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Title page

Once upon a time in the far south: Influence of local drivers and functional traits on plant invasion in the harsh sub-Antarctic islands

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Once upon a time in the far south: Influence of local drivers and functional traits on plant invasion in the harsh sub-Antarctic islands

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1 **Abstract**

2 **Aim**

3 Here, we aim to: (i) investigate the local effect of environmental and human-related factors on alien
4 plant invasion in sub-Antarctic islands; (ii) explore the relationship between alien species features
5 and their dependence on anthropogenic propagule pressure; and (iii) unravel key traits conferring
6 invasiveness in the sub-Antarctic.

7 **Location**

8 Possession Island, Crozet archipelago (French sub-Antarctic islands).

9 **Taxon**

10 Non-native vascular plants (Poaceae, Caryophyllaceae, Juncaceae).

11 **Methods**

12 Single-species distribution models were used to explore the effect of high-resolution topoclimatic and
13 human-related variables on the occurrence of six of the most aggressive alien plants colonizing
14 French sub-Antarctic islands. Furthermore, the interaction between alien species traits and their
15 response to anthropogenic propagule pressure was analysed by means of a multi-species distribution
16 model. This allowed identifying the features of species that were associated to low dependence on
17 human-assisted introductions, and were thus potentially more invasive.

18 **Results**

19 We observed two main invasion patterns: low-spread species strongly dependent on anthropogenic
20 propagule pressure and high-spread species limited mainly by harsh climatic conditions. Differences
21 in invasiveness across species mostly related to their residence time, life history and plant height,
22 with older introductions, perennial and low-stature species being more invasive.

23 **Main conclusions**

24 The availability of high-resolution data improved our understanding of the role of environmental and
25 human-related factors in driving alien species distribution on sub-Antarctic islands. At the same time,
26 the identification of alien species features conferring invasiveness may help anticipating future
27 problematic invasions.

28

29 **Keywords: alien plants, anthropogenic propagule pressure, invasiveness, plant invasion,**
30 **species distribution models, sub-Antarctic islands, topoclimate**

31 **Running title: plant invasion in sub-Antarctic islands**

32

33 1. Introduction

34 Sub-Antarctic islands, archipelagos scattered within the 54-48°S latitudinal ring, are extremely
35 remote territories which harbour a unique biodiversity with a high degree of endemism (Shaw, 2013).
36 As a consequence of their relatively recent discovery and environmental harshness, these islands have
37 long remained pristine and largely free of human disturbances. Yet, due to the gradual relaxation of
38 these natural barriers, sub-Antarctic islands are now listed among the most threatened environments
39 on Earth. In particular, invasion by alien plants, boosted by ongoing climate changes and increasing
40 human disturbances (Duffy & Lee, 2019; Hughes et al., 2019), has become one of the main threats to
41 the endemic biodiversity of these territories, and is bound to rise in the next decades (Lebouvier et
42 al., 2011; Hughes, Pertierra, Molina-Montenegro, & Convey, 2015). Over the past century, alien
43 plants have been increasingly introduced in the sub-Antarctic region (Frenot et al., 2005; Huiskes et
44 al., 2014). European whalers and scientific activities, respectively in the 19th and 20th century,
45 determined the first main introduction events (Convey & Lebouvier, 2009; Shaw, 2013). Later on and
46 since the mid-twentieth century, climate warming, strong changes in precipitation regimes and the
47 widespread impacts of non-native vertebrates have progressively favoured the establishment of cold-
48 tolerant alien plants on sub-Antarctic islands (Shaw, 2013; Pertierra et al., 2017; Duffy & Lee, 2019).
49 Nevertheless, despite their demonstrated impacts on native biodiversity, little attention has been given
50 to plant invasions compared to animal invasions on these islands (le Roux et al., 2013), leaving a
51 knowledge gap in the mechanisms underpinning plant invasion processes in these unique
52 environments (Greve, Mathakutha, Steyn, & Chown, 2017).

53 The outcome of any biological invasion is jointly determined by propagule pressure (i.e. frequency
54 of propagules introduction), abiotic conditions (i.e. physico-chemical features of the invaded
55 environment) and biotic features (i.e. alien species characteristics and interactions with the recipient
56 community), with anthropogenic disturbances affecting all three (Richardson & Pyšek, 2006; Catford,
57 Jansson, & Nilsson, 2009; Lembrechts et al., 2016). The relative importance of these factors is,
58 however, context-dependent and species-specific (Catford et al., 2009). In sub-Antarctic islands, due
59 to the high specialization but low diversity of the native flora, biotic interactions are thought to play
60 a minor role (le Roux et al., 2013; Duffy et al., 2017; Moser et al., 2018), so it is mainly the first two
61 factors that determine the distribution and spread of alien plants. First, invasions depend on human-
62 induced propagule pressure: the frequency of propagule introduction correlates with the number of
63 ship landings and is highest in the vicinity of human facilities (Huiskes et al., 2014). Second, local
64 abiotic conditions are strongly limiting, and particularly the climatic mismatch between the conditions
65 prevailing within the alien species' native range and the conditions prevailing in the sub-Antarctic
66 can strongly constrain invasions (Frenot et al., 2005). Some alien plants are more limited during the
67 introduction phase, while others quickly become relatively independent of human-related propagule-
68 pressure and seem only climatically limited. Once established, the species which are the least
69 dependent on continuous introductions are the most likely to spread widely and become invasive
70 (Richardson & Pyšek, 2006; Catford et al., 2009). Therefore, quantifying the degree of alien species
71 dependence on propagule pressure might aid at identifying potentially invasive species.

72 A lower dependence on human-related propagule pressure is potentially related to certain species
73 features which are more generally known to affect invasiveness. First of all, alien species with longer
74 residence times are more likely to become independent of anthropogenic propagule pressure (Wilson
75 et al., 2007; Pyšek et al., 2015). Second, certain plant traits are considered key for profiling successful
76 invaders (Pyšek & Richardson, 2008): invasive alien plants across most environments are growing
77 faster and taller than non-invasive alien species, and typically produce resource-acquisitive leaves
78 and many small seeds (van Kleunen, Weber, & Fischer, 2010; van Kleunen, Dawson, & Maurel,

79 2015). More specifically, Mathakutha et al. (2019) performed a first functional comparison between
80 invasive and non-invasive alien species colonizing the sub-Antarctic Marion Island, reporting that
81 species generally considered invasive had lower plant height, smaller leaf area, lower frost tolerance
82 and higher specific leaf area than other alien species. Nevertheless, it is still unclear which traits can
83 actually make some alien plants less dependent on human-related propagule pressure, and thus more
84 likely to become invasive, especially in the sub-Antarctic islands. This knowledge could facilitate the
85 early screening of highly invasive alien plant species in these environments (Frenot et al., 2005;
86 Mathakutha et al., 2019).

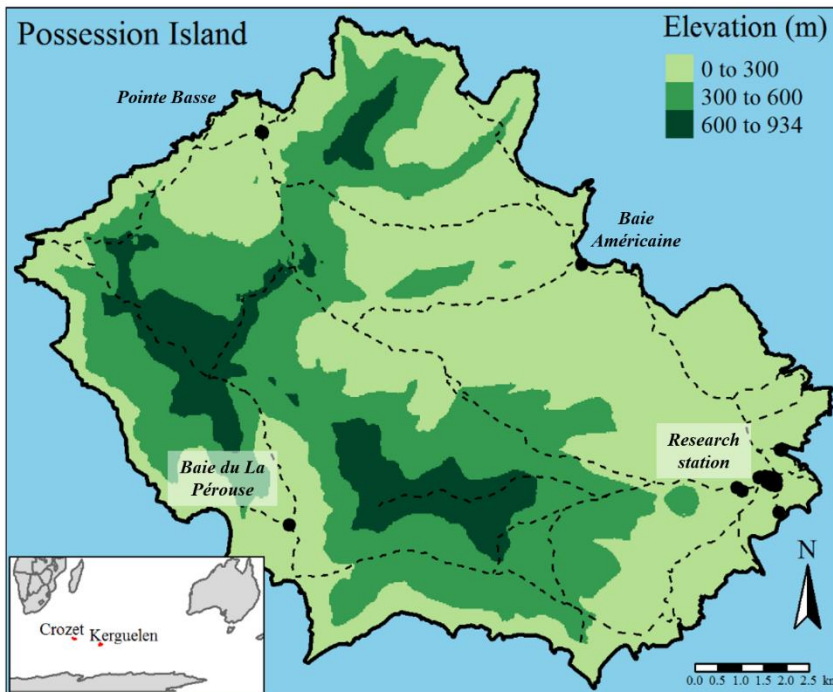
87 Correlative species distribution models (SDMs) are statistical tools that model the species-
88 environment relationship relying on geo-referenced occurrence data and spatial environmental layers
89 (Guisan, Thuiller, & Zimmermann, 2017). Such models already proved to be valuable tools for
90 analysing alien plant invasion in Antarctica and the sub-Antarctic regions. For instance, Pertierra et
91 al. (2017) modelled the distribution of *Poa annua* and *Poa pratensis* in the Antarctic peninsula as a
92 function of bioclimatic variables, while Duffy et al. (2017) generated future scenarios of invasion
93 across Antarctica and the sub-Antarctic regions using climate-based SDMs. Whilst these previous
94 SDM applications have revealed large-scale determinants of alien plant invasion in the Antarctic
95 biogeographic region, they have up till now failed to account for how environmental and
96 anthropogenic factors regulate alien plant distributions at a spatial resolution that is meaningful for
97 local management. This is chiefly due to the lack of high-resolution environmental (e.g. climatic,
98 topographic) and human-related data layers, which limits the implementation of SDMs at fine spatial
99 resolutions in remote areas (Gutt et al., 2012). A more general limitation inherent to the use of SDMs
100 for modelling biological invasion is that SDMs allow mapping into the geographical space only a
101 snapshot of the current alien species-environment relationship net of dispersal and biotic constraints
102 (i.e. realized distribution), while necessarily underestimating the actual area potentially suitable to a
103 species for establishing and maintaining a viable population (i.e. potential distribution; see Jiménez-
104 Valverde et al., 2011 and Srivastava, Lafond, & Griess, 2019).

105 The sub-Antarctic Possession Island constitutes an ideal arena to analyse alien plant invasions in the
106 sub-Antarctic region. The availability of historical vegetation observations allows retracing the
107 invasion history of most alien plant species on the island. Moreover, this island witnessed past human
108 colonization and climate changes comparable to the other sub-Antarctic islands, allowing inference
109 on the mechanisms underpinning alien plant invasion in these unique areas. Previous work showed
110 that there is considerable variation in the spread of alien plants established on Possession Island, with
111 some species clustering close to their introduction locations and others spreading widely and far from
112 the initial introduction sites (Frenot et al., 2005), which allows testing for differences in the
113 dependence on human introductions. In the present study, we model the distribution of the most
114 relevant alien plant species colonizing Possession Island using a combination of environmental and
115 human-related spatial data derived at an unprecedented high spatial resolution (i.e. 30-m) for these
116 latitudes that we related to long-term monitoring observations of plant occurrences. Our aim is to test
117 the local effect of environmental and anthropogenic factors on alien plant invasion in sub-Antarctic
118 ecosystems. We hypothesise that both abiotic and human-related factors jointly define the local
119 occurrence of alien plant species, but that these two factors will not be equally important among
120 species. Furthermore, to identify plant characteristics conferring high invasiveness in sub-Antarctic
121 ecosystems, we investigate how plant functional traits affect species dependence on anthropogenic
122 propagule pressures. In this regard, our working hypothesis is that the most invasive species share
123 specific functional characteristics allowing them to become independent of human-assisted
124 introductions and spread widely once established.

125

126 2. Materials and methods

127 2.1 Study area



128

129 *Figure 1 – Map of Possession Island showing: gross topography using three altitudinal belts (0-300 m; 300-600 m; 600-*
130 *934 m); human settlements (black dots); and hiking paths (dashed lines). The inset map reports the geographical location*
131 *of French sub-Antarctic islands, which include Crozet and Kerguelen archipelagos.*

132 The study was carried out on Possession Island in the Crozet archipelago, which is included in the
133 *Réserve naturelle nationale des terres australes françaises* (RNN TAF) and listed as UNESCO World
134 Heritage site since 2019. Possession Island (Figure 1) is characterized by a complex topography, with
135 an altitudinal gradient ranging from 0 to 934 m above the sea level (*Pic du Mascarin*) over a relatively
136 short spatial extent (147 km²). The island is characterized by a typical sub-Antarctic climate, with
137 mean annual temperature of 5.6 °C and annual precipitation of 2,300 mm (Météo France, data: 1960-
138 2019). Frequent and strong western winds occur throughout most of the year.

139 The first human settlements date back to the 19th century, when whalers and sealers established on
140 the north-east side of the island during the hunting season, facilitating a first series of alien species
141 introductions. In 1963, a permanent research station (*Alfred Faure*, hereafter the ‘research station’)
142 was built on the easternmost area of Possession Island, fostering a new invasion front. Beyond the
143 research station, other shelters (inhabited for short periods) are currently present on each side of the
144 island: north (*Pointe Basse*); south-west (*Baie du La Pérouse*); and north-east (*Baie Américaine*).
145 Among these, the research station is by far the biggest human settlement and main hub of propagule
146 introduction. The vegetation at Possession Island has experienced relatively low grazing pressure
147 from sheep in the past (Convey & Lebouvier, 2009), in comparison to other sub-Antarctic islands
148 where introduced large herbivores still strongly affect the distribution of alien plants (Shaw, 2013).

149 2.2 Study species

150 Despite the 68 alien species recorded on Possession Island (see page 99 of the RNN TAF management
151 plan 2018-2027: https://taaf.fr//content/uploads/sites/2/2019/09/180607-Volet-A_pour-CNPN.pdf),

152 only few have established persistent populations (Frenot, Gloaguen, Massé, & Lebouvier, 2001). In
153 this study, we restricted our analysis to those alien plants that are either known to be generally
154 widespread on sub-Antarctic islands or are particularly widespread on Possession Island, and for
155 which sufficient occurrence data were available (total number of presences > 100). Specifically, we
156 selected the following six species from three different families: *Poa annua* and *Poa pratensis*
157 (Poaceae); *Cerastium fontanum*, *Sagina procumbens* and *Stellaria alsine* (Caryophyllaceae); and
158 *Juncus bufonius* (Juncaceae). The two grasses, *P. annua* and *P. pratensis*, have colonised most of the
159 sub-Antarctic islands (Shaw, 2013) and are the longest-established alien plants in the Antarctic
160 Peninsula (Perterra et al., 2017). *Cerastium fontanum* and *S. procumbens* are currently widely
161 distributed in this environment (Frenot et al., 2005; Shaw, 2013) with, in particular, *S. procumbens*
162 exhibiting the highest rate of spread among the alien plants of Marion and Prince Edward Islands (le
163 Roux et al., 2013). Finally, both *J. bufonius* and *S. alsine* currently occur at significant distances from
164 the research station on Possession Island (Frenot et al., 2001). While the former has been recently
165 observed up to the Maritime Antarctica latitudes (Cuba-Díaz, Fuentes, & Rondanelli-Reyes, 2015),
166 the latter has been singled out by some authors as the potentially most problematic future invasive
167 plant species on Possession Island (Frenot et al., 2001; Convey, Key, & Key, 2010).

168 2.2.1 Species distribution data

169 We analysed the invasion patterns of the six selected alien plant species relying on georeferenced
170 occurrence (presence/absence) data collected within the context of a yearly vegetation monitoring
171 survey carried out by the RNN TAF since 2010. The vegetation sampling is implemented within a
172 system of 675 squared cells of 100 × 100 m each, where floristic data (presence and abundance of
173 vascular plant species) are collected along with habitat characteristics through phytosociological
174 *relevés* (Dengler, 2016). In this study, we used data collected from 2010 to 2017 (3,354 occurrences
175 for the selected species across 1,572 sampled plots).

176 2.2.2 Species features and functional trait data

177 To inform species features (e.g. traits) potentially related to invasiveness, we collected data on plants
178 residence time and functional traits. Residence time positively interacts with propagule pressure in
179 determining plant invasion success (Richardson & Pyšek, 2006; Lockwood, Cassey, & Blackburn,
180 2005; Pyšek et al., 2015), and this relationship was also observed on sub-Antarctic islands (le Roux
181 et al., 2013; Shaw, 2013; Mathakutha et al., 2019). To test how residence time influences alien
182 species' dependence on propagule pressure, we considered the introduction date of the selected plants
183 on Possession Island (Frenot et al., 2001) and used this information to assign them to two groups: old
184 *vs* new resident species (Appendix S1, Table S1.1). In particular, we considered as old resident
185 species those which were firstly observed on Possession Island before the research station was built
186 (1963), while referring to the others as new resident species.

187 We then collated data on seven plant traits commonly used to synthesize species strategies known to
188 be related to invasiveness (van Kleunen et al., 2010; van Kleunen et al., 2015): (1) life history (annual
189 *vs* perennial); (2) plant height; (3) leaf area; (4) specific leaf area (SLA); (5) vegetative reproduction
190 (present *vs* absent, i.e. sexual and vegetative *vs* only sexual reproduction); (6) seed dry mass; and (7)
191 number of seeds per plant. We excluded traits related to flowering since pollinating insects are absent
192 from almost all sub-Antarctic islands (Convey et al., 2010). Life history, plant height and leaf area
193 relate to plant persistence and tolerance to environmental stress (Cornelissen et al., 2003; Pérez-
194 Harguindeguy et al., 2013). In addition, life history is used to assess maximum lifespan and plant
195 height is associated with competitiveness for light and whole plant fecundity (Pérez-Harguindeguy et
196 al., 2013). Specific leaf area is the one-sided leaf area per leaf mass and is associated with resource

197 acquisition and photosynthetic rate (Pérez-Harguindeguy et al., 2013). Reproduction strategy, seed
198 dry mass and number of seeds per plant do not only relate with species persistence, but also with
199 dispersal capacity (Ottaviani et al., 2020). In particular, alien species reproducing predominantly
200 sexually may benefit from lower dispersal limitation and greater genetic diversity (van Kleunen et
201 al., 2015). At the same time, while small and light seeds are better dispersed at longer distances, large-
202 seeded plants may benefit from more stored resources (van Kleunen et al., 2015).

203 Functional trait data collected in areas environmentally analogous to Possession Island were compiled
204 from the literature (other sub-Antarctic islands, Frenot et al., 2005; Marion Island, Mathakutha et al.,
205 2019). Whenever we could not find information collected in comparable environments, we relied on
206 functional trait data included in the TRY database (Kattge et al., 2020). For each alien species, the
207 dominant reproduction strategy in the study area was assessed relying on expert-based knowledge
208 (personal communication, Lebouvier, M., & Bittebiere, A.K.). Species-specific values of the
209 functional traits are reported in table S1.1 (Appendix S1) along with literature sources.

210 2.3 Topoclimatic layers

211 To model the species-environment relationship at fine spatial resolution, we first downloaded coarse-
212 grained temperature (BIO1, BIO5 and BIO6 – annual mean temperature, max temperature of the
213 warmest month and min temperature of the coldest month) and annual precipitation (BIO12) grid
214 layers at 1-km resolution (at the equator) from the CHELSA database (Karger et al., 2017) and then
215 disaggregated their spatial resolution using physiographically informed models fitted through
216 geographically weighted regression (GWR; Fotheringham & Rogerson, 2008). This downscaling
217 technique allows statistically predicting the local value of the coarse-grain CHELSA climatic
218 variables as a function of environmental grid layers available at finer spatial resolution (in this study
219 30-m at the equator, hereafter 30-m) and known to drive microclimate heterogeneity (Lenoir, Hattab,
220 & Pierre, 2017; Lembrechts et al., 2019). GWR-derived topoclimatic layers, beyond allowing to
221 model the species-environment relationship at a more meaningful spatial resolution, have already
222 proved to better account for the complex interactions between macroclimate and topography (Lenoir
223 et al., 2017; Lembrechts et al., 2019).

224 As using BIO5 (max temperature of the warmest month) and BIO6 (min temperature of the coldest
225 month) in place of BIO1 did not improve species distribution models, we ultimately used BIO1
226 (hereafter mean temperature) and BIO12 as topoclimatic predictors. A full description of the
227 downscaling procedure is reported in Appendix S2 along with the results of the GWR models.

228 2.4 Human-related layers

229 As human disturbances are known to favour the establishment of alien plants through propagule
230 introduction and alteration of habitat conditions, we generated a 30-m resolution layer reporting the
231 distance between each human settlement (the research station, *Baie du La Pérouse*, *Pointe Basse* and
232 *Baie Américaine*) and any location on the island. Specifically, assuming that human disturbance is
233 stronger in more accessible areas, we derived a least cost distance grid layer providing a measure of
234 accessibility. Terrain slope changes between both orthogonally and diagonally neighbouring raster
235 cells were used to compute the cost of reaching any location on Possession Island starting from any
236 human settlement and following all potential paths of raster cells (function “accCost”, “gdistance” R
237 package; Etten, 2018). High costs were thus associated with locations not easily reachable from
238 human settlements due to high topographic roughness (Appendix S3, Figure S3.2).

239 A network of hiking paths has been designed by RNN TAF to restrict human movements for wildlife
240 conservation purposes, and walking these paths currently constitutes the only authorized way to move

241 across the island. As humans are a critical vector of propagule introduction and dispersal on sub-
242 Antarctic islands, we derived a 30-m resolution raster layer reporting the distance between any
243 location on Possession Island and the closest hiking path using the function “distance” from the
244 “raster” R package (Hijmans, 2019) (Appendix S3, Figure S3.2).

245 *2.5 Alien species distribution modelling*

246 The occurrence probability of the six studied alien plant species was separately modelled as a function
247 of the topoclimatic (mean temperature and annual precipitation) and human-related variables (path
248 distance and least cost) by means of logit binary generalized linear models (GLM). The single-species
249 distribution models (single-SDMs) were trained and tested on datasets obtained through a re-sampling
250 procedure of the presence/absence data performed in the environmental space to reflect all available
251 environmental conditions on Possession Island (Lenoir et al., 2010; Hattab et al., 2017; see Appendix
252 S4). All four topoclimatic and human-related predictors were retained to fit the single-SDMs as the
253 relative variance inflation factor (function “vif”, R package “car”; Fox & Weisberg, 2019) was always
254 below a threshold of 3. Second-order polynomial terms were included in the model to allow for
255 intermediate niche optima of the species or in case lack-of-fit tests detected consistent departure from
256 linearity in the profile of Pearson residuals (function “residualPlots”, R package “car”; Fox &
257 Weisberg, 2019). The statistical significance of each predictor was tested using type II analysis of
258 deviance (function “Anova”, R package “car”; Fox & Weisberg, 2019). We then computed the
259 likelihood profile-based 95% confidence intervals of the regression parameters.

260 Single-SDMs predictive performance was measured using the true skill statistic (TSS, equal to
261 sensitivity + specificity – 1; function “ecospat.max.tss”, R package “ecospat”; Broennimann, Di Cola,
262 & Guisan, 2018) computed on the testing datasets obtained through the environmental matching
263 described in Appendix S4. We used the TSS as it has desirable properties of other accuracy measures
264 (e.g. Kappa and AUC), while being unaffected by prevalence (Allouche, Tsoar, & Kadmon, 2006).
265 Also, we computed the deviance-based R^2 value as a measure of goodness-of-fit of each single-SDM.

266 The occurrence probability estimated by the full single-SDMs (including both topoclimatic and
267 human-related predictors) for each alien plant species was mapped on a 30-m raster grid layer to
268 visualise their predicted distribution across Possession Island.

269 *2.6 Relationship between plant traits and alien species dependence on propagule pressure*

270 As preliminary analyses, we measured the relative importance of human-related variables in
271 determining alien species occurrence in the single-SDMs. To this aim, we used the sum of Akaike
272 weights (w), which provides an easily interpretable measure of variable importance (it ranges from 0
273 to 1, with a high value for a given variable indicating its high importance relative to the others;
274 Burnham & Anderson, 2002). Then we graphically related the species-specific values of the
275 functional traits to the sum of weights to look for relationships between plant traits and the importance
276 of human-related variables (see Appendix S7).

277 Secondly, we investigated how the interaction between human-related variables and plant traits
278 affected alien species occurrence in a multi-species distribution model (multi-SDM), focusing on
279 those functional traits that showed some relationship with the dependence on human-related variables
280 in the single-SDMs. To this aim, we modelled the occurrence of all alien species together as a function
281 of topoclimatic and human-related variables by means of a logit binary GLM, including the
282 interaction between species identity and topoclimatic variables on the one hand and the interaction
283 between species functional traits and human-related variables on the other hand. This allowed
284 exploring how the effect of human-related variables on alien species occurrence varied according to

285 plant traits, while controlling for species-specific responses to topoclimate. To select the most
286 parsimonious model, we fitted all possible sub-models including different combinations of the
287 functional traits-anthropogenic variables interaction terms (function “dredge”, R package “MuMIn”;
288 Barton, 2019), always retaining the species-topoclimate interaction terms and the main effect of path
289 distance and least cost in each candidate sub-model. Then, we computed the sum of Akaike weights
290 for each model term and used the evidence ratio as a measure of the relative importance of variables
291 (Massol et al., 2007; Burnham & Anderson, 2002). Specifically, we computed the evidence ratio of
292 the *i*-th variable (ER_i) as the odds of its sum of Akaike weights:

$$293 \quad ER_i = \frac{w_i}{I - w_i}$$

294 The evidence ratio was then compared with its expected value (ER_{null}) under the “null hypothesis”
295 that the variable explained as much deviance as a randomly generated explanatory variable, and
296 would thus be as likely as not to be incorporated in the best models. As all the variables were tested
297 in a balanced design, $ER_{null} = 1$ in all tested cases. Following Massol et al. (2007), the effect of a
298 variable *i* was deemed unlikely if $ER_i < 0.37 \times ER_{null}$, implausible when $0.37 \times ER_{null} < ER_i < ER_{null}$,
299 plausible when $ER_{null} < ER_i < 2.72 \times ER_{null}$, and likely when $ER_i > 2.72 \times ER_{null}$. These thresholds
300 correspond to differences in Akaike information criterion equal to +2 or -2, which are commonly
301 admitted as a good rule-of-thumb gap to compare model performance.

302 **3. Results**

303 *3.1 Effect of topoclimatic and human-related variables on single species distribution*

304 Predictive performances of the single-SDMs varied greatly across species (Table 1): high values of
305 TSS were observed for *P. pratensis*, *S. alsine* and *J. bufonius* (0.80-0.82), while low values were
306 obtained for the remaining species (from 0.09 to 0.29). The R^2 values showed a similar trend, with
307 the highest value obtained for *J. bufonius* (0.48) and the lowest for *C. fontanum* (0.02).

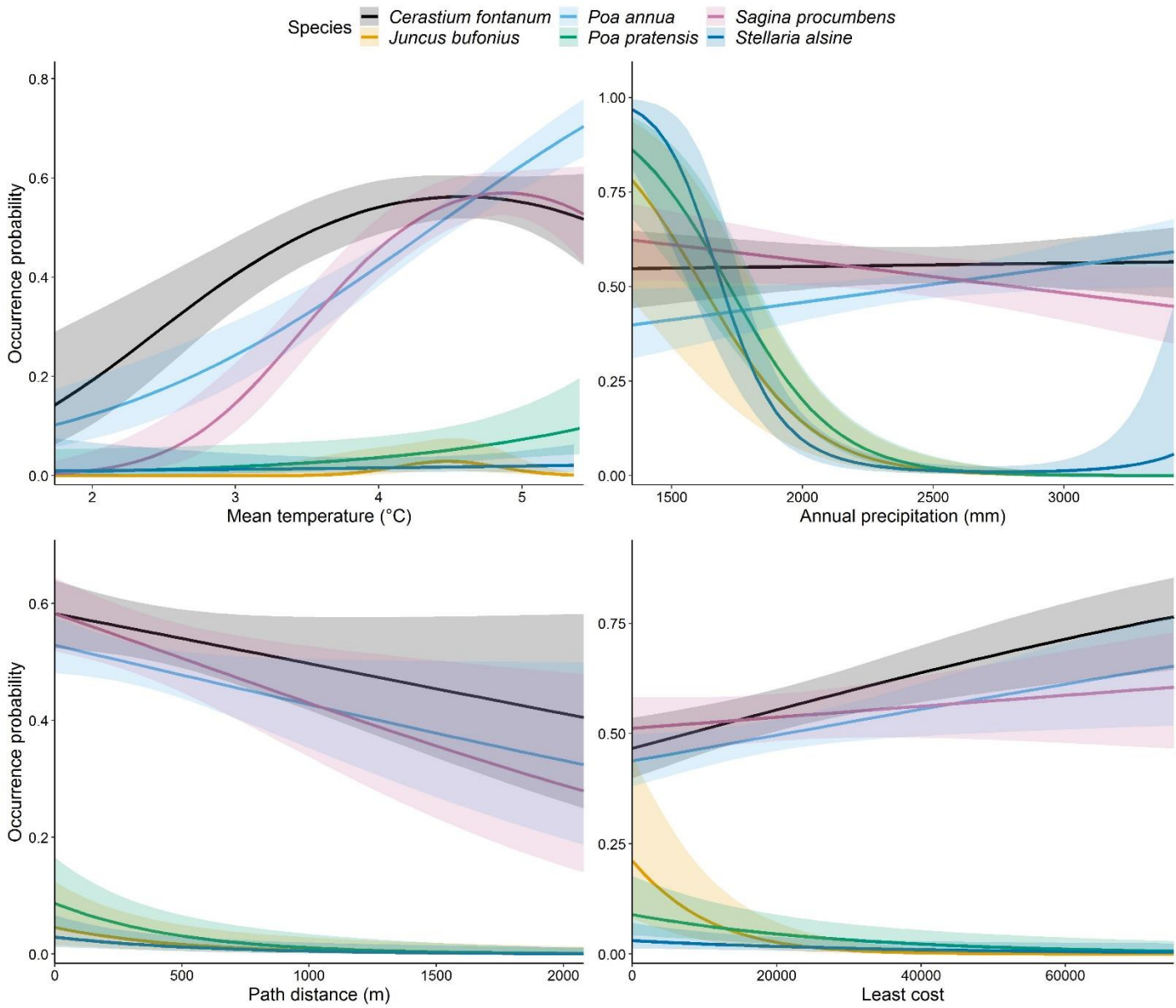
308 Overall, the occurrence of *P. pratensis*, *S. alsine* and *J. bufonius* appeared to be strongly conditioned
309 by both topoclimatic and human-related variables, while *C. fontanum*, *P. annua* and *S. procumbens*
310 were less affected by human-related variables (Table 1, Figures 2 and 3).

311 All alien species, except *S. alsine*, exhibited a significant positive or humped-shaped relationship with
312 mean temperature (Table 1), meaning that their occurrence probability increased with increasing
313 temperature (Figure 2, Appendix S5). More specifically, the occurrence probability of *J. bufonius*, *S.*
314 *procumbens* and *C. fontanum* peaked at mean temperature values around 4.5 °C, while the presence
315 of *P. pratensis* and *P. annua* increased more or less linearly with temperature.

316 Annual precipitation significantly affected the presence of *P. pratensis*, *S. alsine* and *J. bufonius*,
317 while it had a minor influence on the occurrence of the other species (Table 1). In particular, the odds
318 of finding *P. pratensis* and *J. bufonius* decreased approximately by 90% for each 500 mm increment
319 in annual precipitation, while the occurrence probability of *S. alsine* sharply decreased for annual
320 precipitation values above 1,500 mm (Figure 2).

321 All species except *C. fontanum* exhibited a significant negative relationship with path distance (i.e.
322 the occurrence probability of the species decreased at increasing distances from the hiking paths),
323 though its influence varied among species (Table 1, Figure 2, Appendix S5). In this regard, the odds
324 of finding *P. pratensis*, *S. alsine* and *J. bufonius* decreased respectively by 20%, 16% and 19%
325 moving 100 m away from the paths, while the odds of finding *P. annua* and *S. procumbens* decreased
326 by 4% and 6%, respectively.

327 Least cost distance to settlements appeared to influence the occurrence of all analysed species except
328 *S. procumbens* (Table 1). In particular, the odds of finding *P. pratensis*, *S. alsine* and *J. bufonius*
329 decreased, respectively, by 17%, 13% and 44% for each increment of 5,000 units of cost of travelling
330 a given path from a human settlement (Figure 2, Appendix S5). On the contrary, *C. fontanum* and *P.*
331 *annua* showed a positive relationship with least cost, with their odds of occurring increasing
332 respectively by 9% and 5% for each increment of 5,000 units of cost of travelling a given path from
333 a human settlement (Figure 2 and Appendix S5).



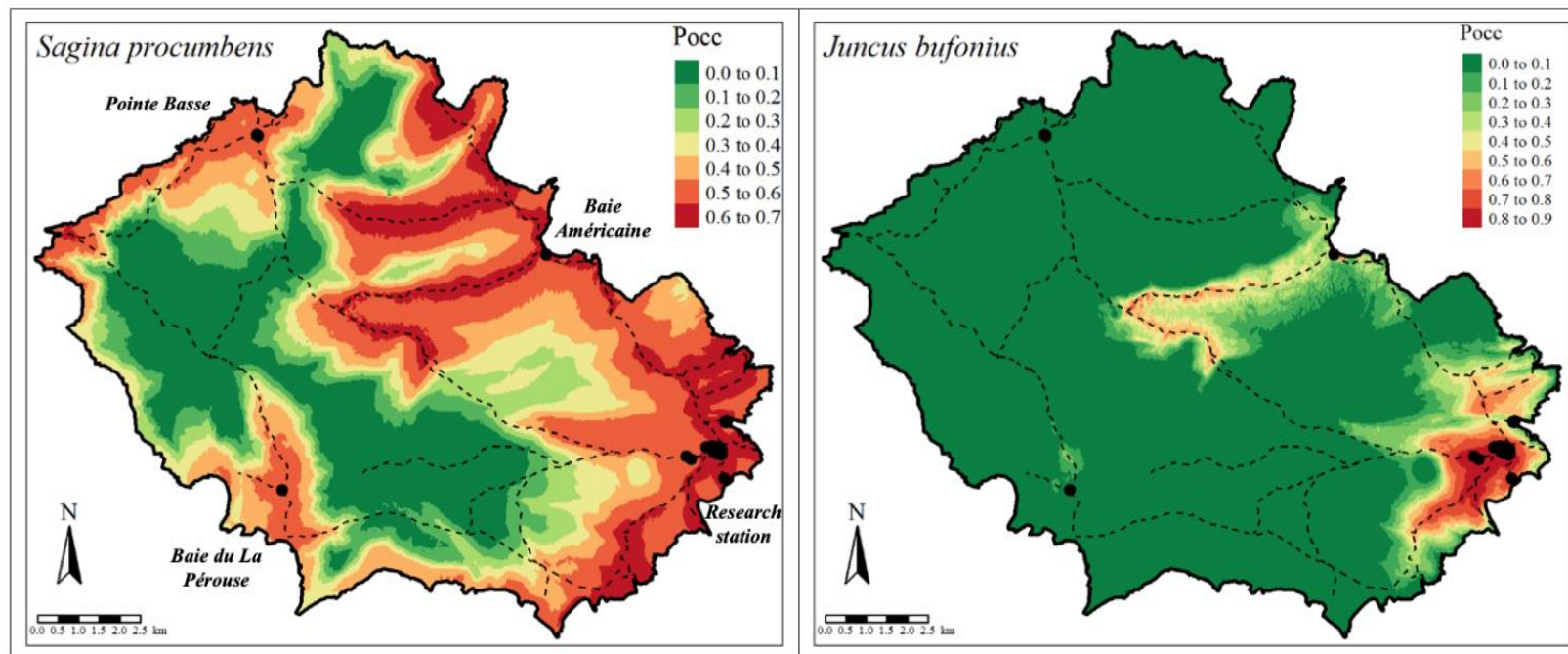
334

335 *Figure 2 – Response curves of the analysed alien species in the single-SDMs.*

336 Table 1 – Single-SDM type II analysis of deviance tables and performance measures (R^2 and TSS). LR: Likelihood Ratio statistic; Df: degrees of freedom; p-val: p-value (***) $p <$
 337 0.001; ** $p < 0.01$; * $p < 0.05$).

Predictors	<i>Poa pratensis</i>			<i>Juncus bufonius</i>			<i>Stellaria alsine</i>			<i>Poa annua</i>			<i>Sagina procumbens</i>			<i>Cerastium fontanum</i>		
	LR	Df	p-val	LR	Df	p-val	LR	Df	p-val	LR	Df	p-val	LR	Df	p-val	LR	Df	p-val
Mean temperature	5.083	1	*	32.516	2	***	0.312	1	= 0.576	55.538	1	***	62.554	2	***	18.325	2	***
Annual precipitation	106.443	1	***	73.647	1	***	68.406	2	***	4.759	1	*	3.681	1	= 0.055	0.041	1	= 0.840
Least cost	10.837	1	***	40.250	1	***	4.420	1	*	5.778	1	*	1.118	1	= 0.290	12.483	1	***
Path distance	15.623	1	***	8.740	1	**	7.524	1	**	3.927	1	*	6.782	1	**	2.877	1	= 0.089
R^2			0.46			0.48			0.36			0.06			0.10			0.02
TSS			0.80			0.81			0.82			0.19			0.29			0.09

338



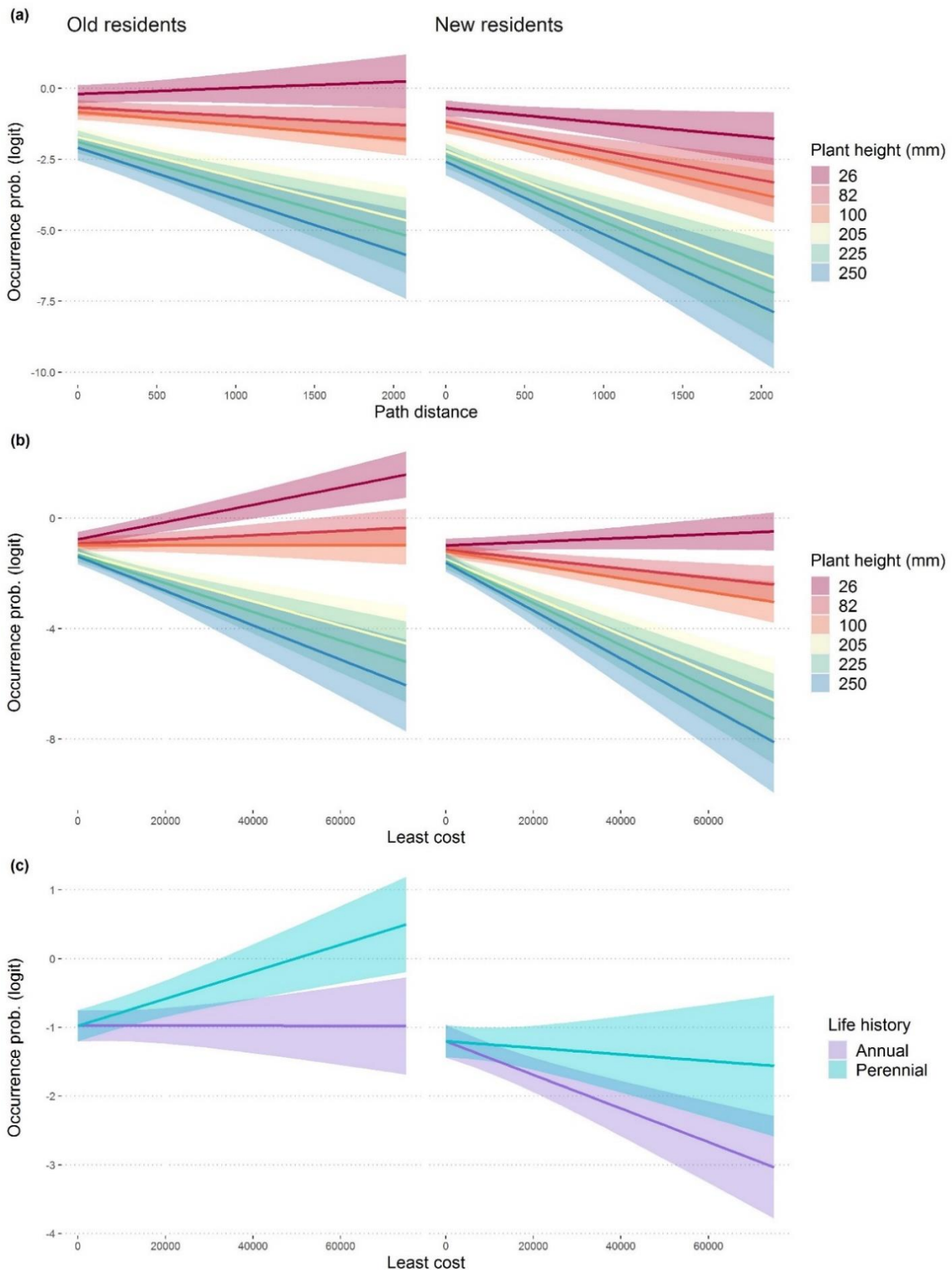
339

340 Figure 3 – Predicted occurrence of *Sagina procumbens* and *Juncus bufonius*. Pocc: occurrence probability. Dashed lines represent hiking paths, while black dots represent human
 341 settlements. Occurrence maps of the other alien species are reported in Appendix S6 (Figure S6.4 and S6.5).

342 *3.2 Plant traits and species dependence on propagule pressure*

343 In the preliminary analyses, residence time, life history, vegetative reproduction and plant height
344 showed some relationship with the sum of weights of the human-related variables in the single-SDMs
345 (Appendix S7, Figure S7.6 and S7.8), while seed- and leaf-related traits clearly showed no
346 relationship (Appendix S7, Figure S7.7 and S7.9).

347 Then, the multi-SDM confirmed significant interactions of residence time, life history and plant
348 height with the human-related variables (Appendix S7, Figure S7.10). Residence time and plant
349 height appeared to interact with both human-related variables, while life history seemed to interact
350 only with least cost in determining alien species occurrence. In particular, the effect of human-related
351 variables on alien species occurrence varied with plant height. For instance, the occurrence
352 probability of taller plants sharply decreased when moving away from human facilities, while a
353 weaker and sometimes opposite trend was observed for plant species of shorter statures (Figure 4a,b
354 and Appendix S7, Figure S7.11). In addition, old residents were on average less affected by the
355 human-related variables than new residents (Figure 4a,b and Appendix S7, Figure S7.11a). Finally,
356 perennials appeared to be on average less negatively affected by least cost distance to human
357 settlements than annuals (Figure 4c and Appendix S7, Figure S7.11b,c).



358

359 *Figure 4 – Effect of the interaction between human-related variables and plant features on alien species occurrence*
360 *probability (logit scale). Panel (a): effect of the path distance-plant height interaction on old and new resident occurrence*
361 *probability. Panel (b): effect of the least cost-plant height interaction on old and new (annual) resident occurrence*
362 *probability. Panel (c): effect of least cost distance to human settlements on annual and perennial (100 mm height) alien*
363 *species occurrence (for both old and new residents). All plots are reported on a logit scale.*

364

365 4. Discussion

366 As hypothesised, both environmental and human-related variables locally affected alien plant species
367 occurrence on Possession Island, though with differences among the studied species. Overall, results
368 confirmed the key role of human-related propagule pressure in favouring alien plant species
369 establishment and spread on sub-Antarctic islands (Frenot et al., 2005; le Roux et al., 2013; Shaw,
370 2013), though we also observed a significant effect of abiotic conditions. Indeed, climate barriers
371 seemed to prevent alien plant species occurrence in the most environmentally stressful areas of the
372 island, as found in sub(ant)arctic mountain regions by Lembrechts et al. (2016). In particular, our
373 results suggested the existence of two main invasion patterns arising from the species-specific
374 dependence on human-related propagule pressure (Frenot et al., 2005; Shaw, 2013): low-spread
375 species (*P. pratensis*, *S. alsine* and *J. bufonius*) strongly relying on human-assisted dispersal along
376 hiking trails and in the vicinity of human settlements; and high-spread species (*C. fontanum*, *P. annua*
377 and *S. procumbens*) mostly limited by harsh climatic conditions at high altitudes. Differences in plant
378 invasiveness appeared to be influenced by residence time, life history and plant height, with old
379 residents and perennial short species being more invasive.

380 Due to their dependence on human-related variables, low-spread species were predicted to occur
381 mainly close to hiking paths and human settlements, pointing to the importance of anthropogenic
382 activities as key drivers of continuous propagule pressure favouring species establishment (Whinam
383 et al., 2005; Pickering & Mount, 2010). Once introduced through ship-to-shore transport, propagules
384 are then likely to be dispersed on hiking paths through trampling (Whinam et al., 2005). However,
385 the harsher environmental conditions characterizing the west side of Possession Island also limit the
386 occurrence of low-spread species to the east. In particular, the west-east gradient of annual
387 precipitation (Appendix S2, Figure S2.1) clearly overlaps with the low-spread species distribution
388 (Figure 3 and Appendix S6), suggesting that their establishment might be prevented in areas with
389 abundant precipitation. Nevertheless, the precipitation gradient is also connected to human presence,
390 so that in the western side of the island (less inhabited and more preserved) anthropogenic propagule
391 pressure is weaker. In any case, our results evidenced that low-spread species may lack important
392 adaptations to successfully colonise less disturbed areas with limiting abiotic conditions, while
393 remaining relegated to areas of high human presence.

394 On the contrary, high-spread species appeared weakly (yet positively) influenced by human-related
395 variables, suggesting that, in spite of the undisputed importance of anthropogenic activities in
396 promoting alien plants establishment (Whinam et al., 2005; Huiskes et al., 2014), high-spread species
397 may possess key traits releasing them from direct dependence on anthropogenic propagule pressure.
398 Consequently, these species appeared to be mostly limited by the extreme climatic conditions of the
399 high and cold inner sectors of Possession Island. This result is in line with the findings from
400 Chwedorzewska et al. (2015), who documented the rapid expansion of *Poa annua* from the Arctowski
401 research base (King George Island) towards wilder areas of the maritime Antarctic Peninsula.
402 Nevertheless, the low predictive performance of high-spread SDMs indicates that the occurrence of
403 these species is poorly explained by the influence of topoclimatic and human-related variables, so
404 that other factors not considered here (e.g. soil properties, plant-soil microbiota interactions, snow
405 cover) may play an important role in driving their distribution at even finer spatial resolutions. In this
406 regard, better performances of the SDMs for high-spread species could have probably been achieved
407 using alien species abundances, which are more informative of the relative habitat suitability than
408 presence-absence data (Howard et al., 2014).

409 Critically, although we managed to obtain relatively high-resolution topoclimatic data, it is important
410 to realize that the CHELSA climate for the island (1) might lack the accuracy it has at temperate
411 latitudes, being based on extrapolations from a single weather station, and (2) represents air
412 temperature only, while short plants as those analysed here relate more strongly to soil and near-
413 surface temperatures (Convey, Coulson, Worland, & Sjöblom, 2018; Lembrechts et al., 2019). This
414 highlights the need for *in-situ* soil- and near-surface temperature measurements in remote locations
415 to get more ecologically meaningful climate data (Lembrechts et al., 2020).

416 Although the small set of analysed alien plant species calls for caution in interpretation, we confirmed
417 here that certain plant traits confer greater invasiveness in sub-Antarctic environments. By relating
418 plant traits to species responses to human-related variables and analysing the effect of their interaction
419 on alien species occurrence, we found evidence that low-stature was a key feature that discriminated
420 invasive from non-invasive alien plant species under the harsh abiotic conditions of Possession Island.
421 Noteworthy, residence time and life history also appeared to affect species invasiveness.

422 As similarly reported by Mathakutha et al. (2019), we found that high-spread species were of shorter
423 statures than low-spread species. Consistently, we observed a sharper decrease in the occurrence
424 probability of taller plants moving away from both hiking paths and human settlements. As plant
425 height is generally associated with species adaptations to harsh environments (Cornelissen et al.,
426 2003) and, specifically, low-stature has been attributed to frost avoidance mechanisms in high
427 mountains (Márquez, Rada, & Fariñas, 2006; Ladinig, Hacker, Neuner, & Wagner, 2013), species of
428 shorter statures may be reasonably favoured in windy and cold sub-Antarctic environments
429 (Mathakutha et al., 2019) and therefore be more easily released of human dependence. Indeed, the
430 importance of functional traits providing tolerance to abiotic stress increases with environmental
431 harshness, even under strong anthropogenic disturbance (Zefferman et al., 2015). Further, our results
432 supported the hypothesis that residence time positively affects invasiveness (Lockwood et al., 2005;
433 Pyšek et al., 2015), though with some exceptions. Generally, old residents (e.g. *C. fontanum* and *P.*
434 *annua*) were less dependent on human-related propagule pressure and more widely spread than new
435 resident species. Nevertheless, among the old residents, *P. pratensis* was strongly dependent on
436 human-related variables and was still mostly restricted to the original introduction sites. On the other
437 hand, *S. procumbens*, a new resident, has been able to spread extensively and quicker than the other
438 (old residents) high-spread species. However, this might be due to the difference in plant height of
439 the two species: while *P. pratensis* is among the tallest analysed species, *S. procumbens* is the
440 shortest. The multi-SDM showed that perennials were slightly less dependent on human presence
441 than annuals (Figure 4c). Although annuals might benefit from high dispersal abilities (e.g. abundant
442 light seeds) and usually spread quicker and wider (Pertierra et al., 2017), perennials can sustain short
443 growing seasons (Frenot et al., 2001; Shaw, 2013) and potentially colonise harsher environments
444 (Dietz & Edwards, 2006). In our case, short perennials (e.g. *C. fontanum*) might be favoured over tall
445 annuals (e.g. *J. bufonius*) due to the interaction between stress-tolerant traits, such as plant height,
446 and high abiotic tolerance.

447 Albeit the interaction between vegetative reproduction and human-related variables was not included
448 in the most parsimonious multi-SDM, alien species may still benefit from sexual reproduction, as
449 suggested from the lower importance of human-related variables for the occurrence of alien plants
450 reproducing sexually in the single-SDMs (Appendix S7). As discussed above, the high dispersal
451 potential of sexually reproducing alien species, together with the ability to form rich seed banks
452 (Wódkiewicz et al., 2014), may foster their extensive spread as, for instance, observed for *P. annua*
453 in the Antarctic Peninsula (Pertierra et al., 2017). Nonetheless, by reproducing vegetatively,
454 perennials might outcompete annuals in maintaining viable and persistent populations during

455 unfavourable seasons. Finally, in spite of their acknowledged importance in conferring invasiveness
456 in sub-Antarctic islands (Mathakutha et al., 2019), we found no evidence of the role of seed and leaf
457 traits in affecting species dependence on human-related variables. This is possibly due to the small
458 set of analysed alien species or to the lack of abundance data, which might have prevented the
459 emergence of further functional traits-anthropogenic variables relationships.

460 Despite some limitations inherent to our dataset (e.g. limited number of species, lack of alien species
461 abundance data) and other typical limitations specific to invasive species distribution modelling (e.g.
462 underestimation of invasion potential, see Jiménez-Valverde et al., 2011), our approach allowed
463 identifying fine-scale drivers of alien plant species distribution, along with the most likely features
464 that favour their spread beyond sources of continuous human-assisted introductions. Combining
465 information on both plant invasiveness and sub-Antarctic islands invasibility, our study provides
466 relevant insights for anticipating future problematic invasions in these remote and unique
467 environments.

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478 **Authors’ contribution**

479 DR, MB, FM and JL conceived the idea; MB analysed the data with FM, MC and JL; MB led the
480 writing of the manuscript. All authors contributed critically to the drafts and gave final approval for
481 publication.

482 **Data availability statement**

483 Data and R code available on Zenodo: <https://doi.org/10.5281/zenodo.4287498>

484 **Conflict of interest disclosure**

485 The authors of this article declare that they have no financial conflict of interest with the content of
486 this article.

487 **References**

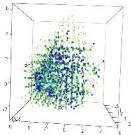
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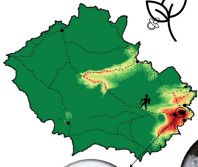
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LOW-SPREAD SPECIES



HIGH-SPREAD SPECIES

