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Title page

Once upon a time in the south: local drivers of plant invasion in the harsh sub-Antarctic islands

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Once upon a time in the south: local drivers of plant invasion in the harsh sub-Antarctic islands

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1 **Abstract**

2 **Aim**

3 To investigate the local effect of environmental and human-related factors on alien plant invasion in
4 sub-Antarctic islands. To explore the relationship between alien species features and dependence on
5 anthropogenic propagule pressure to unravel key traits conferring invasiveness in the sub-Antarctic.

6 **Location**

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

8 **Taxon**

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

10 **Methods**

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

17 **Results**

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

22 **Main conclusions**

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

27

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

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

31

32 **1. Introduction**

33 Sub-Antarctic islands are extremely remote territories which harbour a unique biodiversity with a
34 high degree of endemism (Shaw, 2013). As a consequence of their relatively recent discovery and
35 environmental harshness, these islands have long remained pristine and largely free of human
36 disturbances. Yet, due to the gradual relaxation of these natural barriers, sub-Antarctic islands are
37 now counted among the most threatened environments on Earth. In particular, invasion by alien
38 plants, boosted by ongoing climate changes and increasing human disturbances (Duffy & Lee, 2019;
39 Hughes et al., 2019), has become one of the main threats to the endemic biodiversity of these
40 territories, and is bound to rise in the next decades (Lebouvier et al., 2011; Hughes, Pertierra, Molina-
41 Montenegro, & Convey, 2015). Over the past century, alien plants have been increasingly introduced
42 in the sub-Antarctic region (Frenot et al., 2005; Huiskes et al., 2014). European whalers and scientific
43 activities, respectively in the 19th and 20th century, determined the first main introduction events
44 (Convey & Lebouvier, 2009; Shaw, 2013), while, since the mid-twentieth century, climate
45 modifications have progressively made sub-Antarctic islands more suitable to cold-tolerant alien
46 species (Shaw, 2013; Pertierra et al., 2017; Duffy & Lee, 2019). Nevertheless, despite their
47 demonstrated impacts on native biodiversity, little attention has been given to plant compared to
48 animal invasions in these islands (Molina-Montenegro et al., 2012; le Roux et al., 2013), leaving a
49 knowledge gap in the mechanisms underpinning plant invasion processes in these unique
50 environments (Greve, Mathakutha, Steyn, & Chown, 2017).

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

70 A lower dependence on human-related propagule pressure is potentially related to certain species
71 features which are more generally known to affect invasiveness. First of all, alien species with longer
72 residence times are more likely to become independent of anthropogenic propagule pressure (Wilson
73 et al., 2007; Pyšek et al., 2015). Second, certain plant traits are considered key for profiling successful
74 invaders (Pyšek & Richardson, 2008): invasive alien plants across most environments are growing
75 faster and taller than non-invasive alien species, and typically produce resource-acquisitive leaves
76 and many small seeds (van Kleunen, Weber, & Fischer, 2010; van Kleunen, Dawson, & Maurel,
77 2015). More specifically, Mathakutha et al. (2019) performed a first functional comparison between

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

85 Correlative species distribution models (SDMs) are statistical tools that model the species-
86 environment relationship relying on geo-referenced occurrence data and spatial environmental layers
87 (Guisan, Thuiller, & Zimmermann, 2017). SDMs already proved to be valuable tools for analysing
88 alien plant invasion in Antarctica and the sub-Antarctic regions. For instance, Pertierra et al. (2017)
89 modelled the distribution of *Poa annua* and *Poa pratensis* in the Antarctic peninsula as a function of
90 bioclimatic variables, while Duffy et al. (2017) generated future scenarios of invasion across
91 Antarctica and the sub-Antarctic regions using climate-based SDMs. Whilst these previous SDM
92 applications have revealed large-scale determinants of alien plant invasion in the Antarctic
93 biogeographic region, they have up till now failed to account for how environmental and
94 anthropogenic factors regulate alien plant distributions at the fine spatial resolutions meaningful for
95 local management. This is chiefly due to the lack of high-resolution environmental (e.g. climatic,
96 topographic) and human-related data layers, which limits the implementation of SDMs at fine spatial
97 resolutions in remote areas (Gutt et al., 2012).

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

118

119 **2. Materials and methods**

120 *2.1 Study area*

121 The study was carried out on Possession Island in the Crozet archipelago, which is included in the
122 *Réserve Naturelle Terres Australes Françaises* (RN-TAF) and listed as UNESCO World Heritage
123 site since 2019. Possession Island (Longitude: 51.7469, Latitude: -46.4046; EPSG: 4326) is
124 characterized by a complex topography, with an altitudinal gradient ranging from 0 to 934 m above
125 the sea level (*Pic du Mascarin*) over a relatively short spatial extent (147 km²). The island is
126 characterized by a typical sub-Antarctic climate, with mean annual temperature of 5.6 °C and annual
127 precipitation of 2300 mm (Météo France, data: 1960-2019). Frequent and strong western winds occur
128 throughout most of the year.

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

140 2.2 Study species

141 Despite the 68 alien species recorded on Possession Island (RN-TAF management plan 2018-2027:
142 https://taaf.fr/content/uploads/sites/2/2019/09/180607-Volet-A_pour-CNPN.pdf), only few have
143 established persistent populations (Frenot, Gloaguen, Massé, & Lebouvier, 2001). In this study, we
144 restricted our analysis to those alien plants that are either known to be generally widespread on sub-
145 Antarctic islands or are particularly widespread on Possession Island, and for which sufficient
146 occurrence data were available (total number of presences > 100). Specifically, we selected the
147 following species: *Poa annua* and *Poa pratensis* (Poaceae); *Cerastium fontanum*, *Sagina procumbens*
148 and *Stellaria alsine* (Caryophyllaceae); and *Juncus bufonius* (Juncaceae). The two grasses, *P. annua*
149 and *P. pratensis*, have colonized most of the sub-Antarctic islands (Shaw, 2013), and are the longest-
150 established alien plants in the Antarctic Peninsula (Pertierra et al., 2017). *Cerastium fontanum* and *S.*
151 *procumbens* are currently widely distributed in this environment (Frenot et al., 2005; Shaw, 2013)
152 with, in particular, *S. procumbens* exhibiting the highest rate of spread among the alien plants of
153 Marion and Prince Edward Islands (le Roux et al., 2013). Finally, both *J. bufonius* and *S. alsine*
154 currently occur at significant distances from the research station on Possession Island (Frenot et al.,
155 2001). While the former has been recently observed up to the Maritime Antarctica latitudes (Cuba-
156 Díaz, Fuentes, & Rondanelli-Reyes, 2015), the latter has been singled out by some authors as the
157 potentially most problematic future invasive plant species on Possession Island (Frenot et al., 2001;
158 Convey, Key, & Key, 2010).

159 2.2.1 Species distribution data

160 We analysed the invasion patterns of the six selected alien plant species relying on georeferenced
161 occurrence (presence/absence) data collected within the context of a yearly vegetation monitoring
162 survey carried out by the RN-TAF since 2010. The vegetation sampling is implemented within a
163 system of 675 squared cells 100x100-m, where floristic data (presence and abundance of vascular
164 plant species) are collected along with habitat characteristics through phytosociological *relevés*

165 (Dengler, 2016). In this study, we used data collected from 2010 to 2017 (3354 occurrences for the
166 selected species across 1572 sampled plot).

167 2.2.2 *Species features and functional trait data*

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

178 We then collated data on seven plant traits commonly used to synthesize species strategies known to
179 be related to invasiveness (van Kleunen et al., 2010; van Kleunen et al., 2015): (1) life history (annual
180 vs perennial); (2) plant height; (3) leaf area; (4) specific leaf area (SLA); (5) vegetative reproduction
181 (present vs absent, i.e. sexual and vegetative vs only sexual reproduction); (6) seed dry mass; and (7)
182 number of seeds/plant. We excluded traits related to flowering since pollinating insects are absent
183 from almost all sub-Antarctic islands (Convey et al., 2010). Life history, plant height and leaf area
184 relate to plant persistence and tolerance to environmental stress (Cornelissen et al., 2003; Pérez-
185 Harguindeguy et al., 2013). In addition, life history is used to assess maximum lifespan and plant
186 height is associated with competitiveness for light and whole plant fecundity (Pérez-Harguindeguy et
187 al., 2013). Specific leaf area is the one-sided leaf area per leaf mass and is associated with resource
188 acquisition and photosynthetic rate (Pérez-Harguindeguy et al., 2013). Reproduction strategy, seed
189 dry mass and number of seeds per plant do not only relate with species persistence, but also with
190 dispersal capacity (Ottaviani et al., 2020). In particular, alien species reproducing predominantly
191 sexually may benefit from lower dispersal limitation and greater genetic diversity (van Kleunen et
192 al., 2015). At the same time, while small and light seeds are better dispersed at longer distances, large-
193 seeded plants may benefit from more stored resources (van Kleunen et al., 2015).

194 Functional trait data collected in areas environmentally analogous to sub-Antarctic islands were
195 compiled from the literature (Frenot et al., 2005; Mathakutha et al., 2019). Whenever we could not
196 find information collected in comparable environments, we relied on functional trait data included in
197 the TRY database (Kattge et al., 2020). For each alien species, the dominant reproduction strategy in
198 the study area was assessed relying on expert-based knowledge (personal communication, Lebouvier,
199 M., & Bittebiere, A.K.).

200 2.3 *Topoclimatic layers*

201 To model the species-environment relationship at fine spatial resolution, we first downloaded coarse-
202 grained temperature (BIO1, BIO5 and BIO6 – annual mean temperature, max temperature warmest
203 month and min temperature coldest month) and annual precipitation (BIO12) grid layers at 1-km
204 resolution (at the equator) from the CHELSA database (Karger et al., 2017) and then disaggregated
205 their spatial resolution using physiographically informed models fitted through geographically
206 weighted regression (GWR; Fotheringham & Rogerson, 2008). This downscaling technique allows
207 statistically predicting the local value of the coarse-grain CHELSA climatic variables as a function
208 of environmental grid layers available at finer spatial resolution (30-m) and known to drive

209 microclimate heterogeneity (Lenoir, Hattab, & Pierre 2017; Lembrechts et al., 2019). GWR-derived
210 topoclimatic layers, beyond allowing to model the species-environment relationship at a more
211 meaningful spatial resolution, have already proved to account better for the complex interactions
212 between macroclimate and topography (Lenoir et al., 2017; Lembrechts et al., 2019).

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

217 *2.4 Human-related layers*

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

228 A network of hiking paths has been designed by the RN-TAF to restrict human movements for
229 wildlife conservation purposes, and walking these paths currently constitutes the only authorized way
230 to move across the island. As humans are a critical vector of propagule introduction and dispersal on
231 sub-Antarctic islands, we derived a 30-m resolution raster layer reporting the distance between any
232 location on Possession Island and the closest hiking path using the function “distance” from the
233 “raster” R package (Hijmans, 2019) (Appendix S3, Figure S3.2).

234 *2.5 Alien species distribution modelling*

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

249 Single-SDMs predictive performance was measured using the true skill statistic (TSS, equal to
250 sensitivity + specificity – 1; function “ecospat.max.tss”, R package “ecospat”; Broennimann, Di Cola,
251 & Guisan, 2018) computed on the testing datasets obtained through the environmental matching
252 described in Appendix S4. We used the TSS as it has desirable properties of other accuracy measures

253 (e.g. Kappa and AUC), while being unaffected by prevalence (Allouche, Tsoar, & Kadmon, 2006).
254 Also, we computed the deviance-based R^2 value as a measure of goodness-of-fit of each single-SDM.

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

258 *2.6 Relationship between plant traits and alien species dependence on propagule pressure*

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

266 Secondly, we investigated how the interaction between human-related variables and plant traits
267 affected alien species occurrence in a multi-species distribution model (multi-SDM), focusing on
268 those functional traits that showed some relationship with the dependence on human-related variables
269 in the single-SDMs. To this aim, we modelled the occurrence of all alien species together as a function
270 of topoclimatic and human-related variables by means of a logit binary GLM, including the
271 interaction between species identity and topoclimatic variables on the one hand and the interaction
272 between species functional traits and human-related variables on the other hand. This allowed
273 exploring how the effect of human-related variables on alien species occurrence varied according to
274 plant traits, while controlling for species-specific responses to topoclimate. To select the most
275 parsimonious model, we fitted all possible sub-models including different combinations of the
276 functional traits-anthropogenic variables interaction terms (function “dredge”, R package “MuMIn”;
277 Barton, 2019), always retaining the species-topoclimate interaction terms and the main effect of path
278 distance and least cost in each candidate sub-model. Then, we computed the sum of Akaike weights
279 for each model term and used the evidence ratio as a measure of the relative importance of variables
280 (Massol et al., 2007; Burnham & Anderson, 2002). Specifically, we computed the evidence ratio of
281 the i -th variable (ER_i) as the odds of its sum of Akaike weights:

$$282 \quad ER_i = \frac{w_i}{1 - w_i}$$

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

291 **3. Results**

292 *3.1 Effect of topoclimatic and human-related variables on single species occurrence*

293 Predictive performances of the single-SDMs varied greatly across species (Table 1): high values of
294 TSS were observed for *P. pratensis*, *S. alsine* and *J. bufonius* (0.80-0.82), while low values were

295 obtained for the remaining species (from 0.09 to 0.29). The R^2 values showed a similar trend, with
296 the highest value obtained for *J. bufonius* (0.48) and the lowest for *C. fontanum* (0.02).

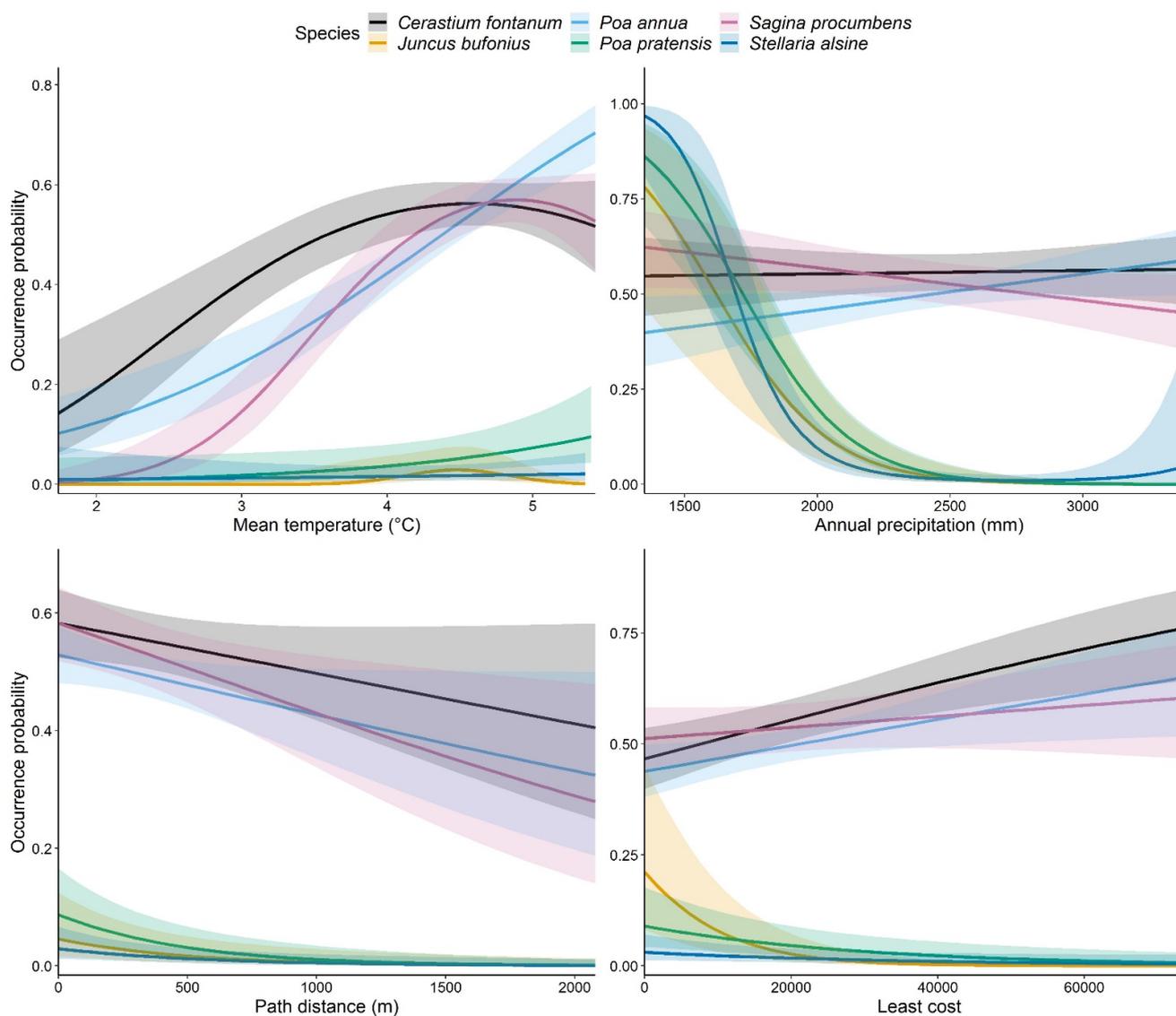
297 Overall, the occurrence of *P. pratensis*, *S. alsine* and *J. bufonius* appeared to be strongly conditioned
298 by both topoclimatic and human-related variables, while *C. fontanum*, *P. annua* and *S. procumbens*
299 were less affected by human-related variables (Table 1, Figure 1, 2).

300 All alien species, except *S. alsine*, exhibited a significant positive or humped-shaped relationship with
301 mean temperature (Table 1), meaning that their occurrence probability increased with increasing
302 temperature (Figure 1, Appendix S5). More specifically, the occurrence probability of *J. bufonius*, *S.*
303 *procumbens* and *C. fontanum* peaked at mean temperature values around 4.5 °C, while the presence
304 of *P. pratensis* and *P. annua* “linearly” increased with temperature.

305 Annual precipitation significantly affected the presence of *P. pratensis*, *S. alsine* and *J. bufonius*,
306 while it had a minor influence on the occurrence of the other species (Table 1). In particular, the odds
307 of finding *P. pratensis* and *J. bufonius* decreased approximately by 90% for each 500 mm increment
308 in annual precipitation, while the occurrence probability of *S. alsine* sharply decreased for annual
309 precipitation values above 1500 mm (Figure 1).

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

316 Least cost distance to settlements appeared to influence the occurrence of all analysed species except
317 *S. procumbens* (Table 1). In particular, the odds of finding *P. pratensis*, *S. alsine* and *J. bufonius*
318 decreased, respectively, by 17%, 13% and 44% for each increment of 5000 units of cost of travelling
319 a given path from a human settlement (Figure 1, Appendix S5). On the contrary, *C. fontanum* and *P.*
320 *annua* showed a positive relationship with least cost, with their odds of occurring increasing
321 respectively by 9% and 5% for each increment of 5000 units of cost of travelling a given path from a
322 human settlement (Figure 1 and Appendix S5).



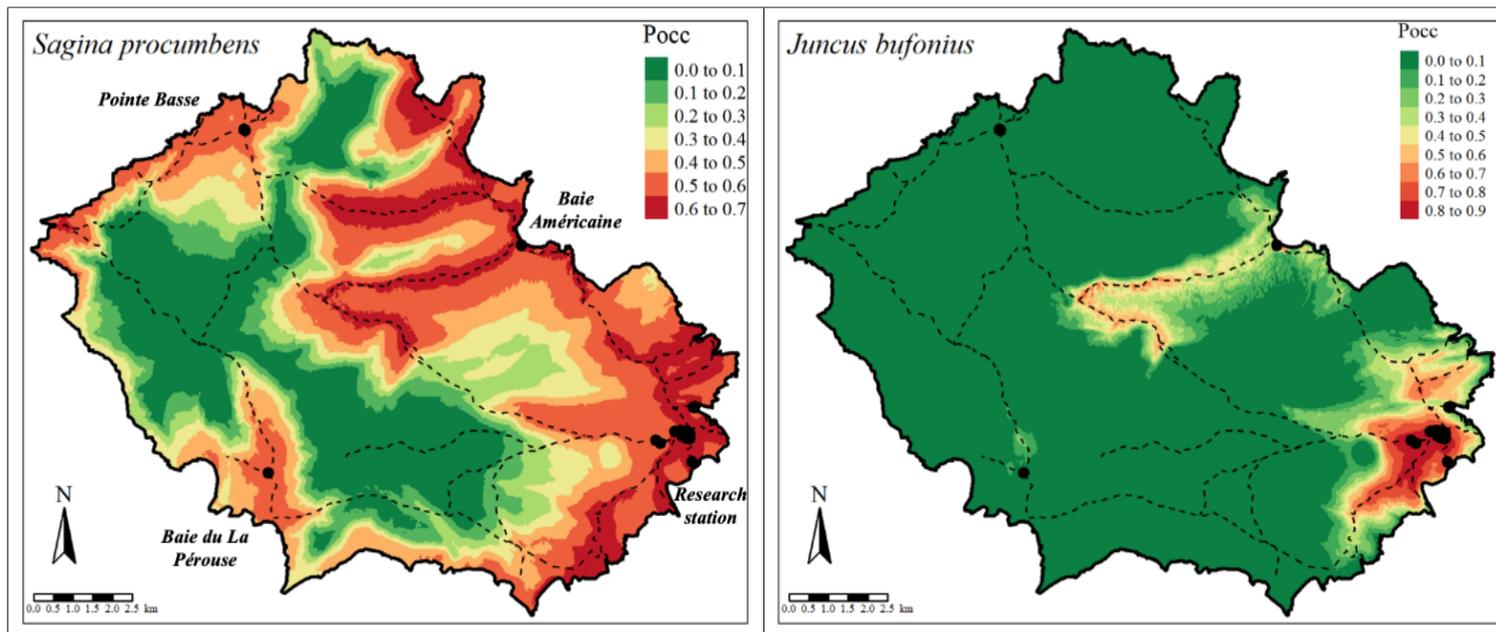
323

324 *Figure 1 – Response curves of the analysed alien species in the single-SDMs.*

325 *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 (***) $p <$*
 326 *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

327



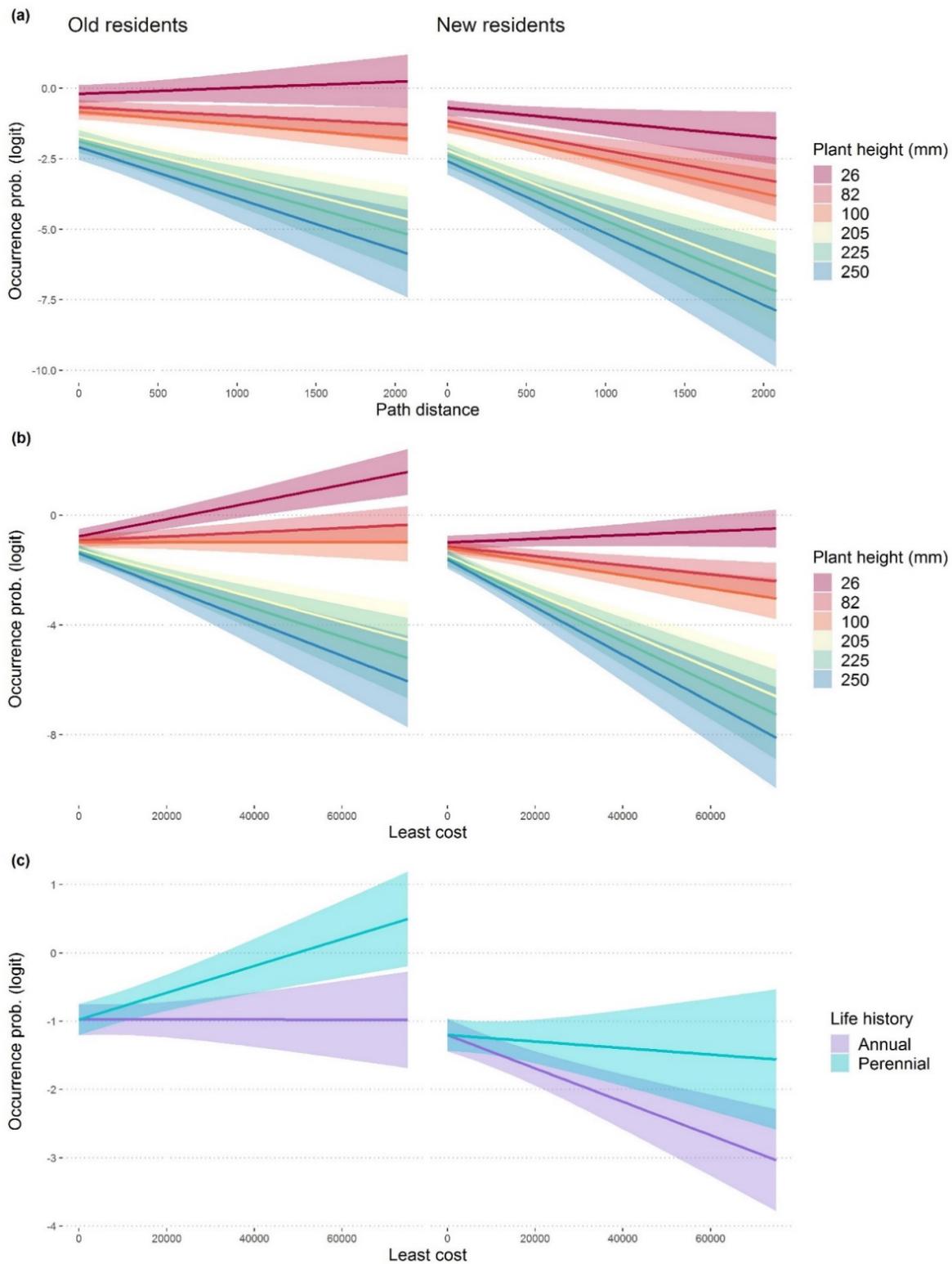
328

329 Figure 2 – Predicted occurrence of *Sagina procumbens* and *Juncus bufonius*. Pocc: occurrence probability. Dashed lines represent hiking paths, while black dots represent human
330 settlements. Occurrence maps of the other alien species are reported in Appendix S6 (Figure S6.4 and S6.5).

331 *3.2 Plant traits and species dependence on propagule pressure*

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

336 Then, the multi-SDM confirmed significant interactions of residence time, life history and plant
337 height with the human-related variables (Appendix S7, Figure S7.10). Residence time and plant
338 height appeared to interact with both human-related variables, while life history seemed to interact
339 only with least cost in determining alien species occurrence. In particular, the effect of human-related
340 variables on alien species occurrence varied with plant height, and while the occurrence probability
341 of taller plants sharply decreased moving far from human facilities, a weaker and sometimes opposite
342 trend was observed for shorter species (Figure 3a,b and Appendix S7, Figure S7.11). In addition, old
343 residents were on average less affected by the human-related variables than new residents (Figure
344 3a,b and Appendix S7, Figure S7.11a). Finally, perennials appeared to be on average less negatively
345 affected by least cost distance to human settlements than annuals (Figure 3c and Appendix S7, Figure
346 S7.11b,c).



347

348 *Figure 3 – Effect of the interaction between human-related variables and plant features on alien species occurrence*
349 *probability (logit scale). Panel (a): effect of the path distance-plant height interaction on old and new resident occurrence*
350 *probability. Panel (b): effect of the least cost-plant height interaction on old and new (annual) resident occurrence*
351 *probability. Panel (c): effect of least cost distance to human settlements on annual and perennial (100 mm height) alien*
352 *species occurrence (for both old and new residents). All plots are reported on a logit scale.*

353

354 4. Discussion

355 As hypothesized, both environmental and human-related variables locally affected alien species
356 occurrence on Possession Island, though with differences among species. Overall, results confirmed
357 the key role of human-related propagule pressure in favouring alien species establishment and spread
358 on sub-Antarctic islands (Frenot et al., 2005; le Roux et al., 2013; Shaw, 2013), though we also
359 observed a significant effect of abiotic conditions. Indeed, climate barriers seemed to prevent alien
360 species occurrence in the most environmentally stressful areas of the island (Lembrechts et al., 2016).
361 In particular, our results suggested the existence of two main invasion patterns arising from the
362 species-specific dependence on human-related propagule pressure (Frenot et al., 2005; Shaw, 2013):
363 low-spread species (*P. pratensis*, *S. alsine* and *J. bufonius*) strongly relying on human-assisted
364 dispersal along hiking trails and in the vicinity of human settlements; and high-spread species (*C.*
365 *fontanum*, *P. annua* and *S. procumbens*) mostly limited by harsh climatic conditions at high altitudes.

366 Due to their dependence on human-related variables, low-spread species were predicted to occur
367 mainly close to hiking paths and human settlements, pointing to the importance of anthropogenic
368 activities as key drivers of continuous propagule pressure favouring species establishment (Whinam
369 et al., 2005; Pickering & Mount, 2010). Once introduced through ship-to-shore transport, propagules
370 are then likely to be dispersed on hiking paths through trampling (Whinam et al., 2005). However,
371 the harsher environmental conditions characterizing the west side of Possession Island also limit the
372 occurrence of low-spread species to the east. In particular, the west-east gradient of annual
373 precipitation (Appendix S2, Figure S2.1) clearly overlaps with the low-spread species distribution
374 (Figure 2 and Appendix S6), suggesting that their establishment might be prevented in areas with
375 abundant precipitation. Nevertheless, the precipitation gradient is also connected to human presence,
376 so that in the west side of the island (less inhabited and more preserved) anthropogenic propagule
377 pressure is weaker. In any case, our results evidenced that low-spread species may lack important
378 adaptations to successfully colonize less disturbed areas with limiting abiotic conditions, while
379 remaining relegated to areas of high human presence (Lembrechts et al., 2018).

380 On the contrary, high-spread species appeared weakly (yet positively) influenced by human-related
381 variables, suggesting that, in spite of the undisputed importance of anthropogenic activities in
382 promoting alien plants establishment (Whinam et al., 2005; Huiskes et al., 2014), high-spread species
383 may possess key traits releasing them from direct dependence on anthropogenic propagule pressure.
384 Consequently, these species appeared to be mostly limited by the extreme climatic conditions of the
385 high and cold inner sectors of Possession Island. Furthermore, the low predictive performance of
386 high-spread SDMs indicate that the occurrence of these species can only be partly explained by the
387 influence of topoclimatic and human-related variables, so that other factors not considered here (e.g.
388 soil properties, plant-soil microbiota interactions, snow cover) may also play an important role in
389 driving their distribution at even finer spatial resolutions.

390 Critically, although we managed to obtain relatively high-resolution topoclimatic data, it is important
391 to realize that the CHELSA climate for the island 1) might lack the accuracy it has at temperature
392 latitudes, being based on extrapolations from a single weather station only, and 2) represents air
393 temperature only, while short plants as those analysed here relate more strongly to soil and near-
394 surface temperatures (Lembrechts et al., 2019). This highlights the need for *in-situ* soil- and near-
395 surface temperature measurements in remote locations to get more ecologically meaningful climate
396 data.

397 Although the small set of analysed alien plant species calls for caution in interpretation, we confirmed
398 here that certain plant traits confer greater invasiveness in sub-Antarctic environments. By relating

399 plant traits to species responses to human-related variables and analysing the effect of their interaction
400 on alien species occurrence, we found evidence that low-stature was a key feature that discriminated
401 invasive from non-invasive alien species on Possession Island. However, residence time and life
402 history also appeared to affect species invasiveness.

403 High-spread species were shorter than low-spread species (Mathakutha et al., 2019). Consistently, we
404 observed a sharper decrease in the occurrence probability of taller plants moving away from both
405 hiking paths and human settlements. As plant height is generally associated with species adaptations
406 to harsh environments (Cornelissen et al., 2003) and, specifically, low-stature has been attributed to
407 frost avoidance mechanisms in high mountains (Márquez, Rada, & Fariñas, 2006; Ladinig, Hacker,
408 Neuner, & Wagner, 2013), shorter species may be reasonably favoured in windy and cold sub-
409 Antarctic environments (Mathakutha et al., 2019) and therefore be more easily released of human
410 dependence. Indeed, the importance of functional traits providing tolerance to abiotic stress increases
411 with environmental harshness, even under strong anthropogenic disturbance (Zefferman et al., 2015).
412 Further, our results supported the hypothesis that residence time positively affects invasiveness
413 (Lockwood et al., 2005; Pyšek et al., 2015), though with some exceptions. Generally, old residents
414 (e.g. *C. fontanum* and *P. annua*) were less dependent on human-related propagule pressure and more
415 widely spread than new resident species. Nevertheless, among the old residents, *P. pratensis* was
416 strongly dependent on human-related variables and was still mostly restricted to the original
417 introduction sites. On the other hand, *S. procumbens*, a new resident, has been able to spread
418 extensively and quicker than the other (old residents) high-spread species. However, this might be
419 due to the difference in plant height of the two species: while *P. pratensis* is among the tallest analysed
420 species, *S. procumbens* is the shortest. The multi-SDM showed that perennials were slightly less
421 dependent on human presence than annuals (Figure 3c). Although annuals might benefit from high
422 dispersal abilities (e.g. abundant light seeds) and usually spread quicker and wider (Pertierra et al.,
423 2017), perennials can sustain short growing seasons (Frenot et al., 2001; Shaw, 2013) and potentially
424 colonize harsher environments (Dietz & Edwards 2006). In our case, short perennials (e.g. *C.*
425 *fontanum*) might be favoured over tall annuals (e.g. *J. bufonius*) due to the interaction between stress-
426 tolerant traits, such as plant height, and high abiotic tolerance.

427 Though the interaction between vegetative reproduction and human-related variables was not
428 included in the most parsimonious multi-SDM, alien species may still benefit from sexual
429 reproduction, as suggested from the lower importance of human-related variables for the occurrence
430 of alien plants reproducing sexually in the single-SDMs (Appendix S7). As discussed above, the high
431 dispersal potential of sexually reproducing alien species may foster their extensive spread as, for
432 instance, observed for *Poa annua* in the Antarctic Peninsula (Pertierra et al., 2017). Nonetheless, by
433 reproducing vegetatively, perennials might outcompete annuals in maintaining viable and persistent
434 populations during unfavourable seasons. Finally, in spite of their acknowledged importance in
435 conferring invasiveness in sub-Antarctic islands (Mathakutha et al., 2019), we found no evidence of
436 the role of seed and leaf traits in affecting species dependence on human-related variables. This is
437 possibly due to the small set of analysed alien species, which might have prevented the emergence of
438 further functional traits-anthropogenic variables relationships.

439 Overall, our approach allowed identifying fine-scale drivers of alien species distribution on sub-
440 Antarctic islands, along with the most likely features that favour their spread beyond sources of
441 continuous human-assisted introductions. Despite some limitations (e.g. limited number of species),
442 our study opens avenues for a more targeted management of alien plant invasions in these unique
443 environments, potentially allowing to anticipate future problematic invasions.

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452 **Authors’ contribution**

453 DR, MB, FM and JL conceived the idea; MB analyzed the data with FM and MC; MB led the writing
454 of the manuscript. All authors contributed critically to the drafts and gave final approval for
455 publication.

456 **Data availability statement**

457 Data and R code available on Zenodo: <https://doi.org/10.5281/zenodo.3951465>

458 **Conflict of interest disclosure**

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