

Barriers to globally invasive species are weakening across the Antarctic

Grant A. Duffy  | Bernard W. T. Coetzee | Guillaume Latombe |
 Alexander H. Akerman | Melodie A. McGeoch | Steven L. Chown

School of Biological Sciences, Monash University, Clayton, Vic., Australia

Correspondence

Grant A. Duffy, School of Biological Sciences, Monash University, Clayton, Vic., Australia.
 Email: grant.duffy@monash.edu

Present addresses

Global Change Institute, University of the Witwatersrand, Johannesburg, South Africa and
 Organisation for Tropical Studies, Scientific Services, Kruger National Park, Mpumalanga, South Africa

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Abstract

Aim: Biological invasions are a substantial threat to Antarctic biodiversity and a priority conservation policy focus for Antarctic Treaty Parties and the sovereign states of surrounding islands. Key to their strategies is prevention, including assessment of establishment risk for alien species. Despite establishment of some of the worst globally invasive species across the Antarctic region, assessments of establishment potential of these species are non-existent. Here, we address this deficit and determine whether these invasive species constitute a significant conservation threat to the broader Antarctic region both now and in response to future regional climate change.

Location: Antarctica and the Southern Ocean islands (45°–90° S).

Methods: We used ensemble species distribution models to assess the current and future climate suitability of the Antarctic region for 69 of the worst globally invasive species and 24 insect and plant species that have already established somewhere in the region.

Results: The Antarctic continent is unsuitable for all of the worst globally invasive species under current conditions, but areas of the Antarctic Peninsula are predicted to become climatically suitable for up to six globally invasive species within the next century. By contrast, all Southern Ocean islands are presently climatically suitable for additional non-native species, with the threat increasing in the future.

Main conclusions: Our findings demonstrate that climate, which is often cited as a key barrier to alien species establishment, may afford some protection to continental Antarctica, but that this protection is not currently extended to the Southern Ocean islands. Furthermore, existing climatic barriers to alien species establishment will weaken as warming continues across the region. This not only illustrates the value of applying distribution modelling methods to this largely ice-covered region, but demonstrates how these methods can be used to inform targeted surveillance of introduction pathways and sites that have the highest risk of establishment of invasive alien species.

KEY WORDS

alien species, biological invasions, environmental niche, invasive species risk-assessment, species distribution modelling, sub-Antarctic Islands

1 | INTRODUCTION

Owing to its climate and geographic isolation, the Antarctic region has historically been afforded protection from biological invasions. This security has not, however, been absolute. Following the discovery of the continent and its surrounding islands, alien species have been introduced to the region both purposefully and accidentally (Frenot et al., 2005). Deliberate introductions of alien species to the Antarctic region are now unlikely, but accidental introductions, including intraregional transfer amongst islands and biogeographic regions (Hughes & Convey, 2010; Lee & Chown, 2011), remain a threat. Furthermore, the chance of accidental introductions is thought to be increasing because of both changing climates and increasing invasion pressure (Chown et al., 2012; Perttierra et al., 2016; Shaw, 2013).

Although the absolute number of recorded biological invasions to the Antarctic remains relatively low compared to trends globally (Hughes & Convey, 2010; McGeoch, Shaw, Terauds, Lee, & Chown, 2015), the region has proven susceptible to the ecological impacts of biological invasions when they have occurred (Courchamp, Chapuis, & Pascal, 2003; Frenot et al., 2005; Lebouvier et al., 2011). In consequence, biological invasions have been identified as one of the primary conservation risks of the broader Antarctic (Chown et al., 2012; Tin, Liggett, Maher, & Lamers, 2014). Accordingly, a suite of measures has been adopted, either to prevent the transfer to and establishment of alien species in the region, or to control or eradicate species that are already present (Shaw, 2013). Eradication attempts are, however, costly and, while often successful, may have unexpected effects on local systems (Bergstrom et al., 2009; Hughes, Perttierra, Molina-Montenegro, & Convey, 2015). Much focus is now therefore on preventative measures, which improve the detection of potentially invasive species and identify sites that are particularly at risk of alien species establishment (Committee for Environmental Protection, 2011; Hughes & Convey, 2012).

Species distribution models (SDMs) have proven useful for understanding the process of biological invasions and form an important component of risk assessments for them both now (e.g., Gallien, Douzet, Pratte, Zimmermann, & Thuiller, 2012; Jiménez-Valverde et al., 2011; Thuiller et al., 2005) and into the future as climates continue to change (Bellard et al., 2013; Petitpierre et al., 2016). Although potential drawbacks and pitfalls are associated with the use of SDMs (see Guillera-Arroita et al., 2015 for discussion), they provide an insightful, first-order means to assess the capability of alien species to establish in any given region. Such assessments can subsequently improve preventative measures through targeted monitoring for particular species (at areas of entrainment and/or arrival, and for particular vectors or paths) and/or surveillance of at-risk sites (e.g., Crall et al., 2013; Latombe et al., 2016; McGeoch et al., 2016).

Broad-scale SDM studies are, however, rarely undertaken for the largely ice-covered Antarctic region (Chown et al., 2012; Gutt et al., 2012; though see Hughes, Worland, Thorne, & Convey, 2012; Perttierra et al., 2016, 2017; for localized studies). Moreover, they

have not been applied to assessments of risk from the world's most significant invaders (IUCN, 2016), which include species that have not only established at sites across the broader Antarctic region, but in several cases have also had significant impacts where they have done so. These include, for example, black rat (*Rattus rattus*), house mouse (*Mus musculus*) and feral pig (*Sus scrofa*; Chapuis, Boussès, & Barnaud, 1994; Chimera, Coleman, & Parkes, 1995; Frenot et al., 2005; Wanless et al., 2009). Assessment of risks from these species, the impacts of which have also been forecast to grow with changing climates (e.g., Angel, Wanless, & Cooper, 2009), and information on which to build appropriate mitigation measures now and into the future are, as a result, unavailable. This situation contrasts strongly with that for the rest of the globe, where explicit assessments of the changing nature of threats from the world's worst invasive species have been made (Bellard et al., 2013). It also represents a significant evidence gap for the key conservation policy priority of the Antarctic Treaty Consultative Parties and the nations that manage the islands surrounding the continent (Berkman, Lang, Walton, & Young, 2011; Shaw, 2013).

Here, we provide explicit SDM-based assessments of establishment likelihood for the world's worst terrestrial invaders and a suite of cold-tolerant species that have already proven to be invasive to parts of the region. In doing so, we also demonstrate how currently available climate datasets can be used to achieve this goal, so illustrating the potential for adopting the approach for any suite of species. We do this through the expansion of broad-scale SDMs of globally invasive species (Bellard et al., 2013) to include the Antarctic continent and its surrounding islands. Although continued ice melt may expose new areas for colonization (Frenot, Gloaguen, & Trehen, 1997), land use for human purposes in the region is minimal, owing to the general absence of agriculture, industry and urbanization (Tin et al., 2014). We therefore apply SDMs using climatic data, which represent present-day and future conditions predicted under ongoing climate change (RCP8.5; Moss et al., 2010), rather than relying on the use of both climatic and land use data (Bellard et al., 2013).

2 | METHODS

2.1 | Species distribution data

2.1.1 | The world's worst terrestrial invaders

Following the assessment made by Bellard et al. (2013), the International Union for the Conservation of Nature (IUCN) list of 100 of the world's worst invasive alien species (Invasive Species Specialist Group of the International Union for Conservation of Nature, 2016), hereafter referred to as the 100 worst, was used to model globally invasive species. The list was constructed by the IUCN by including species based on an assessment of their ecological and socio-economic impacts. A single representative species was selected where multiple, closely related species had comparable impacts as invasive species, such that the 100 worst list spans a broad taxonomic range of

exemplar alien invasive species known to have significantly negative ecological impacts.

Marine and freshwater species on the 100 worst list were excluded from analyses. Nine species on the list (*Anoplophora glabripennis*, *Aphanomyces astaci*, *Batrachochytrium dendrobatidis*, *Bemisia tabaci*, Banana bunchy top virus and its primary vector *Pentalonia nigronervosa*, *Cinara cupressii*, *Coptotermes formosanus*, *Ligustrum robustum*, *Platydemus manokwari* and *Trogoderma granarium*) were excluded from distribution modelling because there were no or few recorded presence data available for these species. The mosquito, *Culex quinquefasciatus*, which is a primary host of the protozoan *Plasmodium relictum* (van Riper, van Riper, Goff, & Laird, 1986), was used in lieu of modelling the distribution of the parasite itself. *Cecropia peltata* records were combined with records of the congener *C. schreberiana*, and *Polygonum cuspidatum* was replaced with the synonym *Fallopia japonica*, as these species are considered species-complexes.

In total, 69 of the 100 species identified on the 100 worst list were used in our analyses (Table S1). Thirty-two plants, 12 invertebrates, 22 vertebrates, two fungi and one protist were used. These included widely known invaders, such as black wattle (*Acacia mearnsii*), common wasp (*Vespula vulgaris*) and black rat (*Rattus rattus*). Of the 69 species used, eight (*Capra hircus*, *Felis catus*, *Oryctolagus cuniculus*, *Mus musculus*, *Rattus rattus*, *Sturnus vulgaris*, *Sus scrofa*, *Ulex europaeus*) have already been introduced to at least one sub-Antarctic island, and two (*Mustela erminea*, *Rubus ellipticus*) are congeners of species that have been introduced or were the subject of introduction attempts (Headland, 2012; McGeoch et al., 2015).

2.1.2 | Cold-tolerant species

In addition to the 69 terrestrial species from the 100 worst list, 24 cold-tolerant insect and plant species were also modelled (Table S2). This species list was compiled from published lists of non-native plant (McGeoch et al., 2015) and insect (Chown & Convey, 2016) species that occur across the Antarctic region. These species were classified as cold-tolerant through virtue of their occurrence in the broader Antarctic region and are subsequently referred to as such. All selected species have been recorded within five or more Antarctic biogeographic regions. Although they met the criterion of being recorded from five or more biogeographic regions (Chown & Convey, 2016), the insects *Ptinus tectus*, *Hofmannophila pseudospretella* and *Endrosis sarcitrella* were excluded from analyses as they have only been recorded within sub-Antarctic human settlements or research bases. The insects *Jacksonia papillata*, *Myzus ascalonicus*, *Psychoda parthenogenetica* and *Apterothrips apteris* were also excluded from analyses as there were few occurrence records for these species.

2.1.3 | Occurrence point data

All georeferenced occurrence records, with no known coordinate issues, for terrestrial species included in the 100 worst list or in

our list of cold-tolerant species were downloaded from the Global Biodiversity Information Facility (GBIF; gbif.org) using the RGBIF package (Chamberlain, Ram, Barve, & McGlinn, 2015) in R Statistical Software (R Development Core Team, 2016). The number of geo-referenced occurrence points available for each species varied considerably (Tables S1 and S2). After the removal of conspicuously erroneous data (e.g., points with 0.00° coordinates indicating default georeferencing), all points within each 0.25° cell (WGS84 geographic coordinate system, global extent) were aggregated such that each cell containing any occurrence records was represented by only one presence point at the centroid of the cell.

2.2 | Climate data

The modelling approach adopted here focuses on climate suitability, an important determinant of alien species establishment (Bellard, Leroy, Thuiller, Rysman, & Courchamp, 2016; Duncan & Forsyth, 2006) and therefore uses only climatic variables. The effects of non-climatic and fine-resolution drivers of species distributions, such as land use, soil composition and microclimate, are not therefore captured by these SDMs. Owing to the difficulties of incorporating them into SDMs, the direct effects of wind, which is expected to intensify across the region (Mayewski et al., 2015), are also absent from our analyses, despite their influence on Antarctic species (e.g., Weimerskirch, Louzao, de Grissac, & Delord, 2012). The SDMs assess the general climatic-niche suitability of a broad suite of alien species at a large spatial extent, to identify areas where current and future climates are suitable for species establishment. Because the costs of eradication of invasive alien species have proven high in the region (e.g., AUD\$ 24.7 million for rabbit and rodent eradication on Macquarie Island, Springer, 2016), especially compared with the relative efficiency of biosecurity procedures (Shaw, 2013), the overprediction (i.e., a false-positive for habitat suitability) that is sometimes characteristic of SDM-based approaches, particularly those that focus solely on climate, is appropriate in a risk-assessment context (see discussion in Jiménez-Valverde et al., 2011).

Climate data were downloaded from the NASA Earth Exchange Global Daily Downscaled Projections (NEX-GDDP; <https://cds.nccs.nasa.gov/nex-gddp>; Thrasher, Maurer, McKellar, & Duffy, 2012) dataset. This dataset comprises spatially downscaled (0.25° resolution) outputs from 21 global climate models developed for the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC AR5). Daily data of maximum temperature, minimum temperature and precipitation, from five global climate models (ACCESS1.0, BNU-ESM, CESM1-BGC, CSIRO Mk3.6.0 and GFDL-ESM2M) were retrieved from the NEX-GDDP data server. An averaged global climate model was also created, taking the arithmetic mean of each cell across all five models. Monthly averages were calculated for all six climate models (five original climate models and one averaged model) of each variable for current (1996–2005), 2050 (2046–2050) and 2100 (2096–2100) time periods under the RCP8.5 future climate scenario. RCP8.5 represents a scenario with a median 4.6°C temperature increase above pre-industrial temperatures by 2100 (Moss et al., 2010). Although RCP8.5 is considered a “worst-case” future climate scenario,

observed emissions continue to track a pathway that would see realization of this scenario (Peters et al., 2013).

Data layers, which contain surface-skin (i.e., terrestrial and marine) measures of temperature and precipitation, were masked using a 0.25° resolution mask of global land masses, which was rasterized from the Thematic Mapping World Borders 0.3 shapefile (thematicmapping.org). The smallest Southern Ocean islands, defined here as oceanic islands between 45 and 65 degrees south, were manually added to this mask so that at least one 0.25° cell occupied by each island was preserved even if the land area represented only a small proportion of the total cell area. Marine variables can be used as reasonable surrogates for terrestrial variables of Southern Ocean islands (Chown, Hull, & Gaston, 2005). Where possible, monthly climate-model averages for each island were qualitatively validated against observed climate averages from long-term meteorological station data (Climate Normals, NOAA; Australian Bureau of Meteorology; UK Met Office) to ensure that they were representative of the currently observed climate. Comprehensive meteorological data for all Southern Ocean islands are, unfortunately, extremely sparse and rarely extend beyond individual stations located at research bases.

From each triplet of masked monthly maximum and minimum temperature data, and monthly mean precipitation data, climate layers analogous to those of the WorldClim dataset (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) were derived using the *dismo* package (Hijmans, Phillips, Leathwick, & Elith, 2015) in R Statistical Software (R Development Core Team, 2016). Five environmental variables, representative of averages, extremes, and variance of temperature and precipitation, were selected from this new dataset for use in modelling. Selected climate variables (corresponding WorldClim variable in parentheses) were mean diurnal temperature range (bio2), maximum temperature of warmest month (bio5), minimum temperature of coldest month (bio6), precipitation of driest month (bio14) and precipitation seasonality (bio15). The variance inflation factor (VIF) was calculated for each set of climate variables to test for collinearity. All variables had VIF values <10 and therefore collinearity of environmental variables was minimal. The six resultant climate datasets (one from the five-model average and five from original global climate models, each with five environmental variable layers) were used to run separate SDM analyses as outlined below and in Appendix S1.

2.3 | Species distribution modelling

Alien species climate suitability was modelled under current and future climates through the application of ensemble SDMs. Ensemble modelling uses a suite of different SDMs to estimate climate suitability by consensus. This provides a more robust methodology than using singular SDMs and reduces the impact of individual model biases (Araújo & New, 2007). Ten SDM methodologies contributed to the ensemble models created in this study (Artificial Neural Network, BIOCLIM, Boosted Regression Trees, Classification Tree Analysis, Flexible Discriminant Analysis, Generalized Additive Model, Generalized Linear Model, Maximum Entropy, Multiple Adaptive Regression Splines, Random Forest; Thuiller, Lafourcade, Engler, &

Araújo, 2009). All SDMs, excluding those in the SDM ensemble that used modified GLM and Maxent settings as described in Appendix S1, were built using default parameters using the *biomod2* package (version 3.1; Thuiller et al., 2009) in R Statistical Software (R Development Core Team, 2016).

Full ensemble SDMs for each of the species selected for analysis were first calibrated using each of the six different datasets of current global environmental data (i.e., the averaged climate data plus each of the five global climate models individually) and occurrence records for each species. As GBIF occurrence data are presence only and most SDM methodologies also require absence data (Thuiller et al., 2009), five sets of pseudo-absence points were generated for each species. These data points were sampled from a global background extent as, owing to the invasive ability of species considered to be the "world's worst invasive alien species" (Invasive Species Specialist Group of the International Union for Conservation of Nature, 2016), all continents and regions were assumed to be accessible to the 69 species taken from the 100 worst list. The same assumption was made for species on the cold-tolerant list to facilitate direct comparisons. Following recommendations by Barbet-Massin, Jiguet, Albert, and Thuiller (2012), 1,000 random pseudo-absence points were created for species with occurrence records that occupied few ($\leq 1,000$) 0.25° cells, while sets of 10,000 pseudo-absence points were created for species with a greater number ($> 1,000$) of cells containing occurrence records. SDM performance was assessed with the true skills statistic (TSS), which is more accurate than kappa statistics and is independent of prevalence, or the proportion of sites with presence records (Allouche, Tsour, & Kadmon, 2006). Occurrence and pseudo-absence data were randomly divided, with 70% of data used for model calibration with the remaining 30% reserved for model evaluation. Calibration and evaluation were repeated three times for each of the five sets of pseudo-absences of each SDM (i.e., a total of 15 calibrations/evaluations for each SDM) with data randomly assigned to calibration or evaluation for each repetition. TSS values can range from -1 to +1 where a value of +1 indicates perfect model performance, and a value ≤ 0 indicates performance no better than random (Allouche et al., 2006). To exclude poorly performing models, only models with a TSS score higher than 0.7 were used for subsequent model projection and to create maps of climate suitability.

Ensemble models built using each of the six climate datasets (averaged climate data plus each of the five global climate models individually) were projected onto corresponding current, and 2050 and 2100 climate layers of the Antarctic region to create relative suitability maps for all species under current and future climate conditions. Relative climate suitability maps for each species were converted to binary suitable/unsuitable maps using the probability threshold that maximized TSS score (Allouche et al., 2006; Bellard et al., 2013). Binary maps for all species were summed to produce maps of the predicted potential number of these alien species under current and future conditions across the Antarctic region.

Extrapolation detection analyses (EXDET; Mesgaran, Cousens, & Webber, 2014; Broennimann, Di Cola, & Guisan, 2016) were used to assess the climate analogy between the reference extent of each species (i.e., current climate from all occurrence and pseudo-absence

points) and the current and future climates of each of the Southern Ocean islands. The results of these analyses were used to identify any regions where models were required to extrapolate into novel climate conditions. Negative values indicate novel conditions at the univariate level, and values ≥ 1 indicate novel combinations of climate variables. Values between 0 and 1 indicate projection into an analogous climate.

Although ensembles of multiple statistical techniques provide a robust alternative to using a single SDM method (Araújo & New, 2007), performance is context-sensitive, and some methods have been identified as generally better than others (Elith et al., 2006; Wenger & Olden, 2012). A range of sensitivity analyses were therefore performed to test the robustness of model outcomes. These analyses and their results are presented in Appendix S1.

3 | RESULTS

Regardless of minor species-specific differences, the broader patterns described below held true across all climate models and were robust to alterations in SDM methodologies. Hereafter, we present and discuss the results of the full 10-model ensemble SDM performed using default options and climate data averaged across all five global climate models (full dataset available at <https://doi.org/10.4225/03/5902b67f2f229>). Results from all other models are presented in Appendix S1 and in the other supporting material (Tables S9–S18).

3.1 | The world's worst terrestrial invaders

Species distribution models predicted climate suitability for 31 of the 69 modelled species from the 100 Worst list across the entire Antarctic region under current climate conditions (Tables 1 and S3; Figures 1a and 2a; Figs S1–S3). Under the RCP8.5 future climate scenario, the number of terrestrial invasive species on the 100 worst list for which the climate of the region is suitable increased to 38 species in 2050 and 47 species in 2100. Climatic suitability for the modelled species varied greatly, however, between the Southern Ocean islands and the Antarctic continent.

The climate of the Antarctic continent and nearby maritime Antarctic islands was unsuitable for all 69 species on the 100 worst list under current conditions (Figure 1a; Fig. S1). Under 2050 conditions, the climates of the northernmost tip of the Antarctic Peninsula, and the South Shetland and South Orkney Islands were identified as suitable for up to four species of the 100 worst (Figure 1a). In 2100, the climate of the Antarctic Peninsula and associated islands is predicted to have altered such that is suitable for as many as six of the 100 worst over a broader spatial extent (Figure 1a). Regardless, only a small area of the Antarctic Peninsula shows climate suitability for terrestrial species on the 100 worst list under either current or future conditions. The climate of the rest of the Antarctic continent remained unsuitable to all 69 of the terrestrial 100 worst species under future climate conditions (Fig. S3).

By contrast, all but one of the Southern Ocean islands were predicted to be currently climatically suitable for multiple species

TABLE 1 Mean (averaged across all cells covered by each island or island group), number of terrestrial species from the 100 worst list (Table S1; Invasive Species Specialist Group of the International Union for Conservation of Nature, 2016) for which the climate of the Southern Ocean islands is predicted to be suitable under current and future climate conditions

	Island	Current	2050	2100
I	Bouvet	0.0 0.0 _{2.0}	0.0 0.0 _{3.0}	2.0 6.0 _{8.0}
II	Prince Edward	15.5 19.0 _{21.0}	18.5 22.5 _{23.5}	22.0 29.0 _{33.0}
III	Crozet	12.0 13.8 _{16.2}	16.0 16.4 _{22.4}	20.6 24.4 _{31.8}
IV	Kerguelen	11.6 15.0 _{16.5}	14.5 18.2 _{22.0}	20.1 24.4 _{31.9}
V	Heard & McDonald	3.5 6.0 _{9.5}	5.0 7.5 _{14.5}	10.0 15.5 _{21.5}
VI	Macquarie	15.0 21.0 _{23.0}	18.0 22.0 _{28.0}	24.0 29.0 _{34.0}
VII	Auckland	22.0 24.5 _{26.5}	24.5 29.5 _{30.0}	31.0 34.0 _{36.0}
VIII	Campbell	19.0 22.0 _{23.0}	21.0 23.0 _{26.0}	27.0 30.0 _{32.0}
IX	Bounty	16.0 19.0 _{22.0}	19.0 23.0 _{29.0}	24.0 30.0 _{36.0}
X	Antipodes	20.0 21.0 _{22.0}	19.0 21.0 _{26.0}	24.0 28.0 _{35.0}
XI	W. Falklands	14.5 19.5 _{22.2}	19.5 23.3 _{25.5}	21.5 24.2 _{28.5}
XII	E. Falklands	15.4 19.9 _{21.9}	19.4 23.6 _{25.5}	22.4 24.9 _{28.4}
XII	South Georgia	4.9 5.3 _{8.1}	7.7 10.0 _{14.4}	10.4 15.9 _{26.3}
XIII	South Sandwich	0.4 0.9 _{1.3}	0.9 2.0 _{5.7}	2.3 4.1 _{7.3}

Bold values indicate the number of species predicted using an average of five global climate models, while subscript values either side represent the lowest and highest number of species predicted when performing separate SDM analyses on each of the five climate models. All future climate conditions were under the RCP8.5 scenario.

from the 100 worst list (Figure 2a; Table 1). Under current conditions, Auckland, Campbell, Macquarie and the Antipodes islands have climates that are suitable for the highest number of modelled species (25, 22, 21, 21 species, respectively), while the South Sandwich Islands and Bouvet (Bouvetøya) are climatically suitable for the fewest species (1, 0 species; Figure 2a; Tables 1 and S3). These patterns are consistent under 2050 conditions, with the climates of all islands, except Bouvet and the Antipodes, habitable for an increased number of species (Tables 1 and S3). Under 2100 conditions, Auckland, Campbell and Bounty islands are climatically suitable for the highest number of species modelled (34, 30 and 30 species, respectively; Tables 1 and S3). The climates of all islands were suitable for more alien species on the 100 worst list under future climate conditions than under current conditions (Figure 3; Table 1). Mean TSS scores for models of each species that were above the 0.7 TSS threshold ranged from 0.772 to 1.000 (mean for all 69 species, 0.899; Fig. S7). Variable importance varied amongst species (Fig. S9), with temperature variables, particularly temperature of the coldest month, the most dominant variables. EXDET analyses revealed that although the climates of the majority of islands were analogous to those used for SDM construction (i.e., EXDET values between 0 and 1), non-analogous novel univariate

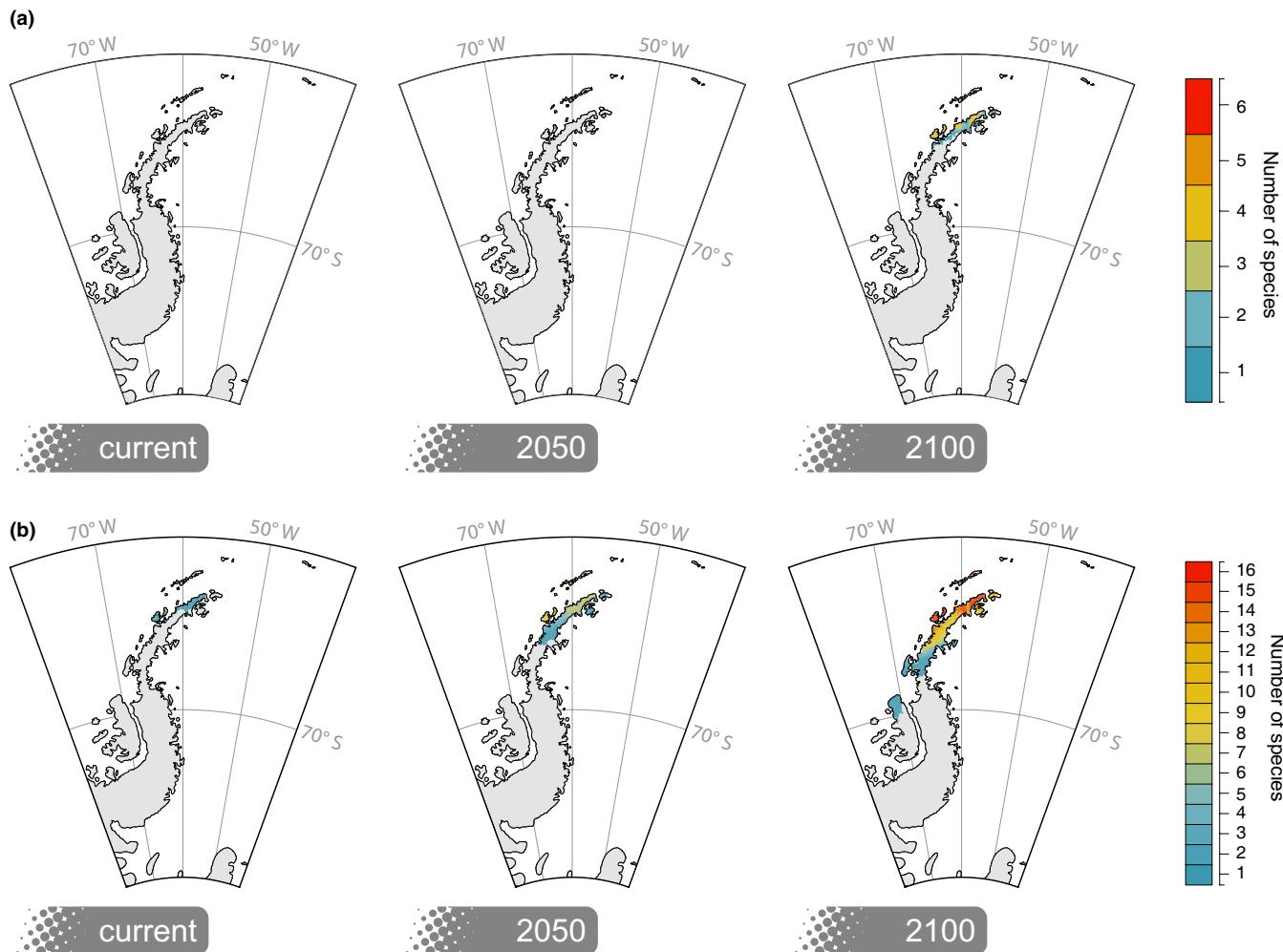


FIGURE 1 Mean number of terrestrial species from the 69 modelled species on the 100 worst list (a; Table S1) and the mean number of the 24 cold-tolerant species modelled (b; Table S2) for which the climate of the Antarctic Peninsula and associated islands was predicted to be suitable under averaged current, RCP8.5 2050 and RCP8.5 2100 conditions

conditions (i.e., negative EXDET values) were recorded for some islands and species (Table S19).

Model outcomes for species on the 100 worst list showed broad agreement with the work of Bellard et al. (2013) despite methodological differences (e.g., the focus here on climate over other habitat variables and use of fifth-generation climate models) between our study and theirs. Bellard et al. (2013) omitted the Antarctic region from their models, but patterns of habitat suitability of modelled species elsewhere across the globe were similar to the patterns of climate suitability reported here (Figs S1–S3). Both studies identified the same regions as being suitable for an increasing number of species on the 100 worst list under future climate change. Likewise, regions predicted to become suitable for fewer species overlapped. This lends confidence to the climatic suitability estimates of the Antarctic region presented here.

3.2 | Cold-tolerant species

Species distribution models predicted that the climate across the entire Antarctic study region was suitable for 22 of the 24 modelled

cold-tolerant species under current and future (2050, 2100) climate conditions (Table 2; Figures 1b and 2b; Figs S4–S6). Based on the five-model average climate data (Table S4), the climate of the entire study region was identified as unsuitable for two of the modelled species, the Anthomyiid fly *Fucellia tergina* and the aphid *Rhopalosiphum padi*, despite their observed occurrence in five and eight Antarctic biogeographic regions, respectively (Chown & Convey, 2016). One cold-tolerant insect (*Agrotis ipsilon*) and eight cold-tolerant plants (*Holcus lanatus*, *Poa annua*, *Poa pratensis*, *Rumex acetosella*, *Sagina procumbens*, *Senecio vulgaris*, *Stellaria media* and *Trifolium repens*) were predicted to find suitable climates across all 14 Southern Ocean island groups under current conditions. The climate of the Antarctic Peninsula and nearby maritime Antarctic islands was suitable for up to four cold-tolerant species under current conditions, with this estimate increasing to 16 cold-tolerant species under 2100 conditions (Figure 1b). Habitat suitability for *Festuca rubra* and *Poa pratensis* was predicted for coastal regions of the continent under 2100 conditions (Fig. S6), although only ice-free areas would be able to accommodate the species and unsuitable soil substrates may preclude colonization.

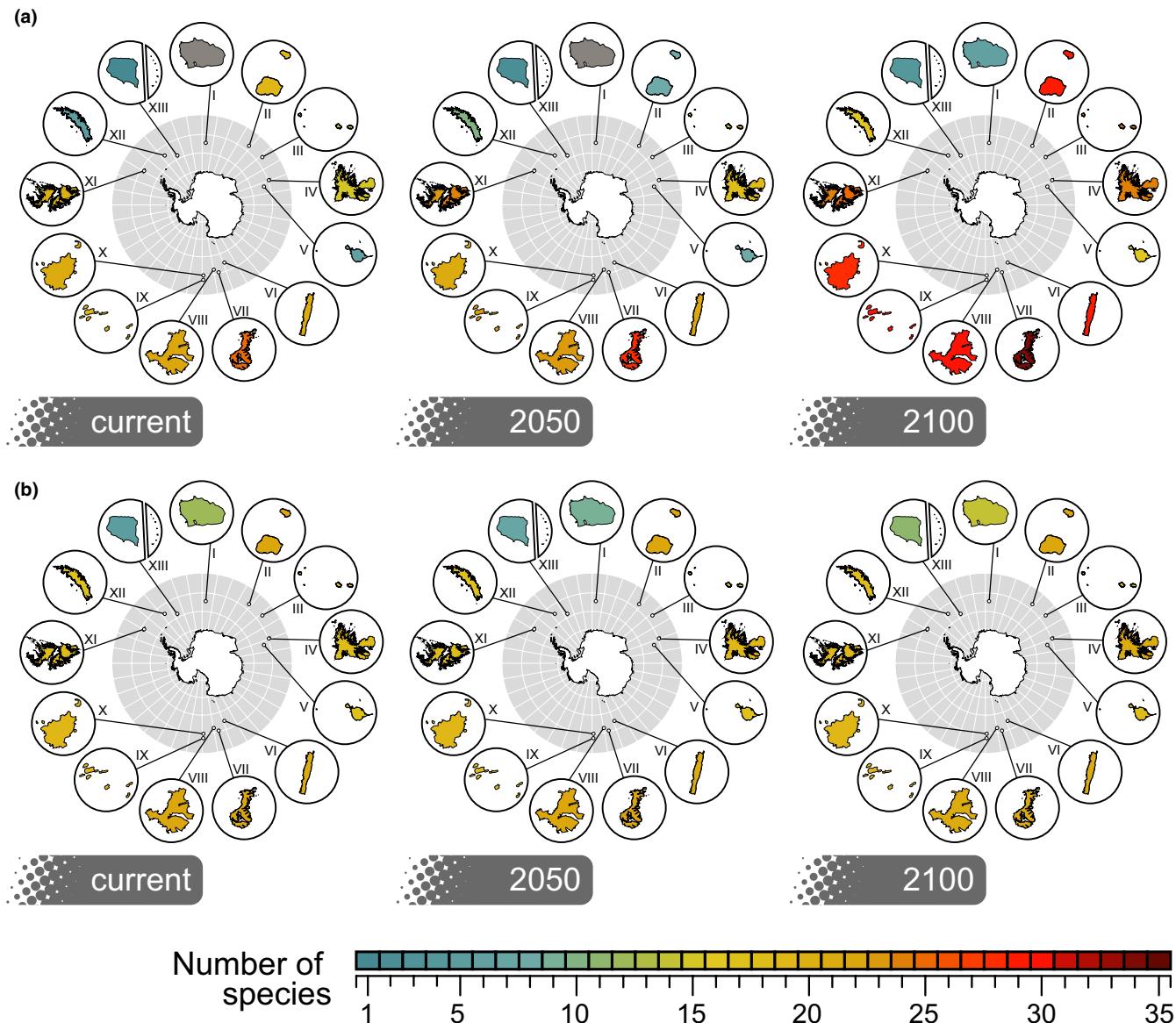


FIGURE 2 Mean number of terrestrial species from the 69 modelled species on the 100 worst list (a; Table S1) and the mean number of the 24 cold-tolerant species modelled (b; Table S2) for which the climates of the Southern Ocean islands are predicted to be suitable under averaged current, RCP8.5 2050 and RCP8.5 2100 conditions. Islands labelled with roman numerals following Tables 1 and 2. Suitable–unsuitable matrices for each modelled species and island are located in Table S11. Not to scale

Under current and 2050 conditions, the climate of every Southern Ocean island was suitable for nine of the modelled cold-tolerant species, increasing to 14 of the modelled cold-tolerant species under 2100 conditions. All islands except Bouvet and South Sandwich were suitable for over two-thirds (16 or more of 24) of the modelled cold-tolerant species under current conditions. The number of cold-tolerant species for which each island was climatically suitable varied spatially, but was generally consistent temporally (Figure 2b; Table 2). While some islands (e.g., Falklands, Kerguelen, South Sandwich) showed small gains in the number of cold-tolerant species for which their climates were suitable between current and 2100 conditions, other islands remained suitable for the same number of cold-tolerant species (e.g., Antipodes), or were suitable for one or two fewer cold-tolerant species (e.g., Auckland Islands). Mean TSS scores for models of each

species that were above the 0.7 TSS threshold ranged from 0.787 to 0.999 (mean for all 24 species, 0.879; Fig. S8). Variable importance varied amongst species (Fig. S10), with temperature variables the most frequently dominant variables. EXDET analyses revealed that although the climates of the majority of islands were analogous to those used for SDM construction (i.e., EXDET values between 0 and 1), non-analogous novel univariate conditions (i.e., negative EXDET values) were recorded for some islands and species (Table S19).

4 | DISCUSSION

Although globally significant invasive species, such as those on the 100 worst list, appear to pose a limited threat to the Antarctic continent

TABLE 2 Mean (averaged across all cells covered by each island or island group), number of cold-tolerant species (Table S2) for which the climate of the Southern Ocean islands is predicted to be suitable under current and future climate conditions

	Island	Current	2050	2100
I	Bouvet	8.0 12.0 13.0	6.0 9.0 15.0	8.0 14.0 17.0
II	Prince Edward	20.0 22.0 22.0	20.0 22.0 22.5	20.0 21.5 22.5
III	Crozet	15.0 16.0 16.6	15.0 16.2 16.6	16.2 17.0 18.2
IV	Kerguelen	17.7 17.7 19.6	17.9 19.2 20.6	19.2 20.5 20.9
V	Heard & McDonald	16.0 16.5 17.0	16.5 17.0 19.0	16.0 17.5 20.5
VI	Macquarie	20.0 21.0 22.0	19.0 21.0 22.0	19.0 21.0 21.0
VII	Auckland	20.5 22.0 22.0	20.5 21.5 22.0	20.0 21.0 23.0
VIII	Campbell	20.0 22.0 22.0	20.0 22.0 22.0	20.0 21.0 22.0
IX	Bounty	18.0 19.0 20.0	17.0 18.0 20.0	19.0 19.0 21.0
X	Antipodes	18.0 19.0 20.0	17.0 19.0 20.0	19.0 19.0 21.0
XI	W. Falklands	17.2 17.7 18.4	17.5 18.2 19.1	18.5 19.2 20.7
XI	E. Falklands	17.0 17.9 18.2	17.2 18.0 19.0	19.0 18.9 20.7
XII	South Georgia	16.8 16.7 17.8	16.9 17.2 18.6	16.7 17.8 20.1
XIII	South Sandwich	4.6 5.0 5.9	4.1 6.6 11.7	6.9 11.3 17.1

Bold values indicate the number of species predicted using an average of five global climate models, while subscript values either side represent the lowest and highest number of species predicted when performing separate SDM analyses on each of the five climate models. All future climate conditions were under the RCP8.5 scenario.

(Figure 1a), the climatic barriers that prevent continental establishment of these temperate and subtropical species (Invasive Species Specialist Group of the International Union for Conservation of Nature, 2016) do not protect the Southern Ocean islands (Figure 2a) and provide little protection from invasion by cold-tolerant species (Figures 1b and 2b). The Antarctic Peninsula will be the most threatened region of the continent under future climate conditions, with the remaining continental land mass unsuitable for all but two cold-tolerant species through to 2100 (Figs S1–S6). Several non-native species are already established on the Antarctic Peninsula (Hughes et al., 2015), and climatic suitability for additional species is particularly concerning as the impacts of alien species on continental Antarctic ecosystems are expected to be severely detrimental to the native biota (Hughes & Convey, 2010). Furthermore, the area most at risk overlaps with those areas that are already subjected to pressures from plant propagules, increasing visitation and changing climate (Chown et al., 2012).

Current climatic barriers may prevent invasion to the Antarctic continent by all of the worst globally invasive species and all but four of the modelled cold-tolerant species, but the milder climates of the Southern Ocean islands are less effective barriers to non-native species establishment (Tables 1 and 2; Figure 2). In part this may account for the higher number of alien species that are presently observed on the Southern Ocean islands compared to the Antarctic continent (Chown et al., 2005; McGeoch et al., 2015). The susceptibility of these

islands is perhaps unsurprising when one considers their climate relative to other invaded regions globally. Current and, in particular, future climates of many of the Southern Ocean islands are within the current climatic range of the South Island of New Zealand (*Te Waipounamu, Aotearoa*; Figure 4) below 1,000 m, a region in which numerous alien species, including at least 40 of the 69 terrestrial species listed on the 100 worst list, have established (Allen & Lee, 2006; Duncan & Forsyth, 2006) and that is within the 45–60° S latitude band used here to classify Southern Ocean islands. This suggests that the current low number of established alien species (McGeoch et al., 2015), relative to New Zealand, across the Southern Ocean islands is indicative of their relative isolation (Chown, Gremmen, & Gaston, 1998), rather than climatic barriers to establishment. Although most Southern Ocean islands have been regularly visited by humans since early exploration in the 16th century, transport to New Zealand is, nevertheless, considerably more frequent than transport to any of the Southern Ocean islands (e.g., data in Chown et al., 2005).

Despite historic isolation, human movements into and across the Antarctic region are becoming more frequent (Hughes & Convey, 2010), increasing the chances of accidental introductions, and the threats posed by the establishment and impacts of alien species (Chown et al., 2012; Shaw, 2013). The introduction risk associated with inter-island transport of species is perhaps the most concerning under current conditions as the climates of all Southern Ocean islands are suitable for additional cold-tolerant species beyond those already present (Figure 2b). Furthermore, biosecurity checks on transport between islands are more difficult to monitor and enforce than those imposed on transport from other continents, exemplified by the Heard and McDonald Islands Management Plan specifically excluding departure to these islands from another sub-Antarctic location (Commonwealth of Australia, 2014). Plant species such as *Sagina procumbens* and *Poa annua*, for which the current climates of all islands were suitable, are already established across almost all sub-Antarctic islands (McGeoch et al., 2015), capable of rapid spread once established (Le Roux et al., 2013), and have a variety of impacts on local ecosystems (Frenot et al., 2005; Haussmann, Rudolph, Kalwij, & McIntyre, 2013). Similarly, once introduced, alien insects tend to disperse rapidly, and many have significant impacts on the local biota (Chown & Convey, 2016).

Alongside increasing human movements, warming from anthropogenic climate change will substantially increase the climate suitability of all of the sub-Antarctic islands for the terrestrial species on the 100 worst list over the course of the next century (Table 1; Figures 2a and 3). Monthly precipitation is predicted to become more variable (Figure 4), which may explain the small temporal variations in the number of cold-tolerant species that certain islands will be suitable for (Figure 2b) as temperature variables were less important in distribution models of cold-tolerant species than they were for species from the 100 worst list (Figs S7 and S8). While the invaders examined here only represent a subset of potential species that may threaten to invade the Antarctic, the general warming trend suggests that an increasing number of globally invasive species will find the region climatically suitable in the future.

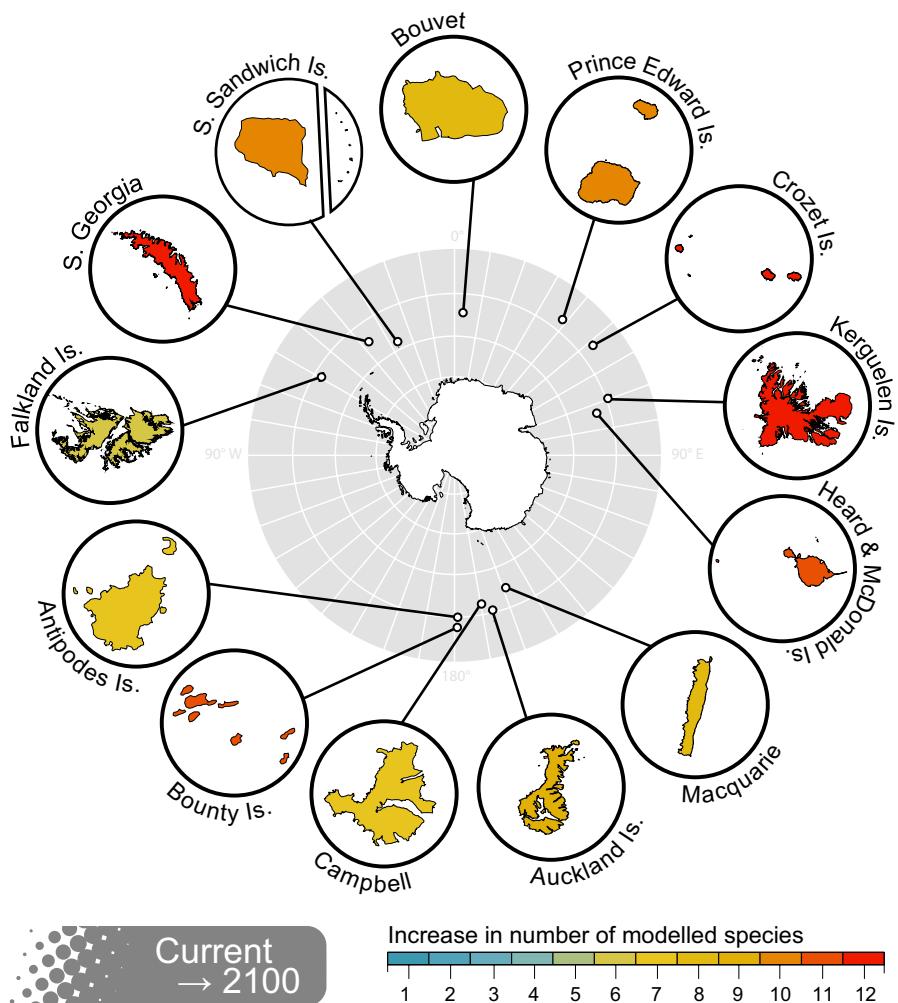


FIGURE 3 Predicted increase in the number of species from models of 69 species from the 100 worst list (Table S1) and 24 species from the list of cold-tolerant species compiled here (Table S2) for which the climates of the Southern Ocean islands are predicted to be suitable, between current and RCP8.5 2100 conditions. Drawn from values in Tables 1 and 2. Not to scale

The methods applied here demonstrate that, overall, SDM approaches are highly applicable for the Antarctic region (in keeping with the more general assessment of Gutt et al., 2012) and can enable either species-specific threats or regional risks to be assessed. There are, nevertheless, certain caveats that must be considered when applying such methods to the Antarctic region. For example, uncertainty in models of the Antarctic climate system, especially with regard to the role and response of sea ice (Frieler et al., 2015; Previdi, Smith, & Polvani, 2015), may limit the predictive ability of future climate models. General uncertainty in future climate projections is reflected in variation amongst the five climate models used here (Tables 1 and 2; Tables S3–S8). Averaging the climate models provides a way to reduce the impact of individual model biases and to ensure that the best approximation, based on current knowledge, of the future climate of the Antarctic region is represented. Regardless, the Antarctic Peninsula region has warmed substantially over the past 50 years (Mulvaney et al., 2013; but see Jones et al., 2016; Turner et al., 2016), is predicted to be one of the fastest warming regions on the planet under multiple future climate models (Hanna et al., 2013), and much work is being done on improving climate model outputs for the Antarctic region (Bracegirdle et al., 2016).

All 10 of the species modelled from the 100 worst list that have previously established on at least one Southern Ocean island have the potential to establish on additional islands based on current climate suitability, yet they have not (Table 3). There are two main hypotheses as to why this may be. The first is that the species has never been introduced to the island (i.e., dispersal to the island is blocked by natural barriers, such as the Southern Ocean, and humans have not purposefully or accidentally introduced the species). Given low numbers of visits to some islands and the recent introduction of more stringent biosecurity measures (e.g., Shaw, 2013), the importance of the dispersal barrier is clear. The second hypothesis is that some factor other than climate has prevented establishment whenever a species has been introduced. Although climate is a key determinant of alien species establishment success (Bellard et al., 2016; Duncan & Forsyth, 2006), the latter hypothesis highlights the importance of considering other factors, such as resource availability and habitat characteristics (e.g., Crall et al., 2013), to improve habitat suitability estimates based initially on climate alone. Habitat characteristics other than climate do play a role in determining species distributions in some Antarctic ecosystems (Haussmann et al., 2013; Smith & French, 1988), but comprehensive data on such characteristics are not readily available for all of the Southern Ocean islands and the broader Antarctic region (though

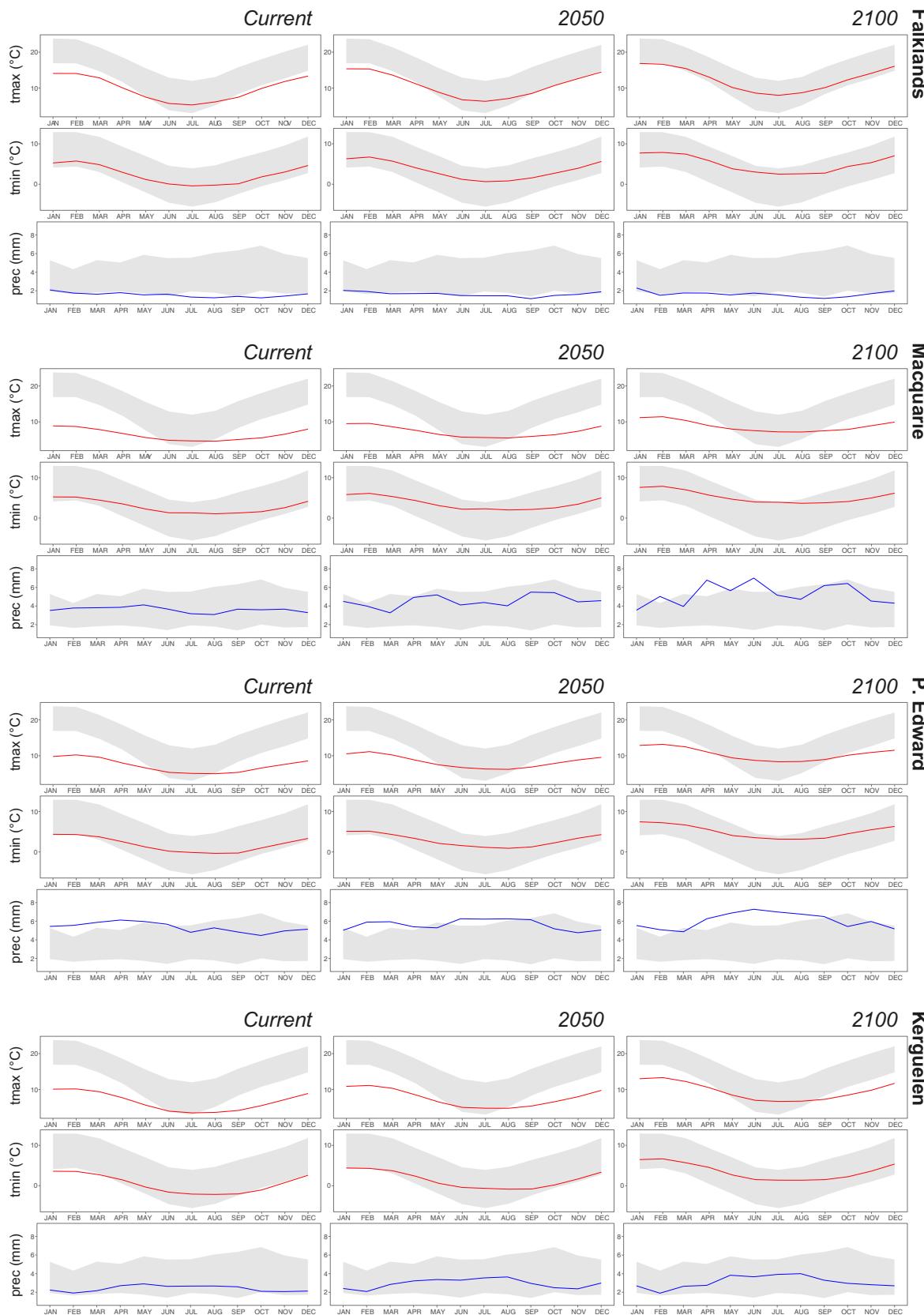


FIGURE 4 Maximum monthly mean temperature (tmax), minimum monthly mean temperature (tmin) and mean monthly precipitation (prec) for four major Southern Ocean island groups (Falkland Islands, Macquarie Islands, Prince Edward and Marion Islands, Kerguelen Islands) under current and future (2050, 2100) climate conditions (averaged from five global climate models). All lines are overlaid onto the range of each respective variable observed on the South Island of New Zealand (<1,000 m elevation) under current environmental conditions (grey shading)

TABLE 3 Climate suitability matrix for terrestrial species from the 100 worst list (Invasive Species Specialist Group of the International Union for Conservation of Nature, 2016) that have been introduced to at least one Southern Ocean island

		European starling <i>Sturnus vulgaris</i>	Gorse <i>Ulex europeus</i>	Feral goat <i>Capra hircus</i>	Feral pig <i>Sus scrofa</i>	Feral cat <i>Felis catus</i>	Rabbit <i>Oryctolagus cuniculus</i>	Stoat <i>Mustela erminea</i>	Rabbit <i>Oryctolagus cuniculus</i>	House mouse <i>Mus musculus</i>	Black rat <i>Rattus rattus</i>
Bouvet	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Prince Edward Islands	0 (0)	1 (0)	0 (0)	1 (0)	1 (0)	0 (1) ^b	1 (0)	1 (0)	1 (0)	1 (1)	1 (0)
Crozet Islands	0 (0)	1 (1)*	1 (0)	1 (1) ^a	1 (1) ^a	1 (1)	1 (1)	1 (0)	1 (1)	1 (1)	1 (1)
Kerguelen Islands	0 (0)	1 (0)	1 (0)	1 (1) ^a	1 (1) ^a	1 (1)	1 (1)* ^a	1 (1)	1 (1)	1 (1)	1 (1)
Heard & McDonald	0 (0)	0 (0)	0 (0)	0 (0)	0 (1) ^a	0 (0)	1 (0)	0 (0)	0 (0)	0 (0)	0 (1)* ^a
Macquarie	0 (0)	1 (0)	0 (1)	1 (1) ^a	1 (0)	1 (1) ^b	1 (0)	1 (0)	1 (1) ^b	1 (1) ^b	1 (1) ^b
Auckland Islands	0 (0)	1 (1)	1 (1)	1 (1) ^b	1 (1)	1 (1)	1 (1)	1 (0)	1 (1) ^b	1 (1)	1 (0)
Campbell	0 (0)	1 (1)	1 (1)	1 (1) ^a	1 (1) ^a	1 (1) ^b	1 (1)	1 (0)	1 (0)	1 (0)	1 (1)* ^b
Bounty	0 (0)	1 (0)	0 (0)	0 (0)	0 (0)	1 (0)	1 (0)	1 (0)	1 (0)	0 (0)	1 (0)
Antipodes	0 (0)	1 (0)	1 (1)	1 (0)	1 (0)	1 (0)	1 (0)	1 (0)	1 (1) ^b	1 (1)	1 (0)
Falkland Islands	0 (1)*	1 (1)	1 (0)	1 (0)	1 (1)	1 (1)	1 (0)	1 (1)	1 (1)	1 (1)	1 (1)
S. Georgia	0 (0)	1 (0)	0 (0)	0 (0)	0 (1) ^a	0 (1) ^a	1 (0)	0 (1) ^a	0 (1)	0 (1)	0 (1)*
S. Sandwich Islands	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

Numbers denote that ensemble species distribution models predicted either a suitable climate on at least one quarter degree cell of each island, 1, or unsuitable climate across the entire island, 0, under current conditions. Numbers in parentheses indicate whether or not the species (* or a congeneric) has been recorded on the island, or at least one island in the group, either currently or in the past. Data on observed occurrences updated from McGeoch et al. (2015) to incorporate recent eradication on Macquarie Island (Springer, 2016) and records of failed introductions and historic occurrences (Clark & Dingwall, 1985; Convey & Lebouvier, 2009; Eastmond, 1883; Goodridge, 1841; Holdgate & Wace, 1961; Kidd, 1876; Lesel & Derenne, 1975; van den Hoff, Burton, & Robins, 2012). Notation indicates where a species did not establish or has become extinct for natural/unknown reasons (^a), or has been the target of a successful eradication programme (^b).

see Terauds et al., 2012; for developments in this area). Biotic interactions, which are often cited as confounders of environment-based SDM studies, are of reduced concern when applying SDM methods to the Antarctic region due to the low levels of interspecific interaction that are characteristic of depauperate Antarctic ecosystems (Lee, le Roux, Meiklejohn, & Chown, 2012).

Conversely, unsuitable climate is indicated for islands where species from the 100 worst list have previously been recorded (Table 3). While these discrepancies appear unusual initially, it should be noted that for reasons that have largely remained obscure, the majority of these species are now extinct from the islands in question (see notation on values contained in Table 3). For example, pigs failed to survive on five of the island groups into which they were introduced (Convey & Lebouvier, 2009). Our analyses suggest climate may have played a role, especially as the persistence of pigs on the Falkland Islands largely owes itself to ongoing human intervention. Another factor to consider is the relatively coarse resolution of the climate data used, which cannot capture the intricacies of small-scale climate variation that likely arise from the topographical heterogeneity that is characteristic of many Southern Ocean islands. Species may therefore have established in meso- or micro-scale climatic refugia (e.g., leeward areas of mountainous islands), which are absent from coarse climate data. For example, the finding that the climates, based on the five-model average, of all islands were unsuitable for two species from the cold-tolerant list (*Fucellia tergina* and *Rhopalosiphum padi*) despite their invasion of at least five Antarctic biogeographic regions indicates that these species are likely to have established in small-scale island climates that were not present in the coarse climate data used. Finally, introductions may have involved either climatically pre-adapted genotypes or some evolutionary change may have occurred (see related discussion in Lee, Slabber, Jansen van Vuuren, van Noort, & Chown, 2007). The inability of correlative methods to represent fully the fundamental niche of a species may also have contributed towards discrepancies between predicted climate suitability and observed species occurrences (Gallagher, Beaumont, Hughes, & Leishman, 2010), particularly in instances where non-analogue climate was indicated (Table S19). The limitations of applying correlative SDMs to a region where environmental conditions lie outside of the model parameters (i.e., no occurrence has been recorded in a climatically similar region) represent a key area where modelling of the occurrence of species in the broader Antarctic region can be improved, especially for islands where non-analogous climates were identified by EXDET analyses (Table S19). Mechanistic niche modelling (Kearney & Porter, 2009) would improve predictions of invasive ranges, but is limited by the general lack of physiological data for many species. Physiological phenotyping should therefore be considered an important focus of future research to determine whether potentially invasive species exhibit the necessary thermal and desiccation tolerances to survive Antarctic climates (e.g., Laparie & Renault, 2014; Lee & Chown, 2016; Lee, Janion, Marais, Jansen van Vuuren, & Chown, 2009; Worland, 2010).

In conclusion, we have shown here that many of the world's worst terrestrial invasive species pose potential current and future risks to the broader Antarctic region. Perhaps more importantly,

we demonstrate that there are now sufficient data in the public domain to model species distributions at a truly global spatial extent, which includes the Antarctic region. Thus, global assessments of pressures on biodiversity, such as those being undertaken for the Convention on Biological Diversity's Strategic Plan for Biodiversity 2011–2020 (Tittensor et al., 2014), can be directly applied to the region (Chown et al., 2017). Indeed, unlike the situation for area protection, where the Antarctic region seems to be lagging globally (Coetzee, Convey, & Chown, 2017), the situation for biological invasions is quite different (Chown et al., 2015). Invasion pathways, sites of possible introduction and status of native and non-native species are generally closely monitored and well managed across the Antarctic region. Thus, understanding of the state of and pressures from biological invasions to the region is developing rapidly. This affords the rare opportunity to monitor and limit the spread of previously introduced non-native species and, ideally, prevent the introduction of species that have the potential to establish.

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BIOSKETCH

Grant A. Duffy is a postdoctoral research associate working on community and macroecology of marine and terrestrial systems. His research uses existing and novel techniques to assess organismal and community responses to environmental change.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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