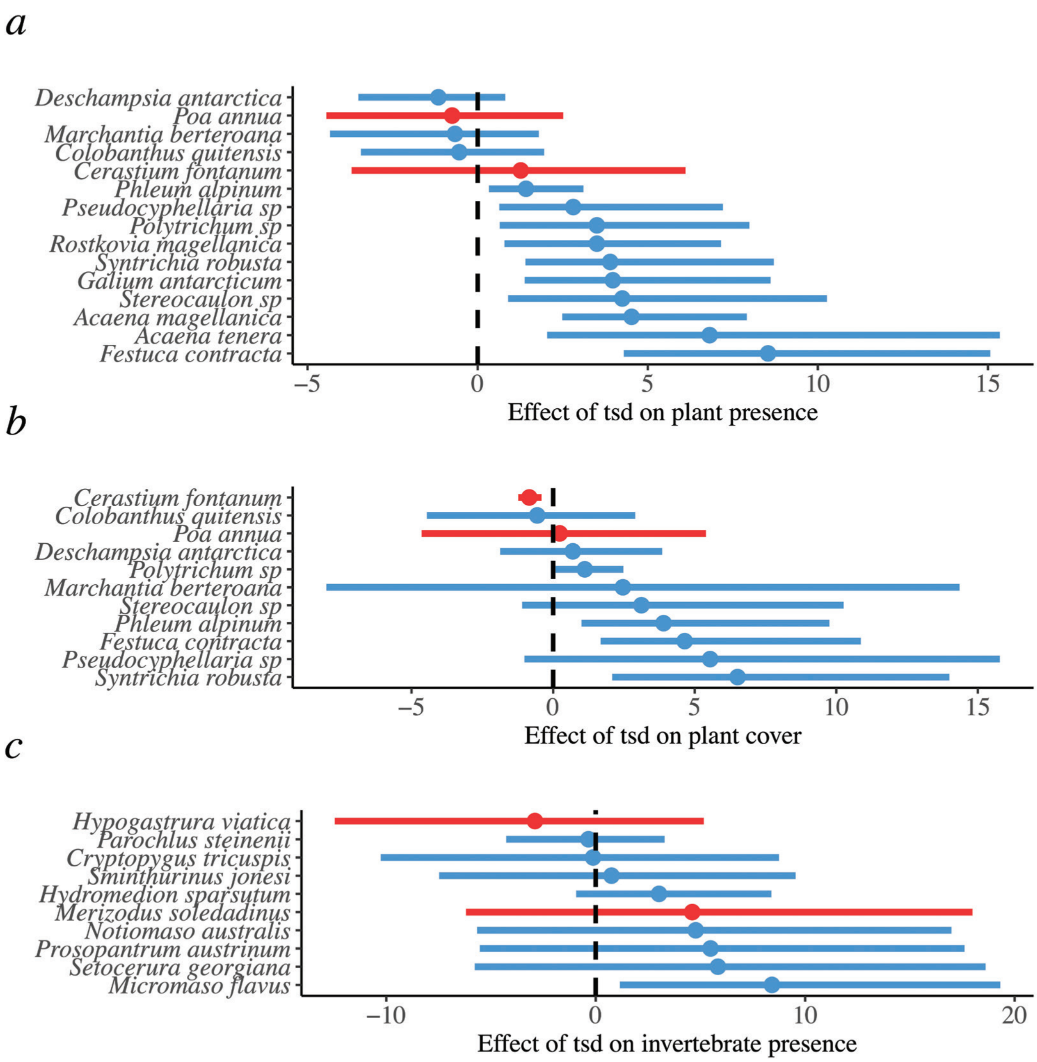

Figure 5. Scaled effect of time since deglaciation (*tsd* in years) on plant presence (**a**), vascular plant cover (**b**) and invertebrate presence (**c**) at tidewater glaciers modelled using Bayesian Inference. Effects on introduced and native species are represented in red and blue, respectively. Points are the mean effects of *tsd* on the logit scale. Intervals represent the Bayesian 95% credible intervals. The vertical dotted lines correspond to the null hypothesis (effect is zero).

Galium antarcticum were more frequent at older deglaciated sites. Similarly, the two lichens *Stereocaulon* sp. and *Pseudocyphellaria* sp. and the mosses *Syntrichia robusta* and *Polytrichum* sp. were more likely to occur in older deglaciated areas, while the presence of the liverwort *Marchantia berteroana* was not affected by *tsd*. The cover of *C. fontanum* decreased with increasing *tsd* (Fig. 5b, Suppl. materials 5, 10), while the cover of *P. annua* showed no evidence of change. Amongst native vascular plants, the cover of *C. quitensis* showed no evidence of change with *tsd*, *D. antarctica* and *P. alpinum* were most abundant at intermediate *tsd* and *F. contracta* had higher cover in older deglaciated areas. Amongst bryophytes and lichens, the cover of *Stereocaulon* sp., *Pseudocyphellaria* sp. and *Marchantia berteroana* showed no evidence of change with *tsd*, while *Polytrichum* sp. was most abundant at intermediate *tsd* and *Syntrichia robusta* increased in cover with *tsd*.

At inland glacier sites, the occurrence of the invasive *Taraxacum officinale* agg. did not differ between old and recent areas of deglaciation (Fig. 6a, Suppl. materi-

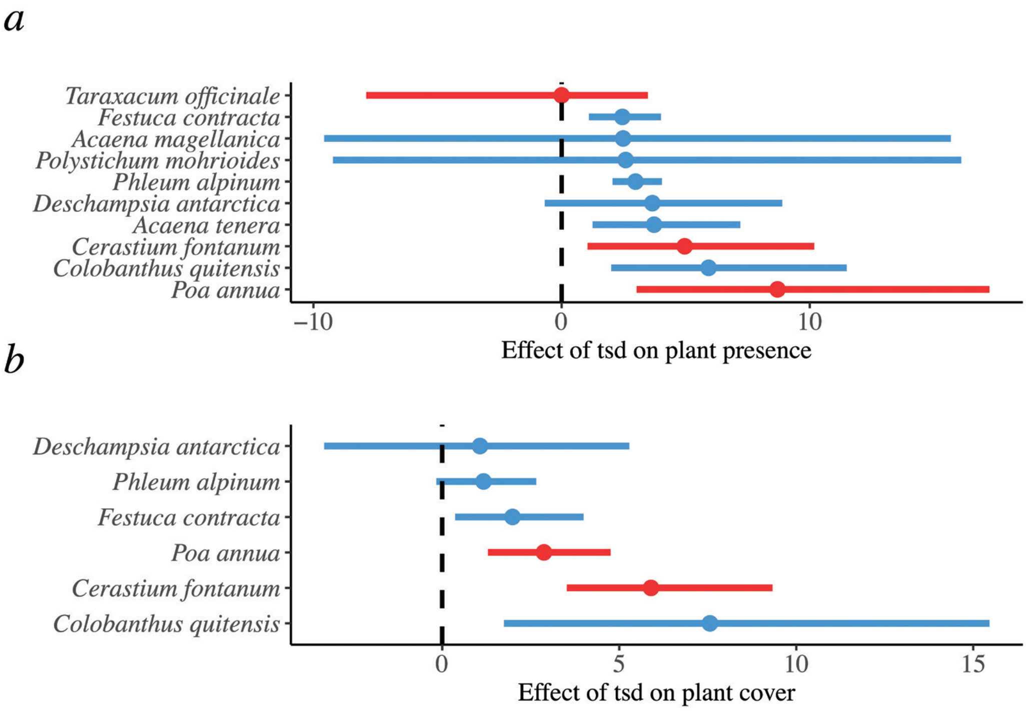

Figure 6. Effect of time since deglaciation (*tsd*) on vascular plant presence (**a**) and vascular plant cover (**b**) at inland glaciers modelled using Bayesian Inference. Effects on introduced and native species are represented in red and blue, respectively. Points are the mean effects of *tsd* on the logit scale. Intervals represent the Bayesian 95% credible intervals. The vertical dotted lines correspond to the null hypothesis (effect is zero).

als 5, 10), while the invasive *P. annua* and *C. fontanum* were more frequent in older deglaciated locations. The native *D. antarctica*, *A. magellanica* and *Polystichum mohrioides* did not significantly differ between *tsd*, while all other native plants became more frequent in older deglaciated areas. The cover of all plants (with the possible exception of *D. antarctica* and *P. alpinum*) was higher in old deglaciated areas (Fig. 6b, Suppl. materials 5, 10).

At tidewater glacier sites, the native spider *Micromaso flavus* seemed more frequent at older deglaciated sites, but there was no clear effect of *tsd* on the presence of other reliably sampled invertebrates (Fig. 5c, Suppl. materials 5, 10).

For both inland and tidewater glaciers, there were notable differences between sites in the presence and cover of species (Suppl. materials 5, 10). The invasive *C. fontanum* was scarce at Lyell Glacier and abundant at Nordenskjöld Glacier, where the introduced springtail *Hypogastrura viatica* was also more common, while *P. annua* was more frequent at Harker Glacier. At inland sites, *T. officinale* agg. was more frequent at Hodges Glacier, while *P. annua* was less abundant at Col Glacier.

Discussion

Colonisation by introduced species

Introduced vascular plants and invertebrates were well represented in the recent stages of community assembly after glacial retreat on South Georgia. Four introduced vascular plants were found on glacial forelands, with *Cerastium fontanum* and *Poa annua* being very frequent, while *Taraxacum officinale* agg. and *P. pratensis* were rarely observed. Around tidewater glaciers, *C. fontanum* and *P. annua* occurred across a broad range of *tsd* and *C. fontanum* was more abundant in recently rather than in older deglaciated sites, indicating that these species are effective pioneers on glacial forelands along South Georgia's coast. Notably, flowering specimens of *C. fontanum* were found in areas deglaciated less than five years prior to the survey, approximately 50 m from the terminus of Lyell Glacier. Both species originate from temperate regions of the Northern Hemisphere (POWO 2023, Suppl. material 7), are widespread on South Georgia (Black 2022) and have successfully invaded most islands in the sub-Antarctic (Frenot et al. 2005). *Poa annua* is invasive on the maritime Antarctic South Shetland Islands (Molina-Montenegro et al. 2012; Hughes et al. 2015) and both species are also early colonisers of newly-deglaciated areas on a glacier foreland on the sub-Antarctic Kerguelen Islands (Frenot et al. 1998). At tidewater glaciers on South Georgia, the rapid colonisation by *C. fontanum* and *P. annua* outpaced that of most native vascular plants, with the possible exceptions of *Deschampsia antarctica* and *Colobanthus quitensis*, with these invasive plants effectively short-cutting the successional sequence following glacial retreat. At inland sites, *C. fontanum* and *P. annua* were less common in more recently-deglaciated areas, but direct comparisons with tidewater glaciers are not possible due to methodological differences. In contrast, the dandelion *T. officinale* agg. appeared equally capable of colonising old and recently-deglaciated areas inland, which likely results from its seeds being wind-dispersed over large distances.

We also documented the presence of five introduced invertebrate species on recently-deglaciated forelands, indicating an ability to disperse and survive in challenging environments. This capacity to track glacial retreat is particularly remarkable for three of these invertebrates that are flightless and suggests high mobility through passive dispersal (Hågvar et al. 2020) or active locomotion, as previously reported for the carabid beetle *Merizodus soledadinus* (Convey et al. 2011; Renault 2011; Laparie et al. 2013; Lebouvier et al. 2020). The invasive springtail *Hypogastrura viatica* was frequent on coastal forelands (in particular at Nordenskjöld Glacier), which underlines the high dispersal capacity of this species that is also introduced on other sub-Antarctic islands and in parts of the South Shetland Islands (Frenot et al. 2005; Greenslade and Convey 2012).

What characteristics of introduced plants and invertebrates make them capable of infiltrating the dynamics of colonisation on glacial forelands? The isolation and harsh environment of sub-Antarctic islands generate environmental filters that may provide opportunities for invaders with a mixture of typical invasive traits that guarantee high resource acquisition and efficient dispersal (Laparie et al. 2013; Liao et al. 2021) and pioneer traits such as low plant height and resistance to abiotic stress (Laparie et al. 2012; Mathakutha et al. 2019; Bazzichetto et al. 2021). Both *P. annua* and *C. fontanum* are small annual plants with shallow roots (although *P. annua* can adopt a perennial life cycle and develop into swards), investing heavily in rapid growth and early reproduction and lack the vegetative and longer-lived tissues typical of the perennial native species that allow multi-year survival under stressful abiotic conditions (Frenot and Gloaguen 1994; Frenot et al. 1998; Chwedorzewska et al. 2015; Johner 2020). It is possible that ruderal traits act as pre-adaptations that provide a colonisation advantage as communities develop around receding glaciers.

Possible impacts of introduced species

Although native plants seem to co-occur with the two invasive pioneers *C. fontanum* and *P. annua*, these invasive plants may have impacts on native communities in glacial forelands. During competition experiments in the field in the South Shetland Islands, *P. annua* reduced the biomass and photosynthetic abilities of *C. quitensis* and *D. antarctica* (Molina-Montenegro et al. 2012). On South Georgia, *C. quitensis* and *D. antarctica* might also be the native plants most likely to experience direct competition with *C. fontanum* and *P. annua*, given their similar early position in the succession on glacial forelands. Competitive interactions between invasive and native taxa are likely to change with ongoing environmental changes and climate warming, possibly to the advantage of introduced species that generally originate from more temperate regions (Molina-Montenegro et al. 2019; March-Salas and Pertierra 2020; Convey and Hughes 2022; Daly et al. 2023). However, our data also show that *C. fontanum* declines in abundance, while *P. annua* remains equally common in post-glacial plant communities as they are eventually colonised by native perennial plants, suggesting that native plants can be stronger competitors than some invasive annuals. Despite this, the two invasive plants remain a component of plant communities at least 30 years after deglaciation both in inland and coastal forelands and these taxa are now so widespread on South Georgia that large-scale control is not feasible (Black 2022).

Current and future impacts of introduced species will likely vary between glacier locations. For instance, we found that Nordenskjöld Glacier had higher plant cover, but was also more invaded by introduced plants and invertebrates than the two other tidewater sites. Whether these local differences are due to contrasting topography, microclimate, soil quality or disturbance by macrofauna or human activities is still to be investigated, but they deserve consideration when assessing impacts of biological invasions on glacier-associated communities and developing conservation strategies.

Introduced invertebrates may also have impacts on the terrestrial ecosystems of sub-Antarctic islands (Convey et al. 2010; Houghton et al. 2019). In our study, they were restricted to coastal sites, suggesting that inland sites might provide refuges for native taxa (but see Lebouvier et al. (2020) who note that *M. soledadinus* is now invading inland and higher altitude locations on the Kerguelen Islands). However, with very limited representative survey data available away from coastal locations on South Georgia, it is also unclear whether inland areas would be suitable for many/most native taxa given their high degree of isolation, inhospitable conditions and low diversity of habitats. The presence of the predatory *M. soledadinus* is of great concern for the native invertebrate diversity as it can locally drive prey species to extinction, impact the life cycle of co-existing species and fundamentally reshape invertebrate communities (Convey et al. 2011; Lebouvier et al. 2020). The introduced springtail, *H. viatica*, might act as a food source to the introduced predator, as well as competing directly or indirectly with native species, such as *Cryptopygus antarcticus* (Convey et al. 1999). Our results suggest that communities in newly-deglaciated areas may not be exempt from the negative effects of invasive invertebrates that may alter the trajectory of invertebrate community succession compared to when they are absent.

The early expansion of introduced species likely modifies soil characteristics, provides biomass and generates biotic interactions in newly-deglaciated areas

(Badenhausser et al. 2022), which might have consequences for the entire succession process following glacial retreat. In other systems, biological invasions can alter the speed (Gallego-Tévar et al. 2020) and trajectory of primary successions (Flory and Clay 2010), but little is known in the context of glacier-associated communities. Moreover, the impacts of invasive species in glacial forelands may not be exclusively negative (Walther et al. 2009), as some native taxa might benefit from a modified succession. Our study highlights the need for future research to understand if and how introduced taxa can alter the trajectory and speed of colonisation dynamics following glacial retreat.

Community changes and underlying mechanisms along the deglaciation chronosequence

Overall, we found an increase in the cover and diversity of plants along the chronosequences in glacial forelands. This is consistent with the basic process of primary succession following glacial retreat (Jones and Henry 2003; Flø and Hågvar 2013; Vater and Matthews 2015; Glausen and Tanner 2019; Gwiazdowicz et al. 2020; Pothula and Adams 2022) and we can presume that a similar trend would have been found with invertebrate communities if sampling quality had allowed. Although our study did not include sites deglaciated more than 30 years previously, we found evidence that the rate of accumulation of vascular plant species decreased along the chronosequence, which contrasts with proglacial successions across the world (Jones and Henry 2003; Pothula and Adams 2022), eventually reaching a plateau representing a high proportion of the native flora of South Georgia. Contrasting with other regions globally where glacier-associated taxa represent a very small proportion of the overall biodiversity, these differences may relate to the specificity of the flora on sub-Antarctic islands, that typically consists of species with higher dispersal ability and adaptations enabling survival in harsh abiotic conditions (Convey 1996).

There were interspecific differences in the colonisation speed of native plants that may help to disentangle the mechanisms underpinning the deglaciation chronosequence. *Deschampsia antarctica* and *Colobanthus quitensis* were the first native species to colonise tidewater glacier sites alongside two genera of lichen (*Stereocaulon* and *Pseudocyphellaria*), followed by *Phleum alpinum* and, subsequently, *Acaena magellanica*, *A. tenera*, *Festuca contracta*, *Rostkovia magellanica*, *Galium antarcticum* and three bryophyte taxa. Interestingly, *D. antarctica* and *C. quitensis* are the only two native angiosperms in the more extreme maritime Antarctic and are known for their high degree of tolerance to adverse conditions (Cavieres et al. 2016; Clemente-Moreno et al. 2020), which may contribute to their ability to colonise very recently-deglaciated sites on South Georgia. The pattern of primary succession following deglaciation on the sub-Antarctic Kerguélen Islands showed some differences to South Georgia, as cushion-forming *Colobanthus* species and tussock-forming *Poa kerguelensis*, but not *D. antarctica*, were amongst the first colonisers (Frenot et al. 1998). The early succession on South Georgia resembles proglacial communities of glaciers at high latitudes and altitudes where lichens, mosses and some grasses are first to colonise, but later trajectories differ due to the presence of shrubs and trees (Jones and Henry 2003; Nakatsubo et al. 2005; Garibotti et al. 2011; Fickert and Grüninger 2018; Ruka et al. 2023). Regional idiosyncrasies in the successional colonisation of deglaciated areas on sub-Antarctic islands are likely a result of missing species in disharmonious floras which may lead to increased vulnerability of developing native communities to invasive plants with traits largely absent for the native species pool. Even across glaciers of the same type on South Georgia, community composition was largely determined by glacier identity, which underlines the importance of the local microenvironment and the composition of adjacent communities in shaping successions following glacial retreat (Bayle et al. 2023). Native invertebrate communities around tidewater glaciers primarily consisted of mites, springtails, dwarf Linyphiidae spiders, Promecheilidae beetles and winged dipterans, resembling proglacial arthropod communities across alpine, sub-polar and polar ecosystems (Kaufmann 2001; Hodkinson et al. 2004; Franzén and Dieker 2014; Hågvar et al. 2020; Moret et al. 2020; Ruka et al. 2023).

Conclusions

Besides providing an important baseline on the patterns of community assembly along a deglaciation chronosequence in the sub-Antarctic, this study highlights the need for future research that quantifies the impacts of invasive pioneers on the speed and trajectory of ecological succession in glacier-associated ecosystems. While current colonisation dynamics suggest that invasive species infiltrate the sequence without outcompeting native colonisers, further studies are required to determine whether this co-occurrence will persist with ongoing climate change, glacial retreat and habitat transformation. On South Georgia and other sub-Antarctic islands, invasive species will likely track the ongoing and future retreat of glaciers where they are present. Our study illustrates that synergies between the effects of climate change and biological invasions constitute a key research avenue in vulnerable montane, polar and sub-polar ecosystems.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

PT, PC, PB, RN and WD designed the study. PT, PC and WD coordinated logistical support. PT collected and analysed the data. PT and WD drafted the manuscript. PT, PC, PB, RN and WD revised the manuscript. All authors agree to be held accountable for the content of this paper and approve the final version.

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Data availability

The original datasheets containing all species field and laboratory observations and images of surveyed bryophyte and lichen morphospecies can be downloaded as supplementary materials. Samples are stored at the University of Liverpool.

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Supplementary material 1

Positions of all transects (black dots) along former deglaciation fronts (from 1993 to 2017, light to dark purple) in the vicinity of tidewater glaciers or in recent and old deglaciation areas in the vicinity of inland glaciers

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson
Data type: pdf
Explanation note: For the latter, the approximate last known positions of the glacier are highlighted in light purple (Husvik: 1958, Hodges: 1970, Col: 2023).

Link: https://doi.org/10.3897/neobiota.92.117226.suppl1

Supplementary material 2

Adapted Braun-Blanquet scale used in the study of inland glacier sites

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson
Data type: pdf

Link: https://doi.org/10.3897/neobiota.92.117226.suppl2

Supplementary material 3

Results of model selection, based on the posterior likelihood of models for each variable

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson
Data type: pdf
Explanation note: SE indicates standard error. The simplest model with best predictive performance determined was that using pairwise comparisons of the expected log pointwise predictive density (elpd-diff). Point estimates of the expected log pointwise predictive density (elpd_loo), the effective number of parameters (p_loo) and the loo information criterion looic are also provided.

Link: https://doi.org/10.3897/neobiota.92.117226.suppl3

Supplementary material 4

Model traces, conditional effects and posterior predictive check of each modelled variable

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson

Data type: pdf

Link: https://doi.org/10.3897/neobiota.92.117226.suppl4

Supplementary material 5

Summary of effects of time since deglaciation for each glacier site on all variables modelled with Bayesian Inference (including quadratic and interaction terms if retained in the best model)

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson

Data type: pdf

Explanation note: Effects on the presence and cover of taxa are on a logit scale. Effects on unbound count data are on a log scale. The R-hat statistic is provided to assess the convergence of each estimate.

Link: https://doi.org/10.3897/neobiota.92.117226.suppl5

Supplementary material 6

List of species found at tidewater and inland glacier sites

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson

Data type: pdf

Explanation note: Introduced species in bold. Taxonomical information from up-to-date database (POWO 2023; Bánki et al. 2024).

Link: https://doi.org/10.3897/neobiota.92.117226.suppl6

Supplementary material 7

Description of the introduced species observed in the survey (n = 9)

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson

Data type: pdf

Link: https://doi.org/10.3897/neobiota.92.117226.suppl7

Supplementary material 8

Average cover (in %) across transects of the 10 most common vascular plants around tidewater glaciers (*a*, n = 21 transects), inland glaciers (*b*, n = 18 transects)

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson

Data type: pdf

Link: https://doi.org/10.3897/neobiota.92.117226.suppl8

Supplementary material 9

Species sampling curves for each surveyed transect

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson

Data type: pdf

Link: https://doi.org/10.3897/neobiota.92.117226.suppl9

Supplementary material 10

Effect of time since deglaciation on the presence of plant and invertebrate species at tidewater and inland glacier sites modelled with Bayesian Inference

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson

Data type: pdf

Explanation note: Transparent points represent the original data. Lines (tidewater) or points (inland) are the estimated mean effects of *tsd*. Purple, turquoise and yellow areas (Harker: purple, Lyell: turquoise, Nordenskjöld: yellow) or intervals (Husvik: purple, Col: turquoise, Hodges: yellow) represent the Bayesian 95% credible intervals, respectively.

Link: https://doi.org/10.3897/neobiota.92.117226.suppl10

Supplementary material 11

Plant and invertebrate inventory on glacial forelands of South Georgia (2022–2023)

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson

Data type: zip

Explanation note: GPS positions, plant and invertebrate inventories made across tidewater (2022) and inland glaciers (2023) on South Georgia.

Link: https://doi.org/10.3897/neobiota.92.117226.suppl11

Supplementary material 12

Bryophyte and lichen morphospecies observed on glacial forelands of South Georgia (2022–2023)

Authors: Pierre Tichit, Paul Brickle, Rosemary J. Newton, Peter Convey, Wayne Dawson

Data type: zip

Explanation note: Bryophyte and lichen morpho-species were photographed across two 5 × 5 m quadrats at opposite ends of each 30 m transect on forelands of tidewater glaciers. Specimens are recorded in Suppl. material 11.

Link: https://doi.org/10.3897/neobiota.92.117226.suppl12