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ORIGINAL ARTICLE

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Expansion of invasive carabids across elevation and habitats on sub-Antarctic South Georgia

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Abstract

1. Up-to-date information about the extent and underlying drivers of biological invasions is necessary to improve conservation strategies.
2. The flightless, predatory carabid beetles, *Merizodus soledadinus* and *Trechisibus antarcticus*, were introduced to the sub-Antarctic island of South Georgia after 1960. The most recent but opportunistic monitoring of the species' distributions in the late 2000s indicated significant range expansions.
3. We systematically assessed the presence and numbers of carabids and the associated communities at >200 locations on the northern coast of the island in 2023.
4. The ranges of both species have continued to increase over the past 10–15 years, and they are now present from lowland coastal areas to the tops of valleys (>300 m above sea level).
5. We modelled the detectability and abundance of carabids, finding that they occurred across all habitats examined but with greater abundance in dense vegetation.
6. Our survey suggests that *T. antarcticus* is less abundant when *M. soledadinus* co-occurs. While a complete assessment of carabid impacts on native communities is not feasible with our data, we found that some native insects were considerably rarer within the carabids' range than beyond it.
7. Ongoing climate change will likely provide opportunities for carabids to expand their range and become more abundant, highlighting the need for continued monitoring and biosecurity.
8. We recommend regular application of systematic hand searches in favourable habitats, underlain by quantified estimates of search effort. Our transferable research methodology can optimise monitoring of introduced species in regions where field surveys are challenging.

KEYWORDS

alien species, biological invasion, biosecurity, Coleoptera, conservation biology, entomology, habitat preference

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INTRODUCTION

Sub-Antarctic islands are at the forefront of a changing world. Their local climates are rapidly warming due to anthropogenic climate change (Nel et al., 2023), leading to the rapid retreat of glaciers (Gordon et al., 2008) and the expansion of vegetation to higher elevation and newly deglaciated areas (Tichit et al., 2024; van der Merwe et al., 2024). These islands are still impacted by the legacies of the highly destructive Southern Ocean sealing and whaling industries (Bergstrom & Chown, 1999; Convey & Lebouvier, 2009; Frenot et al., 2005; Leihy et al., 2023). In addition, islands, such as South Georgia now receive increasing numbers of visitors through the expanding sector of Antarctic tourism and other human activities, which increases the risks of new non-native species introductions (Tichit et al., 2023).

The unique terrestrial ecosystems of the sub-Antarctic islands, including a significant proportion of endemic species, are vulnerable to these changes in climate, habitat and human activities (Convey, 2007; Frenot et al., 2005; Houghton et al., 2019). Native plant and invertebrate communities have developed through a combination of rare colonisation events from distant areas and evolution in isolation in the islands' relatively harsh but stable conditions (Aguado-Lara et al., 2025; Kuschel & Chown, 1995). Native communities typically have low functional redundancy, or even lack entire guilds, and are thus vulnerable to introduced species with higher competitive abilities (Convey, 1996; Houghton et al., 2019). Over the last two to three centuries, human activities have considerably disrupted the geographical isolation of these remote islands, facilitating the introduction of highly successful non-native species (Convey & Lebouvier, 2009; Molina-Montenegro et al., 2019; Moser et al., 2018). Indeed, sub-Antarctic communities of flying and edaphic insects frequently include more introduced than native species. Climate change could facilitate both the establishment of new, and the further expansion of already-present, non-native species through increased temperatures, amelioration of environmental stresses, and exposure of new ground for colonisation due to the retreat of glaciers that formerly acted as dispersal barriers (Cook et al., 2010; Daly et al., 2023; March-Salas & Pertierra, 2020; Tichit et al., 2024). A large proportion of non-native species that have successfully established or could be introduced on sub-Antarctic islands are insects (Houghton et al., 2019).

The carabid beetles, *Merizodus soledadinus* and *Trechisibus antarcticus*, are striking examples of successful insect invasions on sub-Antarctic islands. Both are flightless predators that were accidentally introduced by humans to South Georgia, probably in relation to research or military activities (Convey et al., 2011; Lebouvier et al., 2020). The species were first noted on South Georgia in 1963 (*M. soledadinus*, at Grytviken and Husvik) and 1982 (*T. antarcticus*, at Husvik, Figures 1 and 2b, Darlington, 1970, Vogel, 1985). Both species were introduced from their native range in southern South America or the Falkland Islands, but the exact introduction pathways are not known. *Merizodus soledadinus* was also introduced to Îles Kerguelen in the southern Indian Ocean in the early 20th century, most likely from the Falkland Islands via sheep farming activities (Lebouvier et al., 2020).

Both species can have negative impacts on native terrestrial communities that have evolved without significant predation pressures in the absence of comparable native predators. On South Georgia, *T. antarcticus* locally decreases the abundance of the native herbivorous beetle *Hydromedion sparsutum* by predating the early larval stages of that species, which in turn may respond with accelerated larval development (Ernsting et al., 1995). The native flightless dipterans, *Eretmoptera murphyi* and *Antrops truncipennis*, may be easy prey for the carabids, and the lack of co-occurrence of carabids with native staphylinid beetles suggests that they may also be negatively impacted (Convey et al., 2011). While the impact of *M. soledadinus* on South Georgia has not been investigated in detail, research from Îles Kerguelen indicates that the species can prey on a broad range of macro-arthropods, to the point that some native species become locally extinct (Daly & Renault, 2025; Lebouvier et al., 2020). Carabid predation on herbivores and detritivores has the potential to alter ecosystem processes and functions such as decomposition and nutrient cycling, but this remains speculative in the absence of dedicated investigations.

More generally, little is known about the ecology of invasive carabids on South Georgia and the latest information on the species' ranges is from opportunistic surveys and observations in the period 2002–2009 (Convey et al., 2011). Between 1995 and 1996 and 2006–2009, *T. antarcticus* expanded from its assumed Husvik introduction site westwards to Fortuna Bay and eastwards along the Busen Peninsula (Figure 2b). Since its first sighting on Thatcher Peninsula in 1963 (Darlington, 1970), *M. soledadinus* has been found at two other disjunct locations around the former whaling station at Husvik and at Jason Harbour, while it rapidly expanded within the Thatcher Peninsula and colonised the Greene Peninsula and Barff Peninsula (Figure 2). Although the distribution of *M. soledadinus* on Barff Peninsula seemed restricted to Corral Bay in 2007, this observation was not based on extensive sampling, and there is no tidewater glacier that could have limited its further dispersal (Convey et al., 2011). An eastward expansion of the species since the 2010s thus seems extremely likely.

Monitoring methods are inevitably imperfect and species such as carabids can remain undetected by chance, especially in sub-Antarctic regions that are difficult to access and with the general lack of specialist expertise or practical experience on the ground. In addition, introduced arthropods are often elusive and patchily distributed. The issue of imperfect detection can be addressed using occupancy and N-mixture abundance models that rely on repeated measurements to explicitly estimate the probability of detecting a species (Murn & Holloway, 2016), thereby providing accurate estimates of their true presence/absence and abundance. By allowing comparison of the probability of detection of different sampling methods and prediction of the sampling effort required to reach sufficient detection rates, occupancy and N-mixture abundance models can considerably improve the monitoring of invasive species.

In early 2023, we surveyed the abundance of *M. soledadinus* and *T. antarcticus* across habitats and elevations in and around their most recently documented range on the north-east coast of South Georgia. Combining repeated sampling and N-mixture models made it possible to disentangle processes underlying patterns in the detection

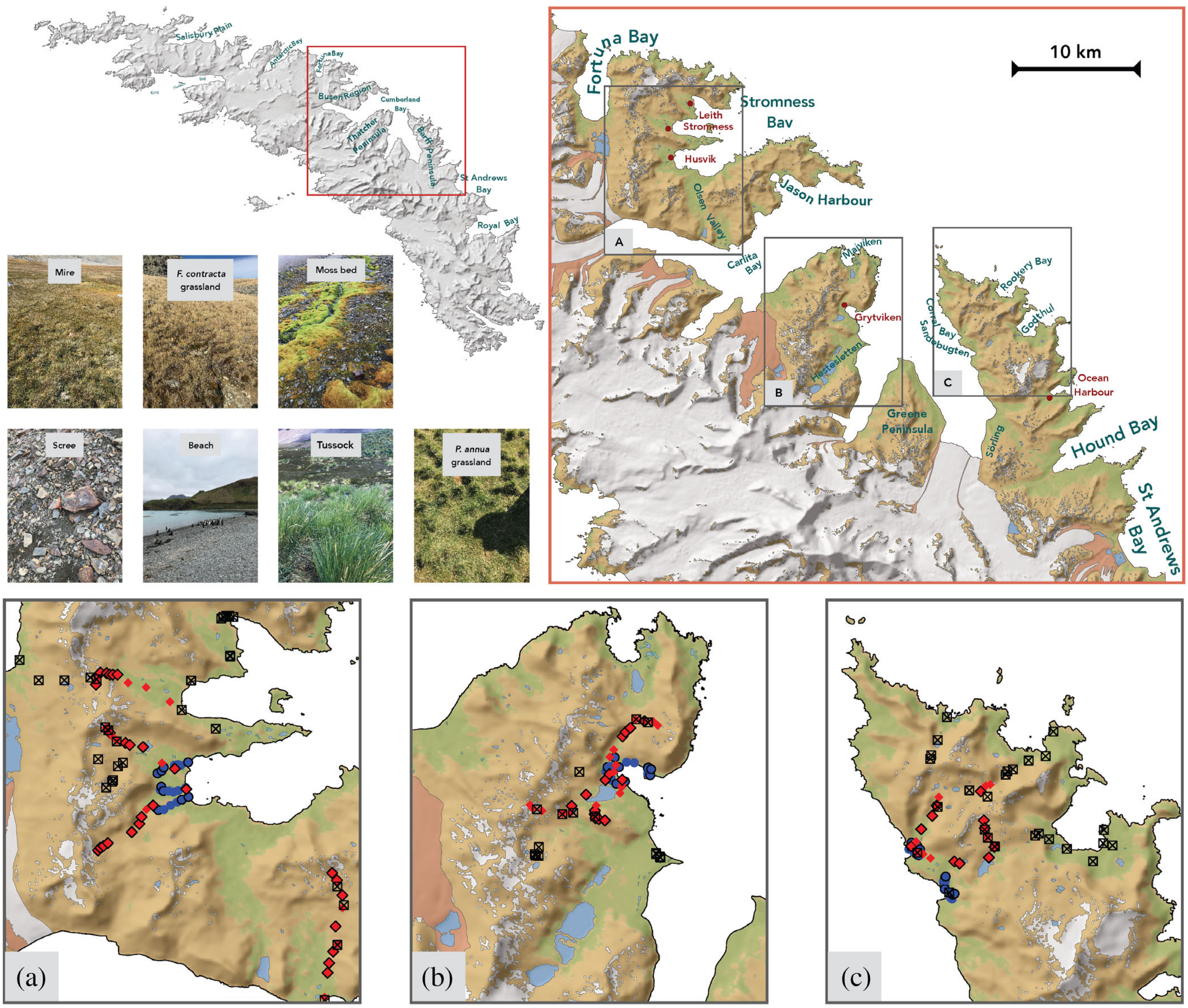

FIGURE 1 *Top left*: Topological map of South Georgia with the surveyed area (red rectangle). *Top right*: Topological and habitat type map of the central north-eastern coast where carabid presence and abundance were systematically surveyed within three regions (grey rectangles) in January–February 2023. *Bottom:* Details of sampling locations in the three regions: Fortuna Bay to Busen Peninsula (a), Thatcher Peninsula (b), Barff Peninsula (c). Systematic sampling was performed with pitfall traps along elevation (red diamonds) and habitat (blue circles) transects, and with quantitative hand searches when possible (black outline). Opportunistic sampling was performed only with quantitative hand searches (black crossed squares).

probability and the abundance of these easily concealed beetles. Our aims were to

1. reveal changes in the geographical distribution of the species 10–15 years after the most recent available observational data (*geographical extent*)
2. confirm whether carabids have expanded from lowland coastal areas to higher elevation (*elevation range*)
3. understand if carabids are more abundant in some habitats than others (*habitat association*)
4. explore the impact of carabid species on each other and on native communities (*Effects of carabids on invasive and native invertebrates*).
5. quantify the ability of two survey methods to detect carabids as a function of habitat and sampling effort (*optimal sampling*)

MATERIALS AND METHODS

Data collection and study area

To achieve our scientific aims, we conducted a field study on the north-east coast of South Georgia between 23 January and 29 February 2023 (Figure 1). We also aggregated quantitative and non-quantitative data from various sampling events that occurred between 2015 and

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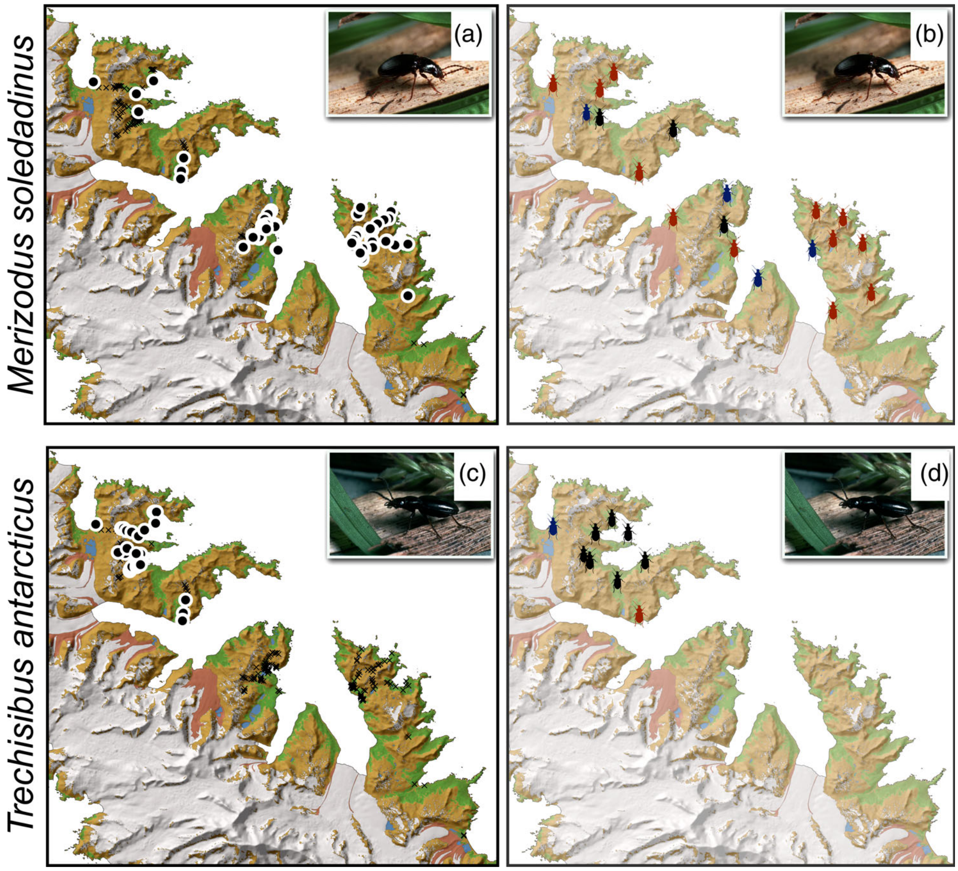

FIGURE 2 Presence/absence (a) and expansion of *M. soledadinus* (b) and presence/absence (c) and expansion of *T. antarcticus* (d) on the north-east coast of South Georgia. (a, c) Points represent sampling locations at which the species was found during opportunistic or systematic surveys in 2023, while small black crosses represent observed absences. (b, d) Approximate spatial occurrences of the beetles prior to 2000 (black), from 2006 to 2009 (blue), from 2015 to 2023 (orange, based predominantly on the present survey). Credit for the carabid pictures: British Antarctic Survey (BAS).

2023 to generate the most up-to-date distribution of South Georgia's introduced invertebrates, including the two carabids.

Our study consisted of repeated surveys of the presence and numbers of non-native carabid beetles and co-occurring invertebrates and plants at 227 sampling locations (Figure 1, Table 1). We focused the search effort on three areas separated by tidewater glaciers where the carabids have previously been reported: the Fortuna Bay to Busen Peninsula region, the Thatcher Peninsula and the Barff Peninsula. We combined systematic surveys, where sampling locations ($n = 184$) were pre-determined along elevation and habitat transects, with opportunistic surveys, where sampling locations ($n = 43$) were directly assigned in the field. Systematic surveys contributed to addressing all our study aims, while opportunistic surveys specifically allowed us to refine the carabids' distributions. We used pitfall traps and quantitative hand searches for systematic surveys, and only quantitative hand searches for opportunistic surveys, such that sampling effort was always quantifiable in the data that we collected.

Systematic surveys along elevation transects

We used systematic surveys along elevation transects to reveal how the abundance of beetles varied with elevation. An elevation transect typically consisted of 10 sampling locations distributed at regular elevations (every 30 ± 10 m) from the coast to the top of a valley (typically about 300 m above sea level (a.s.l.), Figure 1, Table 1). Note that, while sampling locations along elevation transects were randomly assigned, once on site, we sampled the more vegetated areas that were likely more favourable to carabids. This was to prevent all the higher elevation sampling points being located in scree and fellfield habitats that overwhelmingly cover ice-free areas above about 100 m a.s.l on South Georgia (Government of South Georgia & the South Sandwich Islands, 2022b). Therefore, our data allow the effects of elevation on carabids *given the presence of* a favourable habitat to be revealed. We completed nine elevation transects across the study area.

We used two sampling methods during systematic surveys of carabids and other ground-dwelling invertebrates along elevation transects: pitfall trapping and quantitative hand searching under stones. Replicated measurements are necessary to disentangle true absence from imperfect detection in occupancy and N-mixture abundance models (Kellner & Swihart, 2014). To achieve this, three pitfall traps were placed at each sampling location, at the edges of an equilateral triangle with sides of 1 m and approximately centred around the location. In parallel, 10 stones were turned during a hand search. Stones varied in size from about 10–80 cm in diameter. In a few cases,

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TABLE 1 Numbers of sampling points at geographic sites by sampling method. Note that some quantitative hand searches and captures with pitfall traps were carried out at the same sampling location.

	Site	Type	Year	Sampling locations	Quantitative hand search	Pitfall trap	Other method
Barff Peninsula	Corral Bay	Habitat transect	2023	14	6	14	-
	Godthul	Opportunistic	2023	8	8	-	-
	Lurcock Lake	Opportunistic	2023	4	4	-	-
	Reindeer Valley	Elevation transect	2023	13	9	10	-
	Rookery Bay	Opportunistic	2023	6	6	-	-
	Sandebugten	Habitat transect	2023	14	7	13	-
	Whittamore Pass	Elevation transect	2023	12	8	9	-
Fortuna Bay to Busen Region	Carlita Valley	Elevation transect	2023	14	11	10	-
	Fortuna Bay	Opportunistic	2023	4	4	-	-
	Husdal	Elevation transect	2023	10	9	10	-
	Husvik	Habitat transect	2023	27	15	21	-
	Karakkatta Valley	Elevation transect	2023	13	8	10	-
	Leith	Opportunistic	2023	7	7	-	-
	Shackleton Valley	Elevation transect	2023	11	7	10	-
	Stromness	Opportunistic	2023	1	1	-	-
Thatcher Peninsula	Brown Mountain	Elevation transect	2023	11	7	10	-
	Deadmans Cairn	Elevation transect	2023	12	6	10	-
	Echo Pass	Elevation transect	2023	12	6	10	-
	Glacier Col	Opportunistic	2023	4	4	-	-
	Grytviken	Habitat transect	2023	21	10	21	-
	Hestesletten	Opportunistic	2023	4	4	-	-
	Hodges Bowl	Opportunistic	2023	1	1	-	-
Salisbury plain		Additional	2023	4	4	-	-
King Haakon Bay		Additional	2023	>10	-	-	Non-quantitative hand searches (>10)
Hound Bay		Additional	2023	2	-	-	2 hand searches targeted at carabids
St Andrews Bay		Citizen science	2022	3	3	-	-
South Georgia		Additional	2015	89	-	-	89 Tullgren funnels

the number of replicates at each location was not achieved; for example when one pitfall trap was destroyed by wildlife or when few stones were present at a given sampling location. These differences in sampling effort were taken into account in the statistical analysis. Locations were typically sampled with both pitfall trapping and hand searching, allowing for a comparison of their efficiency. When hand searches were not possible at the exact assigned location; for example when no stones of a manageable size could be turned, an additional sampling location was randomly chosen in a neighbouring area (within <50 m) at the same elevation.

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Pitfall traps consisted of 250-ml plastic beakers half-filled with ethanol (96%) and buried with the rim at ground level. The traps were collected after being deployed for approximately 72 h. During hand searches, the types and numbers of invertebrates observed under randomly selected stones within 4 m of the sampling location were recorded. To limit biases, all hand searching observations and taxonomic identifications were performed by the same observer. When possible, invertebrates present under stones were preserved in ethanol to allow accurate taxonomic identification.

Systematic surveys along habitat transects

We surveyed the abundance of beetles in different habitats. Sampling locations were systematically distributed across seven habitat types in coastal lowlands (<65 m a.s.l., Figure 1), identified prior to the surveys based on geomorphology and vegetation composition and structure: *(1)* beaches consisting of pebbles and little or no vegetation, *(2)* mires dominated by rushes such as *Rostkovia magellanica*, *(3)* grasslands dominated by the native *Festuca contracta*, *(4)* moss beds along ponds and streams, *(5)* grasslands dominated by the invasive grass *Poa annua*, *(6)* screes and fellfields with little or no vegetation and *(7)* tussock grasslands dominated by *P. flabellata*. Habitat sampling was replicated two to four times in four bays (Figure 1, Table 1). Sampling locations of the same habitat type within each bay were deliberately spaced to avoid spatial clustering.

Locations were typically sampled with both pitfall trapping and hand searching, allowing for a comparison of their efficiency. When hand searches were not possible at the exact assigned location, for example when no stones of a manageable size could be turned, an additional sampling location was randomly chosen in a neighbouring area (within <50 m) in the same habitat.

Opportunistic surveys

To map the current distribution extent of carabids, we targeted sampling around the suspected distribution edges or when revisiting locations previously surveyed between 2002 and 2009 (Convey et al., 2011). These opportunistic surveys consisted only of quantitative hand searches. We used the same hand searching protocol as in systematic surveys.

Sample processing and vegetation

All sampled invertebrates except Acari and other micro-invertebrates were identified to genus or species level under a microscope using the available literature (Enderlein, 1912; Hendel, 1937; Gressitt, 1970; Convey et al., 1999; Kits, 2011). The two carabids, *M. soledadinus* and *T. antarcticus*, were distinguished using characters listed in Convey et al. (2011); in particular, the smaller size, deeply sinuated thorax and deep frontal furrows of *T. antarcticus* compared to *M. soledadinus*. Identification confidence for each taxon was categorised as 'possible', 'probable' or 'certain', but only the two latter categories were included in the statistical analyses (see Tichit et al., 2026 for the original invertebrate dataset).

To characterise the associated vegetation during habitat surveys and elevation transects, the cover of vascular plant species, mosses, lichens and bare substrate at each sampling location was estimated within a 4×4 m quadrat using a Braun-Blanquet scale (Tichit et al., 2026).

Additional sampling

We also aggregated data from various additional sampling events to generate the most up-to-date distribution of South Georgia's introduced invertebrates, including the two carabids. In February 2023, we conducted a small number of opportunistic hand searches under stones at Salisbury Plain, following the same protocol as described above, in an area that has never been impacted by the carabids (Figure 1). An invertebrate survey using Tullgren funnels was carried out in 2015 by the Government of South Georgia and the South Sandwich Islands (GSGSSI) at various locations on the north-eastern coast of the island. This material was briefly examined to assess the presence of carabids (Tichit et al., 2026). We included published carabid occurrences in glacial forelands established with pitfall traps and quantitative hand searches in 2022 (Tichit et al., 2024). In St Andrews Bay, cruise passengers coordinated by the Polar Citizen Science Collective performed quantitative hand searches in November 2022. Quantified hand searches specifically targeted to assess the presence of carabids were carried out by the plant eradication team in Hound Bay in February 2023. Intensive hand searching without estimation of sampling effort in coastal vegetated habitats was undertaken for half a day during a landing at King Haakon Bay in March 2023 by co-authors Convey and Contador, along with other confirmatory records of non-native invertebrate presence in the Stromness valley and around Grytviken whaling station.

N-mixture models

All statistical analyses were performed in *R* (R Core Team, 2024). The longitude and latitude of sampling points were projected in the WGS 84/South Georgia Lambert coordinate system, while the elevation was extracted from the Copernicus Global Digital Elevation Model (European Space Agency, 2024).

To study the influence of sampling method, elevation and habitat on the recording of the carabids, beetle counts obtained during systematic surveys were modelled with hierarchical N-mixture models using Bayesian inference with function *stan-pcount* from the *Stan*-based package *ubms* (Kellner et al., 2022; Stan Development Team, 2024). These models enable processes underlying the abundance and detection of individuals in count data to be disentangled, thus taking into account imperfect detection. In N-mixture models,

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the response variable was the number of individuals of each carabid species observed during elevation transect and habitat surveys. For *M. soledadinus*, we used all systematic surveys across the three study regions (Figure 1, $n = 184$), while for *T. antarcticus*, we ran models restricted to the Fortuna Bay-Busen Peninsula region where the species occurs ($n = 74$). We assessed the capture method as a predictor of the probability of detection of carabids, while habitat and scaled elevation were covariates of the true abundance. To take spatial autocorrelation between neighbouring sampling points into account, the random effect was modelled using three spatial thresholds of 100, 1000 and 10,000 m for *M. soledadinus* (10, 50 and 100 m for *T. antarcticus*). The predictive performance of each spatial model was compared to a non-spatial null model using the expected log pointwise predictive density (Vehtari et al., 2017). For both species, the spatial RSR models with the intermediate threshold (1000 m for *M. soledadinus*, 50 m for *T. antarcticus*) had highest predictive power and were retained in the analysis (Table S1). Models were run using three chains for 3000 iterations (including 1500 burn-in). Default weakly informative priors were used and the integer upper index of integration, *K*, was set to 30. To verify that the models converged towards reliable predictions, traces of the sampling behaviour of predictors were scrutinised, and the distribution of Pareto *k* diagnostic values was drawn (Tichit et al., 2026). When not otherwise specified, mean estimates are given with a Bayesian 95% credible interval within brackets.

To investigate if the presence of one carabid species was associated with a lower abundance of the other, the same N-mixture modelling procedure was repeated to model *T. antarcticus* counts from the area ranging from Fortuna Bay to the Busen Peninsula region, where both species are present ($n = 74$ locations). Model covariates now included the observed presence of *M. soledadinus* and a restricted spatial regression with smaller thresholds of 10, 50 and 100 m. As previously, the predictive performance of spatial models was assessed in comparison to a non-spatial null model (the abundance of *T. antarcticus* was best modelled with the intermediate threshold of 50 m) and the performance gain from including the presence of *M. soledadinus* as a covariate was estimated by comparing models with and without this added factor.

To investigate whether the presence of carabids was associated with a lower abundance of four common native invertebrates, the same N-mixture modelling procedure was repeated across the study area for four native species. The two endemic herbivorous Promecheilidae beetles, *Perimylops antarcticus* and *Hydromedion sparsutum*, are probably preyed upon by carabids (Ernsting et al., 1995); but *P. antarcticus*, primarily found in more barren habitats at higher elevations, may be less exposed to predation than the coastal *H. sparsutum*. We also included the Acanthodrilidae earthworm *Microscolex* sp. (we did not distinguish between *M. georgianus* and *M. anderssoni*). This soft-bodied and ground-dwelling invertebrate is abundant in coastal habitats and may be a suitable prey item for carabids (especially young instars). The procedure was applied to the most common species of linyphiid spider on South Georgia, *Notiomaso australis*, that may compete with carabids for some smaller prey. These models included the observed presence of *M. soledadinus* as an explanatory variable. As previously, the predictive performance of spatial models was assessed in comparison to a non-spatial null model, and the performance gain from including the presence of *M. soledadinus* as a covariate was estimated by comparing models with and without this added factor.

Detection probability and sampling effort

N-mixture models allowed prediction of the probability (p_{det}) of detecting one carabid under one stone (for hand searches) or in one trap (for pitfall traps). When taking into account the replication level, *R* (typically 10 for hand searches and 3 for pitfall traps), the probability of detecting at least one beetle (i.e. to detect the species' occurrence) given the sampling effort is $p = 1 - \left((1 - p_{det})^N\right)^R$, where *N* is the predicted beetle abundance. This probability can be calculated across habitats (by setting *N* to the average predicted abundance of a species) or in any specific habitat.

RESULTS

Geographical extent

Merizodus soledadinus and *T. antarcticus* were observed, respectively, at 33% and 14% of the 227 sampled locations on South Georgia. We found up to 16 individuals of *M. soledadinus* and 8 of *T. antarcticus* under a single stone during hand searches, while the maximum number of beetles in one pitfall trap was 12 and 7, respectively. Confirming the conclusion of the last available survey (Convey et al., 2011), *T. antarcticus* was only observed in the area ranging from Fortuna Bay to the Busen Peninsula region, while *M. soledadinus* was also present on the Thatcher and Barff Peninsulas (Figure 2a,b). However, our new data extend the known distributions of both species. In the Busen Peninsula region, *T. antarcticus* was found for the first time in Carlita Bay and *M. soledadinus* was observed for the first time in Fortuna Bay, Leith Harbour, Stromness and Carlita Bay. On Thatcher Peninsula, *M. soledadinus* was recorded at Hestesletten. On Barff Peninsula, *M. soledadinus* is now present at numerous locations, including near Lurcock Lake, in Reindeer Valley, Rookery Bay, Godthul and close to Ocean Harbour. In 2015, it was already present at Sörling Valley. Hand searches at Hound Bay in 2023 (>6 stones at $n = 2$ locations) and St Andrews Bay in 2022 (15 stones at $n = 3$ locations) did not reveal the presence of carabids, and none were reported despite intensive hand searches at Salisbury Plain and King Haakon Bay in 2023.

Elevation range

The survey recorded both *T. antarcticus* and *M. soledadinus* from considerably higher altitudes than previously reported on South Georgia,

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from sea level to maximum elevations of 289 m and 314 m a.s.l., respectively (Figure 3a). To assess how the abundance of the carabids changed with elevation, we modelled the probability of detection (p_{det}) and the abundance of the two species using N-mixture models based on counts from hand searches and pitfall traps obtained during elevation transects and habitat surveys within the distribution range of *M. soledadinus* ($n = 184$ sampled locations) and of *T. antarcticus* ($n = 74$ sampled locations). There was a negative effect of elevation on the predicted abundance of *M. soledadinus* (mean estimate [Bayesian 95% credible interval]: −0.9 [−1.5, −0.5]) but not of *T. antarcticus* (−0.1 [−0.6, 0.3], Figure 3b,c, Table S2). Note that, above 65 m a.s.l, the latter corresponds to the effect of elevation in favourable vegetated habitat (typically river and moss bed).

Habitat association

These models also predicted different abundances of both species depending on habitat (Figure 4, Table S2). The predicted abundance of *M. soledadinus* was lowest on beaches (−2.6 [−3.9, −1.4]) (Figure 4a). Scree (−0.1 [−1.3, 1.2]), mires (1.7 [0.6, 2.9]), *Festuca contracta* grasslands (1.9 [0.9, 3.1]) and moss beds (2.2 [1.1, 3.4]) had a moderate positive effect on the predicted abundance. There was a strong positive relationship between the abundance of *M. soledadinus* and *P. annua* (2.9 [1.9, 4.0]) and tussock grasslands (3.7 [2.4, 4.5]). Tussock grasslands (3.0 [1.4, 4.7]), mires (3.0 [1.5, 4.8]) and *F. contracta* grasslands (2.8 [1.3, 4.5]) had a positive effect on the predicted abundance of *T. antarcticus* (Figure 4b).

Effects of carabids on invasive and native invertebrates

To investigate possible effects of the co-occurrence of the two carabid species, we built an N-mixture model restricted to the Fortuna Bay-Busen Peninsula region. Including the observed presence of *M. soledadinus* as an explanatory variable to this model did not improve its quality (Table S1), but there was a negative effect of the observed presence of *M. soledadinus* on the predicted abundance of *T. antarcticus* (−1.4 [−2.5, −0.5]), (Figure 5).

In our N-mixture models of four common native invertebrates, we found clear effects of sampling method on detection probability and of elevation and habitat on abundance, but there were no negative relationships between the predicted abundance of native

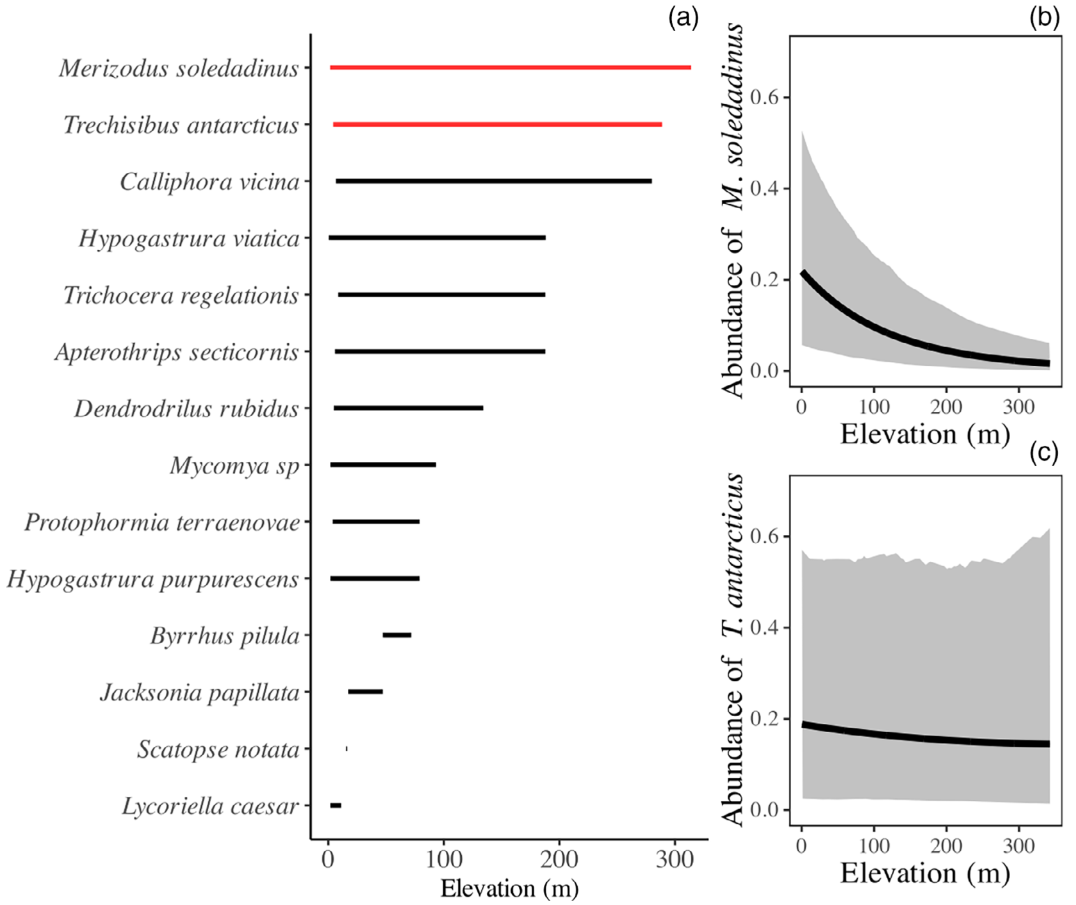

FIGURE 3 Elevation ranges of the two carabids (red) and of 12 other non-native invertebrates (black) found in this study (a). Effect of elevation on the abundance of carabids predicted with Bayesian N-mixture models (b-c). Black lines are the estimated mean effects and grey areas represent the 95% credible intervals.

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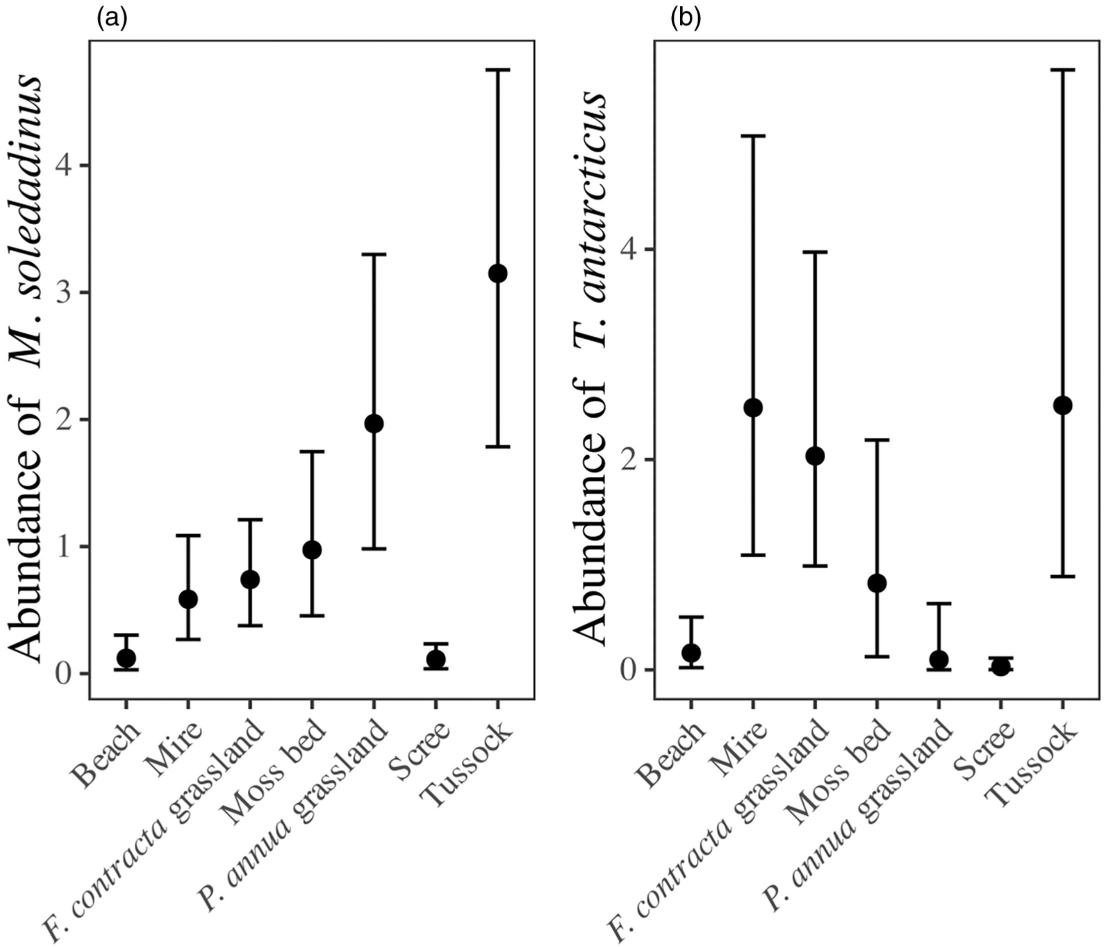

FIGURE 4 Effect of habitat on the abundance of *M. soledadinus* (a) and *T. antarcticus* (b) predicted with Bayesian N-mixture models. Black points are the estimated mean effects and intervals represent the 95% credible intervals.

invertebrates and the observed presence of *M. soledadinus* (Figure S2). Note that all the sampling locations included in the models were within the invaded range of at least one carabid species. On Salisbury Plain, the only quantitatively surveyed site that is beyond these ranges, an average of 1.9 (min = 0, max = 12) individuals of *H. sparsutum* per stone were found in *P. annua* grassland ($n = 16$ stones), while 0.1 (min = 0, max = 3) individuals of these species were found in the same habitat in the invaded range ($n = 83$ stones). Likewise, 0.3 (min = 0, max = 2) native staphylinid beetles (*Halmaeusa atriceps* and *Crymus antarcticus*) per stone were found on Salisbury Plain, while none were observed in the invaded range.

Optimal sampling

The probability of detecting a carabid was higher in a pitfall trap than under a stone (Figure 6a,d). However, when combined with replication level (typically 10 stones were turned while three traps were deployed at each location), the probability of detecting the occurrence of *M. soledadinus* was slightly higher for hand searches (0.69) than for pitfall traps (0.50). The probability of detecting the presence of *T. antarcticus* remained slightly lower for hand searches (0.52) than for pitfall traps (0.71). To refine our understanding of the detection performance of hand searches and pitfall traps, we calculated the modelled probability of detecting at least one carabid for each habitat within the range of each species as a function of search effort (Figure 6b,c,e,f). For *M. soledadinus*, a low search effort in tussock and *P. annua* grasslands (<15 stones turned or <8 pitfall traps) was sufficient to reach near-perfect detection of occurrence (probability >0.95), whereas for *T. antarcticus*, a low search effort in tussock and mires (<20 stones turned or <4 pitfall traps) enabled near-perfect detection.

Other invasive invertebrates

This survey also provided new data on the communities of vascular plants and ground-dwelling invertebrates associated with carabids at the sampling locations. Twelve additional species of non-native invertebrates were observed (*Apterothrips secticornis*, *Byrrhus pilula*, *Mycomya* sp., *Protophormia terranovae*, *Calliphora vicina*, *Dendrodrilus rubidus (Syn: Bimastos rubidus)*, *Scatopse notata*, *Trichocera regelationis*,

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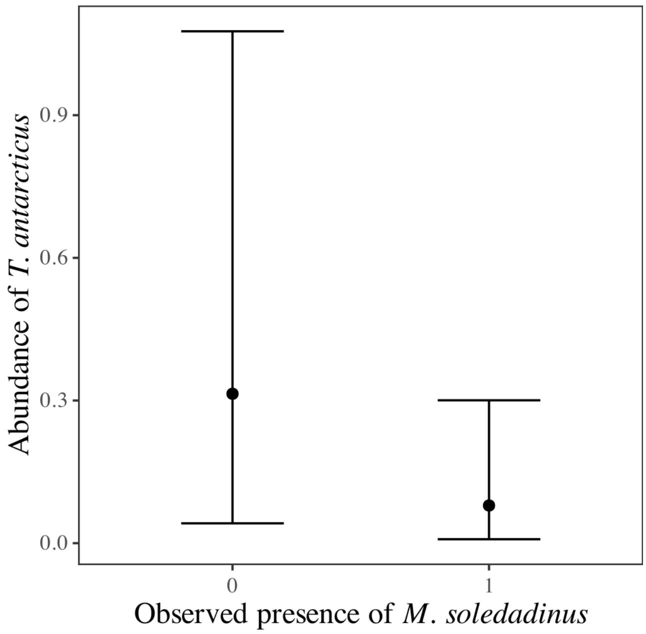

FIGURE 5 Effect of the observed presence/absence of *M. soledadinus* on the abundance of *T. antarcticus* predicted with Bayesian N-mixture models across their common range. Black points are the estimated mean effects and intervals represent the 95% credible intervals.

Hypogastrura purpurescens, *Hypogastrura viatica*, *Jacksonia papillate*, *Lycoriella caesar*), sometimes at locations not previously reported and information on their altitudinal ranges was recorded (Figures S1 and 3a). We documented a likely eastward expansion of the introduced springtail *H. purpurescens* on Barff Peninsula (cf. Greenslade & Convey, 2012). As with the two carabids, the following introduced invertebrates also seem to be colonising inland areas: *C. vicina*, *H. viatica*, *T. regelationis*, *A. secticornis*, *D. rubidus*. This is particularly notable for apparently poorly mobile species, such as the wingless thrips *A. secticornis* and the earthworm *D. rubidus* that were found at 188 and 134 m a.s.l., respectively.

DISCUSSION

We performed a systematic survey of the invasive carabids, *Merizodus soledadinus* and *Trechisibus antarcticus*, on South Georgia and modelled their abundances and underlying drivers using N-mixture models. Such fine-scale models explicitly estimate the ability to detect individuals, thereby informing about the efficiency of sampling methods (Christy et al., 2010; Della Rocca et al., 2020). In this study, we estimated the detection ability of two sampling methods. Although N-mixture models seem particularly suited for non-native species with elusive and heterogeneous distributions, this is to our knowledge the first time that these models have been applied to the study of introduced insects. Our research reveals that carabids have continued to expand their range on South Georgia over the past 10–15 years, including by colonising higher elevations. Carabid abundance was generally affected by elevation and differed between habitat types. We found some indications of a relationship between the presence of *M. soledadinus* and the abundance of *T. antarcticus* and native invertebrates where they co-occur. Here we discuss how these findings relate to the carabids' ecology, what they suggest about the future of the invasion and what they imply for local biosecurity and conservation.

Geographical extent

Trechisibus antarcticus was not found in Carlita Bay in 2006 (Convey et al., 2011), indicating a southward expansion of the species from the core of its distribution. The shortest path implies dispersal from the north-facing section of the Olsen Valley (Figure 1), where the species was already present, requiring a rate of about 200 m/year. The present study does not allow an assessment of whether the species has expanded farther east on Lewin Peninsula, nor westwards beyond the east side of Fortuna Bay, but it was not found further west in Salisbury Plain and King Haakon Bay.

Merizodus soledadinus has substantially expanded its distribution in the Fortuna Bay to Busen Region (Figures 1 and 2). The most parsimonious dispersal path implies a total distance of more than 8 km with a spread rate of about 600 m/year. From Husvik Bay, the species would have dispersed along the coast to reach Stromness Bay and Leith Harbour and then reached Fortuna Bay via the Shackleton Pass. This is surprising, given the high elevation of this Pass (288 m a.s.l.) separating Leith Harbour from Fortuna Bay and suggests that dispersal might have been facilitated by human activities on this popular hiking path (as may have been the case for *T. antarcticus* in the past, Convey et al., 2011). We cannot assess with precision the western limit of the species' ranges, other than their absence in Salisbury Plain and King Haakon Bay. *Merizodus soledadinus* was also found in Carlita Bay, which it may have colonised from Husvik Bay (as for *T. antarcticus*) or from a disjunct population in Jason Harbour. As predicted by Convey et al. (2011), *M. soledadinus* has continued to expand eastwards on Barff Peninsula since it was first reported in Corral Bay, with the species now occurring as far as Godthul and Ocean Harbour where it was not present in 2009. These sites are located about 4.5 and 8 km from Corral Bay but are separated by a mountain range. Assuming dispersal along the coast of the Barff Peninsula from the closest known occurrence in Corral Bay, *M. soledadinus* would have spread at 1–2 km/year. The species does not yet appear to have reached Hound Bay and St Andrews Bay further to the east, but more detailed investigations are required in these areas that were only briefly accessed in this study. In the future, there seems to be no limitation to the continued eastward expansion of *M. soledadinus* due to the lack of tidewater glaciers along the island's coastline as far east as Royal Bay. Using a conservative dispersal rate of 1 km/year along the coast, the species could reach Hound Bay, St Andrews Bay and Royal Bay in about 10, 20 and 40 years, respectively.

The dispersal rates of *M. soledadinus* are consistent with those reported on Îles Kerguelen where the species is also invasive

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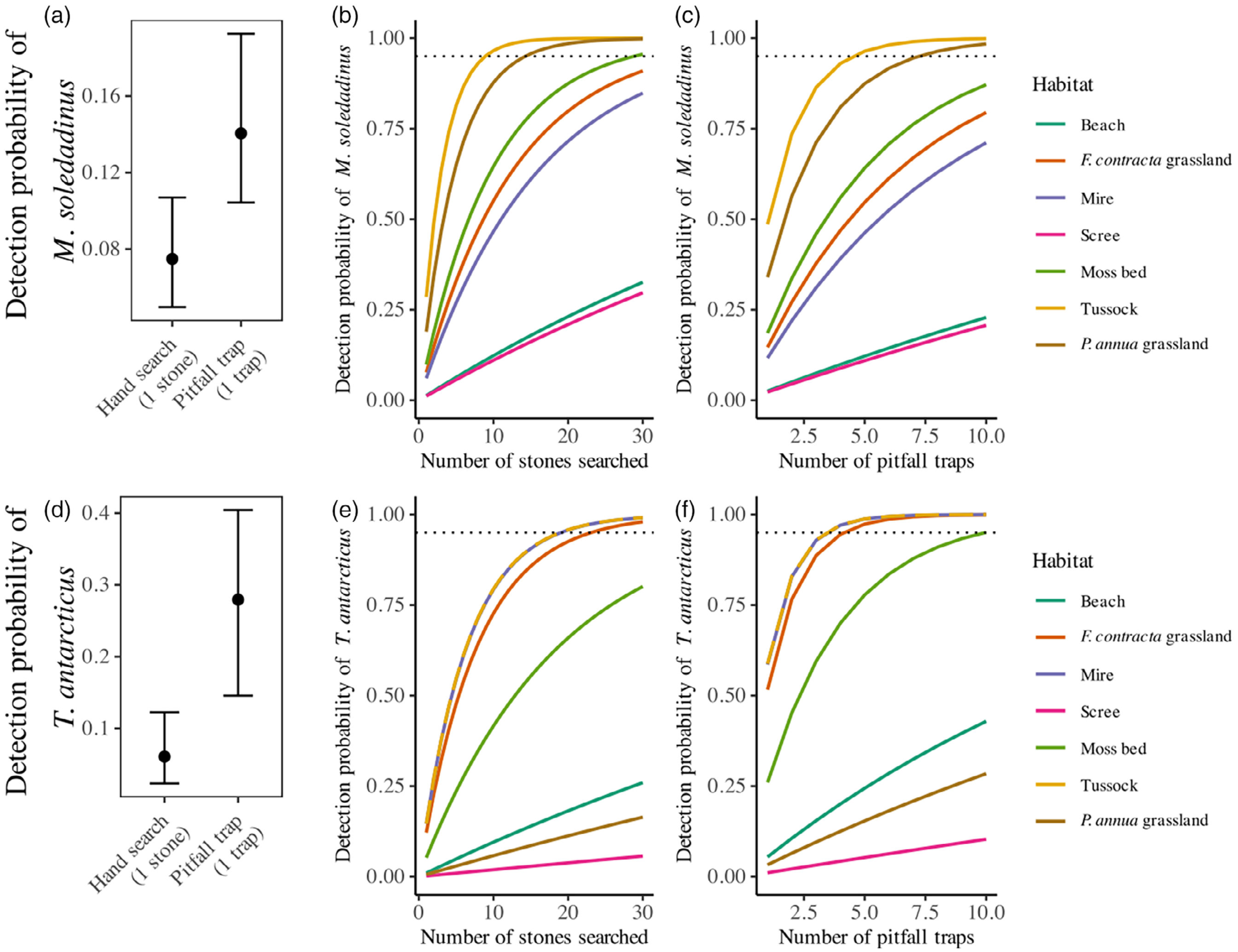

FIGURE 6 Effect of sampling method (hand searching under stones and pitfall traps) on the detection probability of *M.soledadinus* (a) and *T. antarcticus* (d) p_{det} predicted with Bayesian N-mixture models. Black points are the estimated mean effects and intervals represent the 95% credible intervals. Predicted probability p of detecting the occurrence of carabids in different habitats as a function of sampling effort for the hand searches (b, e) and pitfall traps (c, f).

(Lebouvier et al., 2020), but are low compared to other invasive Coleoptera at lower latitudes (median spread rate ≈ 20 km/year, Fahrner & Aukema, 2018). This may be because the two carabid species are flightless and have few opportunities to disperse via human infrastructure or activities that are currently scarce within South Georgia, although boat traffic to Corral Bay may have been the source of the invasion of Barff Peninsula (Convey et al., 2011). Furthermore, geographical barriers (permanent glaciers, mountains) likely restrict the dispersal of flightless insects on South Georgia compared to other regions.

The geographic range of *M. soledadinus* is about three times larger than that of *T. antarcticus*, which is constrained to the Fortuna to Busen Region by tidewater glaciers (Figures 1 and 2). This difference may be a legacy of the initial introduction of the species: *T. antarcticus* was only introduced to Husvik, while *M. soledadinus* was introduced to both Husvik and Grytviken. However, *M. soledadinus* has been able to overcome these barriers at least twice in recent decades (possibly aided by human transport) to invade Greene Peninsula and Barff Peninsula, when *T. antarcticus* has never been reported on, for example, Thatcher Peninsula. One reason for the high spread of *M. soledadinus* may be that the species seems able to disperse across the sea via floating objects such as seaweed or other debris (Renault, 2011). Another possibility is that the presence of *M. soledadinus* on Thatcher Peninsula decreases the chances for *T. antarcticus* to establish, which is supported by our finding that *T. antarcticus* is less abundant when *M. soledadinus* occurs.

Trechisibus antarcticus showed a rapid spread from Husvik into adjacent bays only a decade from its introduction in the 1980s, while the expansion of *M. soledadinus* was modest from its initial introduction locations in the 1960s to 1990s, and only really accelerated from the late 2000s (Convey et al., 2011). This acceleration might be explained by the release of physiological limitations in *M. soledadinus* with local warming on South Georgia.

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Elevation range

It is particularly notable that both carabids, originally introduced to and reported in coastal lowlands of South Georgia (*M. soledadinus* was originally not found above 150 m (Darlington, 1970)), are now detected more than 300 m a.s.l on this island (Figure 3). In favourable vegetated habitat, *M. soledadinus* became less abundant with increasing elevation, while *T. antarcticus* showed no significant decline, suggesting that *T. antarcticus* may have a higher capacity than *M. soledadinus* to survive lower temperatures and to disperse at high elevation. However, when considering that vegetated habitat becomes scarce with increasing elevation where it is restricted to the vicinity of streams and water bodies, both species likely become less abundant in the overall landscape with increasing altitudes. In *M. soledadinus*, this trend may be due to enhanced physiological constraints (decreasing temperature and moisture) and decreasing prey availability with increasing elevation (Ouisse et al., 2016, 2020).

On Îles Kerguelen, *M. soledadinus* increased its altitudinal occurrence from about 100 m to 350 m a.s.l. between the mid-1990s and 2005 (Lebouvier et al., 2020), probably due to habitats at higher elevation becoming increasingly suitable with local warming (Ouisse et al., 2020). On South Georgia, there are no baseline inventories in inland areas to test if the timing of inland expansion is similar, but both carabids have undoubtedly spread to higher elevations since their introduction near whaling stations along the coast.

Habitat association

Both carabids were most strongly associated with highly vegetated and productive habitats (Figure 4). *Merizodus soledadinus* was more abundant in *P. annua* and tussock grasslands and, to a lesser extent, in mires, *Festuca* grasslands and moss beds, while *T. antarcticus* was more abundant in tussocks and mires. Rocky habitats with little vegetation (scree and beach) were least favourable for both species, but they still occurred in these suboptimal habitats, leaving no pristine refuges for prey invertebrates. *Merizodus soledadinus* also occurs across multiple habitat types on Îles Kerguelen, where its habitat association is constrained by the availability of prey and relative humidity (Ouisse et al., 2016; Renault et al., 2015). In laboratory experiments, *M. soledadinus* and *T. antarcticus* sampled on South Georgia were both sensitive to desiccation (Ouisse et al., 2016; Todd & Block, 1997). Consistent with these previous studies, it is likely that both species in our survey are thriving in tussock grassland and other vegetated habitats because of their high moisture and food availability but are less abundant in scree and beach habitats where prey are limited or moisture is low.

The habitat association of the carabids suggests that vegetated habitats can act as a corridor that facilitates their spread, as is the case for other invasive insects (Resasco et al., 2014). Tussock grassland is widespread in coastal lowlands on South Georgia (Government of South Georgia & South Sandwich Islands, 2022b) and can likely facilitate further expansion of the beetles. The association of *M. soledadinus* with *Poa annua* grassland may facilitate its dispersal in coastal areas, although this may not apply to *T. antarcticus*, which was rare in *P. annua* grasslands in our study. *Poa annua* and *P. flabellata* grasslands often host high densities of seals and seabirds that may further assist the dispersal of carabids by carrying substrate and fertilising vegetation (Convey & Hughes, 2022). Our data also indicate that the carabids can disperse towards higher elevations along valleys, where they probably rely on narrow corridors of favourable habitat, such as *Festuca* grasslands and moss beds along streams. Inland valleys may provide shortcuts that accelerate the expansion of the carabids. For example, the likely dispersal of *M. soledadinus* from Corral Bay to Godthul would have required a yearly expansion of about 250 m through Reindeer Valley, rather than about 1 km/year along the coast, as estimated above. Biological invasions can be amplified through interactions with a changing and heterogeneous landscape and climate change (O'Reilly-Nugent et al., 2016). Furthermore, the likely future encroachment of vegetation towards higher elevations on South Georgia would provide additional favourable habitat and dispersal corridors that may accelerate the expansion of the carabids. This may, in turn, increase the predation pressure on native species that are associated with higher altitudes, such as the native beetle *Perimylops antarcticus*. We do not fully understand how expanding vegetation itself will impact native invertebrate populations, so long-term monitoring is required to reveal the combined impacts of carabid predation and advancing vegetation on native invertebrate abundance.

Effects of carabids on invasive and native invertebrates

Notably, our analyses suggest that *T. antarcticus* becomes less abundant in the presence of *M. soledadinus* where their ranges overlap (Figure 5). This correlation might reflect a negative interaction between the two ground-dwelling predators, which could be due to direct predation between the two species or competition for limited prey (Crowder & Snyder, 2010).

On Îles Kerguelen, *M. soledadinus* presence has likely caused the local extinction of native arthropods (Lebouvier et al., 2020). On South Georgia, however, we identified no negative correlation between the observed presence of *M. soledadinus* and the abundance of four common native invertebrates. This difference in impact may be because abundances of *M. soledadinus* were typically much lower on South Georgia than on Îles Kerguelen, where there were sometimes more than 100 individuals under one stone (Lebouvier et al., 2020). This higher carabid density could be explained by a higher prey availability or by the warmer and more favourable local climate on Îles Kerguelen, supporting the idea that temperature has been an important limitation for the expansion of *M. soledadinus* on South Georgia. The earlier introduction on Îles Kerguelen may also play a role, suggesting that future densities of *M. soledadinus* on South Georgia could resemble those currently present on Îles Kerguelen (Lebouvier et al., 2020). Direct comparative studies would be very

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valuable to understand differences in invasion trajectories between Îles Kerguelen and South Georgia.

Another factor that may explain the lack of apparent impact of carabids in our study is that nearly all inventoried native communities are within the range of one or both species of carabids and have thus already been exposed to predation pressure. The only survey site that has never experienced any impact from carabids and can be used as a pristine reference is Salisbury Plain. Opportunistic hand searches in *P. annua* grassland at this location yielded high numbers of the endemic beetle *H. sparsutum* (a known prey of *T. antarcticus*) and of native staphylinid beetles. In contrast, *H. sparsutum* was rare in *P. annua* grassland in the invaded range and staphylinid beetles were not found despite our high sampling effort. Previous research demonstrated that *T. antarcticus* has a negative impact on *H. sparsutum* (Ernsting et al., 1995), while a lack of co-occurrence between staphylinid beetles and carabids was also reported in Convey et al. (2011), suggesting that the latter are also negatively impacted by the carabids. The scarcity of *H. sparsutum* in *P. annua* grasslands in the carabids' invaded range may be a combined effect of opposing pressures, predation by carabids that preferentially target small individuals (Ernsting et al., 1995) and the poor nutritional value of *P. annua* that limits body size (Chown & Block, 1997). Future investigations should compare sites within and beyond the invaded ranges of carabids to thoroughly quantify their impact on native communities.

Merizodus soledadinus from Îles Kerguelen can prey on a wide range of macro-arthropods, including the endemic wingless fly *Anatalanta aptera* (Daly & Renault, 2025; Lebouvier et al., 2020). On South Georgia, the diet of *M. soledadinus* is unknown. Investigating the key food sources of *M. soledadinus* and *T. antarcticus*, for example through gut content metabarcoding or prey choice experiments, would enable identification of which native species are likely to be impacted by carabids. If the diet of carabids on South Georgia is as flexible as on Îles Kerguelen, they may be able, once a preferred prey is depleted, to switch to other native invertebrates, further endangering the fragile communities of the island.

Optimal sampling

We estimated the probability of detecting carabids depending on survey method and predicted the chances of detecting each species as a function of habitat and sampling effort (Figure 6). This information is key to improving the monitoring of invasive carabids on South Georgia (Christy et al., 2010). The same approach would also be valuable to optimise monitoring in wider invasion contexts where species are concealed and fieldwork capacities are limited, such as other sub-Antarctic islands, the Antarctic Peninsula, polar regions and mountain areas. Our models indicate that surveying *M. soledadinus* with hand searches at low elevation under about 15 stones in *P. flabellata* tussocks or *P. annua* grasslands is sufficient to confirm presence/absence with more than 95% certainty. For *T. antarcticus*, survey effort should be slightly higher (>20 stones) and focus on coastal tussock grasslands and mires. *Poa annua* grasslands are not a favoured habitat for the latter species and should be avoided. Note, however, that beetle density may be particularly low close to the species' range limits, meaning that higher sampling effort would be required in those areas.

Implications for biosecurity and conservation

GSGSSI has implemented strict measures to protect the unique ecosystems of South Georgia (Government of South Georgia & the South Sandwich Islands, 2021, 2022c). However, there is no specific monitoring or management strategy in place for *M. soledadinus* and *T. antarcticus* despite the threats posed by the two carabids – and more generally by invasive invertebrates – on native communities of South Georgia (Black, 2022). We acknowledge that the survey of inconspicuous invertebrates in remote areas and, by extension, the implementation of control measures, is challenging. On the other hand, only through monitoring can we gather the information necessary to improve the management of invasive invertebrates and the conservation of native biota. With this study, we identify areas for future research, provide a basis for feasible and targeted monitoring and make recommendations for better biosecurity.

The impacts of carabids on South Georgia's terrestrial ecosystems are still largely unknown. Baseline inventories of ground-dwelling invertebrates in carabid-free sites are needed to assess the wider impacts of these invading insects on native communities. Obtaining quantitative inventories around suspected edges of the distribution (west of Fortuna Bay, Hound Bay and St Andrews Bay) would be particularly valuable to follow these impacts, as these areas will likely be reached by dispersing carabids in the near future, providing opportunities for Before and After Control Impact (BACI) surveys (Christie et al., 2020). The impacts of other introduced invertebrates also require further attention. For example, introduced earthworms may have considerable influence on soil properties, as is the case in other invaded ecosystems (Hendrix, 2006), and introduced Diptera (e.g. *Calliphora vicina*, *Lycoriella caesar*, *Trichocera regelationis*) may alter fundamental processes such as pollination and nutrient cycling (Bartlett et al., 2023; Convey et al., 2010). Many introduced invertebrates are also suitable prey for *M. soledadinus* and *T. antarcticus* and could further facilitate their invasion (Daly & Renault, 2025; O'Dowd et al., 2003).

A monitoring plan is important to document the evolution of the carabid invasion. Repeated surveys at accessible locations in the invaded range will detect changes in carabid abundance. Surveys at distribution edges will enable the following of the predicted spread of carabids and assessment of their impact. Hand searches under stones are a simple and effective quantitative method to monitor carabids and other invertebrates that can easily be performed by non-specialists. To maximise the efficiency of hand searches, our results demonstrate that turning >20 stones, preferentially in moist and densely vegetated habitats (e.g. tussocks, grasslands), and reporting the presence/absence of macro-invertebrates, is probably sufficient to assess the occurrence of carabids and to inventory the associated communities (see above). These surveys have real potential to be

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embedded within other operations on South Georgia (e.g. invasive plant control, building maintenance) or to involve tourist cruise passengers within a citizen-science context. However, the possible benefits of these activities for South Georgia conservation should be traded off with the biosecurity risks and negative environmental impacts that are inherent to (sub-)Antarctic tourism and other human activities around the island (Eijgelaar et al., 2010; Hughes et al., 2014).

Invasive insect monitoring on South Georgia would enable adaptive conservation and management actions. For example, the early detection of a small population of *T. antarcticus* on Busen Peninsula, or of either species west of Fortuna Glacier, will increase chances of successful local eradication with traps or chemical treatments. Robust biosecurity routines and activity restrictions must continue to be applied during terrestrial operations on South Georgia (Government of South Georgia & the South Sandwich Islands, 2022a) to minimise the risk of assisting the spread of carabid beetles, in particular for operations to and from the Fortuna Bay-Busen Peninsula region where *T. antarcticus* is currently restricted, as well as in St Andrews, Royal and Fortuna Bays. Invasive insect monitoring will be required to reassess and optimise these measures in the future.

AUTHOR CONTRIBUTIONS

Pierre Tichit: Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing; project administration; data curation; formal analysis. **Peter Convey:** Conceptualization; investigation; funding acquisition; methodology; writing – review and editing; project administration. **Paul Brickle:** Resources; conceptualization; investigation; funding acquisition; methodology; writing – review and editing; project administration. **Rosemary J. Newton:** Conceptualization; investigation; funding acquisition; methodology; writing – review and editing; project administration; resources. **Tamara Contador:** Investigation; writing – review and editing. **Wayne Dawson:** Conceptualization; investigation; funding acquisition; writing – original draft; methodology; writing – review and editing; formal analysis; project administration; supervision; resources.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The original datasets of invertebrate and plant communities, as well as the model quality checks used in this study are available at https://doi.org/10.5281/zenodo.18297670. Invertebrate samples are stored at the University of Liverpool.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1: Supporting Information

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