Human activities, propagule pressure and alien plants in the sub-Antarctic: Tests of generalities and evidence in support of management

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ABSTRACT

Despite concerns about the richness of plant invaders on islands, and their likely effects on local systems, impacts of these species seem to be small. However, this may be due to an absence of information on impacts, including changing species occupancy and forecast occupancy, rather than lack of impact per se. Here we use the plant invaders on the sub-Antarctic Prince Edward Islands (PEIs) and spatially explicit modeling of presence–absence survey data to demonstrate that the geographic extent of many invasives is increasing and is forecast to lead to occupancy of >60% of the islands' surface area by 2060, with ongoing climate change. In keeping with theory, proximity to human activity, neighboring populations (i.e. propagule pressure) and residence time, along with more minor contributors such as elevation, explain >50% of the variation in the occupancy of each of the six main invasive species on the islands. Human disturbance and changing climates seem to have led to recent increases in the rate of range expansion. Our results suggest that impacts of island plant invaders may be more significant than previously estimated, largely owing to prior data deficiency. More specifically they also suggest that control plans for the PEI (and other Southern Ocean Islands, SOIS) should first target less widely distributed species, which are invasive elsewhere. They also indicate that for the other SOIS, and for Antarctica, surveillance and anticipatory control plans should be in place.

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1. Introduction

The introduction of non-indigenous species is a major cause of biodiversity change, especially on islands. These species modify diversity, alter ecosystem functioning, and often cause population declines (D'Antonio and Dudley, 1995; Blackburn et al., 2004; Pyšek et al., 2012). However, plant invaders are generally thought to be having less significant an impact on island systems than others such as mammals (compare Davis, 2003; Sax and Gaines, 2008 with Blackburn et al., 2004). Indeed, urgent calls for further investigation of island plant invaders have been made (e.g. Sax and Gaines, 2008). Vascular plants are the most species rich of the groups that have been introduced to and become invasive on the islands of the Southern Ocean, which are globally significant by virtue of their location, endemicity, and seabird populations (Convey and Lebouvier, 2009). Nonetheless, the extent of the impacts of invasive plants, by comparison with those of other taxa such as mammals, appears relatively minor (Frenot et al., 2005), and mostly indirect (Frenot et al., 2001; but see also Gremmen et al., 1998). Either the plant invasives are only having a minor impact, or the situation is a consequence of limited explicit investigation of the impacts of invasive plants across the region (for discussion see Vilà et al., 2010; Hulme et al., in press).

If impact for a given area is considered the product of the number of species that has undergone a transition from established to invasive, the range size (or average density or biomass) of each species, and effect per individual or unit biomass (see Parker et al., 1999; McGeoch et al., 2010), few assessments for the Southern Ocean Islands (SOIS) have indeed been made. Investigations of the number and identity of introduced vascular plant species per island are common (Bergstrom and Smith, 1990). However, assessments of changes in the status of species and in their geographic range are less widely undertaken (e.g. Gremmen and Smith, 1999; Scott and Kirkpatrick, 2005). For only one of the 25 SOIS

has a spatially explicit approach been used to document both gains and losses in area of occupancy (Frenot et al., 2001). Investigations of abundance and local impacts are less common still (Gremmen et al., 1998; Scott and Kirkpatrick, 2005).

Remedying this situation is of considerable conservation significance. If invasive plants are having minimal impact across the region, conservation spending might better be directed at other taxa, such as mammals, which do have significant impacts (Frenot et al., 2005). However, if the purported absence of impact is a consequence of limited investigation, impacts will accumulate until they can no longer be ignored, by that time likely being irreversible (Vilà et al., 2011; McConnachie et al., 2012). Perhaps for this reason, most SOIS management plans currently take a precautionary approach, recommending eradication of alien plants where feasible (de Villiers et al., 2005). However, control of plant invaders across the SOIS is uncommon, and has mostly been piecemeal, largely because the information required for prioritization and planning is absent (Grant et al., 2012). For the same reason, few generalities concerning the mechanisms underlying changes in invasion status (e.g. propagule pressure, residence time) have been developed across the region (unlike the case elsewhere – Křivánek et al., 2006; Gravuer et al., 2008), so further hampering invasion management (for general discussion see McGeoch et al., 2012), and failing to capitalize on an opportunity to test theory (e.g. Wilson et al., 2007) in a relatively remote system. Overall, the situation is not conducive to efficient conservation management, especially given forecasts of increasing invasion impacts for the SOIS (Frenot et al., 2005), and for Antarctica, which is prone to invasion by the same suite of species (Chown et al., 2012a).

Here we quantify the spatial distribution and local species richness patterns of introduced plant species at the sub-Antarctic Prince Edward Islands, as an exemplar system for the SOIS region. We model the factors explaining the current distribution and local richness of these species and, in conjunction with data from previous studies, estimate maximum rates of change in distributions on the islands. We also estimate: (1) the extent to which residence time has played a role in determining the current extent of invasion; (2) the likely equilibrium ranges of the species; and (3) the expected distributions of these species in 50 years' time given current rates of spread of each species and realized climate change (le Roux and McGeoch, 2008). In doing so we follow the useful development of such approaches applied to alien plant invasions in both continental and island settings (e.g. Schussman et al., 2006; Senan et al., 2012).

2. Methods

2.1. Site, species and residence time

The Prince Edward Islands (46°54′S, 37°48′E) comprise Marion Island (MI: 293 km^2, 1 230 m elevation) and Prince Edward Island (PEI: 45 km^2, 672 m elevation). They have a cool, oceanic climate and a tundra-type indigenous vegetation, varying from tussock grassland and mires in the lowlands to an impoverished polar desert at the higher elevations (Chown and Froneman, 2008). The islands were discovered in 1673, with the first documented landing in 1803/1804 (Chown and Froneman, 2008). Non-indigenous plants were first recorded in 1873 (Cerastium fontanum on MI; Moseley, 1874). In 1947 the islands were annexed by South Africa, with a continuous scientific presence since then on MI (Chown and Froneman, 2008). The first comprehensive survey of the vascular flora took place in 1965/1966 (Huntley, 1971), and biological research has since been continuous (Chown and Froneman, 2008), with the development of a network of field accommodation (huts) around MI in the 1970s (Fig. 1). Human activity on MI peaked during the feral cat, Felis catus L., eradication pro-

gramme (1986–1991), involving many field workers moving between the huts and the research station. Prince Edward Island is less commonly visited and now has a higher conservation status than MI (de Villiers et al., 2005).

Seventeen non-indigenous vascular plant species have been introduced to and are currently established on MI, although some are of uncertain status (Table 1). Only three non-indigenous species have been recorded on PEI, all of which are still present (Ryan et al., 2003). Since Huntley's (1971) first assessments, comprehensive surveys of the alien vascular plant species on MI have been undertaken on a sporadic basis (Gremmen, 1975, 1981; Bergstrom and Smith, 1990; Gremmen and Smith, 1999), with fewer assessments for PEI (Bergstrom and Smith, 1990; Ryan et al., 2003; Table A1). Several of the previous studies have been comprehensive, with the authors suggesting that the spatial distributions of the species were well documented (Gremmen and Smith, 1999: 407; Ryan et al., 2003: 556).

To assign a year of first detection to each species we examined the literature on non-indigenous vascular plants recorded on the islands, and confirmed previous herbarium records (at Royal Botanical Gardens, Kew, UK). However, for most species, the first year of detection may not reflect the year of establishment owing to the absence of previous surveys (e.g. species recorded by Huntley, 1971) and to the taxonomic difficulty of some groups (Gremmen and van der Meijden, 1995). Thus, residence times (first year of this study (2006) minus year of first detection) should be considered a minimum estimate (Wonham and Pachepsky, 2006).

2.2. Surveys

Data from previous surveys (Table A1) were considered representative of the occurrence of the species unless the authors of the works either suggested that this was not the case or indicated that previous studies may have been so compromised (see Gremmen and Smith, 1999). In previous studies, the occurrence data for many of the species were either described by location or presented as mapped extents of occurrence (sensu Gaston, 1990) (e.g. Bergstrom and Smith, 1990; Ryan et al., 2003). Locality data from these studies were digitized (ARcGIS 9.3.1, ESRI, California) as presence data at a 0.5 × 0.5 min (hereafter half-minute) grid resolution (~926 × 635 m). This was done separately for each species, each of the islands and each of the years for which data were available (Table A1). Although the more cryptic species (e.g. Agrostis castellana) may have gone undetected, we made the assumption that the previous data represented a reasonable estimate of true absence. That is, at least since Gremmen's (1975) assessment, the now digitized data could be considered a minimum assessment of area of occupancy (Gaston, 1990) at a half-minute grid resolution for each species. Although such an assumption is complicated by the fact that the original occurrence maps may have included some half-minute grids unoccupied by the species concerned, the relationship between area of occupancy and extent of occurrence is typically strong (Gaston, 1990). Moreover, we selected the half-minute resolution to minimize this likely problem, acknowledging that resolution has an effect on estimates of occupancy (McGeoch and Gaston, 2002).

For the current survey, the half-minute resolution grid was retained for Marion Island. Over a period of 1 year (April 2006–May 2007) the center point of each grid was visited (below 500 m a.s.l., see Fig. 1 and Appendix 1) and a survey made of all non-indigenous vascular plant species within an 8 × 8 m square. Species absences were formally recorded, as was altitude, substrate type, vegetation type, aspect, and slope (see Chown and Froneman, 2008 for descriptions of substrate and vegetation types). As part of the survey protocol, all alien vascular plant species were also recorded en route to these sites. These 'ad hoc' re-
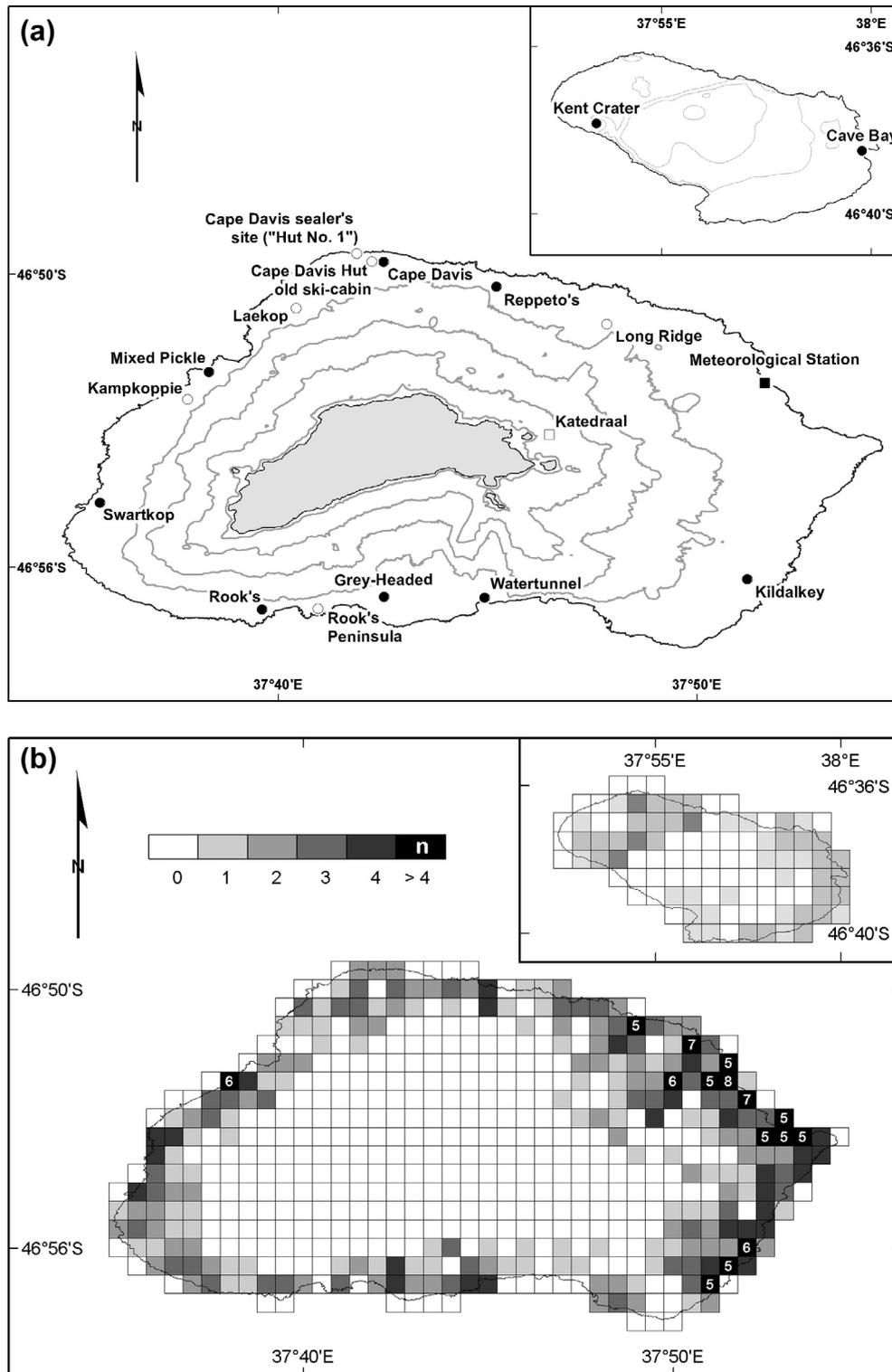
Fig. 1. (a) Topographic map of Marion Island indicating the location of the meteorological and research station (■; filled square), the contemporary field huts (●; filled circles), previous field hut sites (○; empty circles), and one contemporary, high-elevation field hut (□) that was excluded as a putative introduction site given that no indigenous vascular plants occur there. Areas above 840 m a.s.l., the current upper altitudinal limit to vascular plants, are shaded gray. In the inset, the location of two putative introduction sites (Cave Bay and Kent Crater) are mapped. On both maps, 200 m contour lines are plotted. (b) Alien plant species richness across Marion Island (Prince Edward Island in the inset) plotted at a half-minute resolution. Numbers in black cells indicate species richness when greater than four alien species.

cords were made by recording the species, spatial position (hand held GPS receiver, Garmin eTrex Vista, USA), and environmental variables as above, with additional information provided for large patches (Appendix 1). Spatial records were obtained for 2 317 unique localities (2 349 presence records across 14 species). Supplementary surveys for all areas including those above 500 m a.s.l. (Appendix 1) contributed a further 1 343 unique locations and 392 presence records.

The time available for surveys on Prince Edward Island was limited to 7 days in December 2008 (PGR/JDS/SLC) and 4 days in April

Table 1

The established, introduced vascular plant species found on the Prince Edward Islands, including details of original discovery, estimated original occupancy, occupancy based on data from this study, and rate of spread. Original occupancy is presented as the number of half-minute grid cells (~0.589 km^2) occupied when discovered, with more accurate estimates from the original (or a subsequent) source provided in parentheses where available. Current occupancy is also presented as the number of occupied half-minute grid cells, with an estimate of area provided in parentheses (for widespread species calculated as the number of cells multiplied by the total area of one half-minute grid cell; otherwise derived from the published literature or an estimate of patch size based on visual surveys). The species marked with an asterisk are of uncertain status and the mnemonics SS and WS refer to the suspected introduction either by sealers or following the establishment of the research station (after Chown and Froneman, 2008).

Species	Year discovered	Original collection or record attributable to	Estimated original occupancy (half-minute cells)	Estimated current occupancy (half-minute cells)	Rate of spread since discovery (km^2 year^{-1})
Marion Island					
Potamogeton nodosus Poir.*	1965	B.J. Huntley	1	1	0
Elymus repens (L.) Gould	1965 SS	B.J. Huntley	1 (250 m^2)	1 (250 m^2)	0
Agrostis castellana Boiss et Reut.	1975	N.J.M. Gremmen	2 (2 sites)	Unknown[a]	Unknown
Agrostis gigantea Roth	1994 WS	N.J.M. Gremmen	1 (<200 m^2)	1 (<200 m^2)	0
Agrostis stolonifera L.	1965	B.J. Huntley	1	40 (23.6 km^2)	0.56
Alopecurus geniculatus L.	1965 SS	B.J. Huntley	1 (<1 m^2)	1?	0
Festuca rubra L.	1965 SS	B.J. Huntley	1 (<100 m^2)	1 (<100 m^2)	0
Poa annua L.	1948 SS	Dike	1	147 (86.6 km^2)	1.48
Poa pratensis L.	1965 WS	B.J. Huntley	1	21 (12.4 km^2)	0.29
Juncus cf. *effusus* L.*	1965	B.J. Huntley	1	3 (1.8 km^2)	0.03
Luzula cf. *multiflora* (Retz.) Lej.*	1999	M.N. Bester & B. Stewart	1	2 (1.2 km^2)	0.08
Cerastium fontanum Baumg.	1873 SS	H.N. Moseley	1	155 (91.3 km^2)	0.68
Sagina procumbens L.	1965 WS	B.J. Huntley	1	129 (76 km^2)	1.84
Stellaria media (L.) Vill.	1873 SS	H.N. Moseley	1	31 (18.3 km^2)	0.13
Rumex acetosella L.	1953 SS	J.J. Van der Merve	1	2 (1.2 km^2)	0.01
Unidentified shrub*	2004	V.R. Smith	1 (one plant)	1 (one plant)	0
Prince Edward Island					
Poa annua	1966 SS	B.J. Huntley	1	16 (9.4 km^2)	0.22
Cerastium fontanum	1987	D.M. Bergstrom and V.R. Smith	1	7 (4.1 km^2)	0.19
Sagina procumbens	1997	N.J.M. Gremmen and V.R. Smith	1	37 (21.8 km^2)	2.36

[a] *A. castellana* cannot easily be distinguished from *A. stolonifera*, and its distribution is therefore assumed to be equal to or smaller than that of *A. stolonifera*. The grass *Holcus lanatus* was found in 2011 and is not listed here but only occurs at the meteorological station.

2010 (AMT/GM). In consequence, the half-minute resolution survey could not be undertaken. Rather, all previous sites at which alien species had been found were assessed and, during traverses for other work, the position of all occurrences of the three known alien species was recorded. In addition, 100, 1 × 1 m grid cells, haphazardly distributed across the island, were surveyed for the presence or absence of alien vascular plant species. No alien species new to the island were recorded. Additional absence records were generated from the GPS tracks of two observers (AMT/GM) who were recording alien species presences. Therefore, points on their tracks that were not presence records for these species reflect true absences (track points were reduced until all records were separated by at least 30 m). This provided a total of 1 181 unique localities and 215 presence records for the three alien species on Prince Edward Island.

2.3. Analyses

Survey data obtained above were rescaled to the half-minute grid resolution used for both islands for the previous survey data. Given the extent of the survey effort, unoccupied cells were considered real absences for mapping purposes and for the calculation of area of occupancy. The latter was calculated as the product of the number of grid cells occupied by each species and the area of each cell (c. 0.589 km^2). Change in occupancy was calculated per species as the difference in number of half-minute resolution grid cells occupied between two time periods (e.g. 2006 grids minus 1965 grids). The relationship between residence time and current occupancy for the species established on Marion Island was assessed using reduced major axis regression, with significance assessed through permutation (Legendre and Legendre, 1998).

To model the relationship between species occupancy and the environmental variables, presence and absence point data for the six widespread alien species on MI were analyzed using generalized linear models (GLM; spatially non-explicit) and generalized estimating equation models (GEE; spatially explicit) (see Bini et al., 2009 for rationale). Candidate predictor variables included altitude (as linear and quadratic terms because the altitude-diversity relationship is variable, Rahbek, 2005), vegetation type, substrate type, aspect and slope, a variable indicating the distance to the nearest population of the same species, and variables indicating distance from the research station and distance to the closest field hut (as two separate variables). Following a best subsets regression approach, all combinations of predictor variables were modeled. The resulting models were ranked by AIC (Akaike's Information Criterion; GLM) or QIC (quasi-likelihood-under-the-independence-model information criterion; GEE), after the exclusion of models with strongly collinear predictor variables (assessed with the variance inflation factor, VIF; Fox and Monette, 1992; Appendix 1). Analyses were repeated using a larger dataset, including records without vegetation, slope, aspect or substrate data (chiefly *ad hoc* records collected during other fieldwork). A best subsets approach was used again, with five candidate predictor variables (altitude, altitude^2, distance to closest field hut, distance to research station, distance to nearest conspecific population). The altitude^2 term was not included in models of *Agrostis stolonifera* distribution as it never gave a better fit than the linear altitude term and caused models not to converge.

Because MI is warming and drying with pronounced influences on the elevational range of many indigenous vascular plant species (le Roux and McGeoch, 2008), model assessments were also used to make qualitative predictions of further changes to the distribution of the six widespread alien species assuming a similar rate of climate change (and biotic response) over the next 50 years (recalling the possible effects of non-equilibrium conditions on model outcomes, Elith and Leathwick, 2009). The highest occurrence

and the 95th percentile of altitudes at which each species was recorded were used as two measures of the maximum elevations currently environmentally suitable for each alien species. Island area below each species' upper altitudinal limit was then summed (calculations based on a 20 m resolution digital elevation model; see Meiklejohn and Smith, 2008 and Appendix 1) as an estimate of the species maximum potential range. However, due to the scarcity of *Stellaria media*, *A. stolonifera* and *Poa pratensis* in fellfield vegetation and on scoria (present in less than 1% of records in fellfield vegetation; Table A2), their analyses were repeated after these habitat types were excluded.

All alien species presence records were used to calculate alien species richness across Marion Island in the 401 sampled half-minute grid cells. Eleven environmental variables were calculated for each grid cell (Appendix 1) and their relationship with species richness examined using GLM and spatial GEE models.

These analyses were repeated for Prince Edward Island. The distributions of its three alien plant species were modeled using GLM and GEE models, although fewer explanatory variables were available (altitude, altitude^2, the minimum distance to the nearest population of the same species, the distance to two putative introduction sites; Cave Bay and Kent Crater). Alien species richness across the island was also modeled using GLM and GEE models, acknowledging the small range of variation therein, with topographic parameters estimated from a digital elevation model (Appendix 1).

3. Results

3.1. Distribution and spread

Nine alien species have not increased their area of occupancy markedly or at all since their discovery (Table 1; Figs. A1 and A2). By contrast, six species have spread extensively. *S. media* is the one exception with an initial increase in area of occupancy and subsequent decline (Fig. 2). *Luzula* cf. *multiflora* has spread, but not sufficiently to extend beyond two grid cells. At present, *C. fontanum*, *P. annua* and *Sagina procumbens* are the most widespread species, with *S. procumbens* having the fastest rate of spread (Table 1 and Fig. 3).

3.2. Correlates of species distributions

For MI, the best models for the occupancy of the six most widespread alien species, using the extended dataset, all included nearest conspecific population: the likelihood of a species presence increases significantly with proximity to other individuals of the same species (Table 2). Some measure of altitude was also included in all models, although its negative effect typically was weak. The likelihood of presence was predicted consistently by the proximity of the research station and field huts in a smaller group of species, viz. *C. fontanum*, *P. annua*, and *P. pratensis*. In all cases, probability of presence declined with increasing distance from a human use
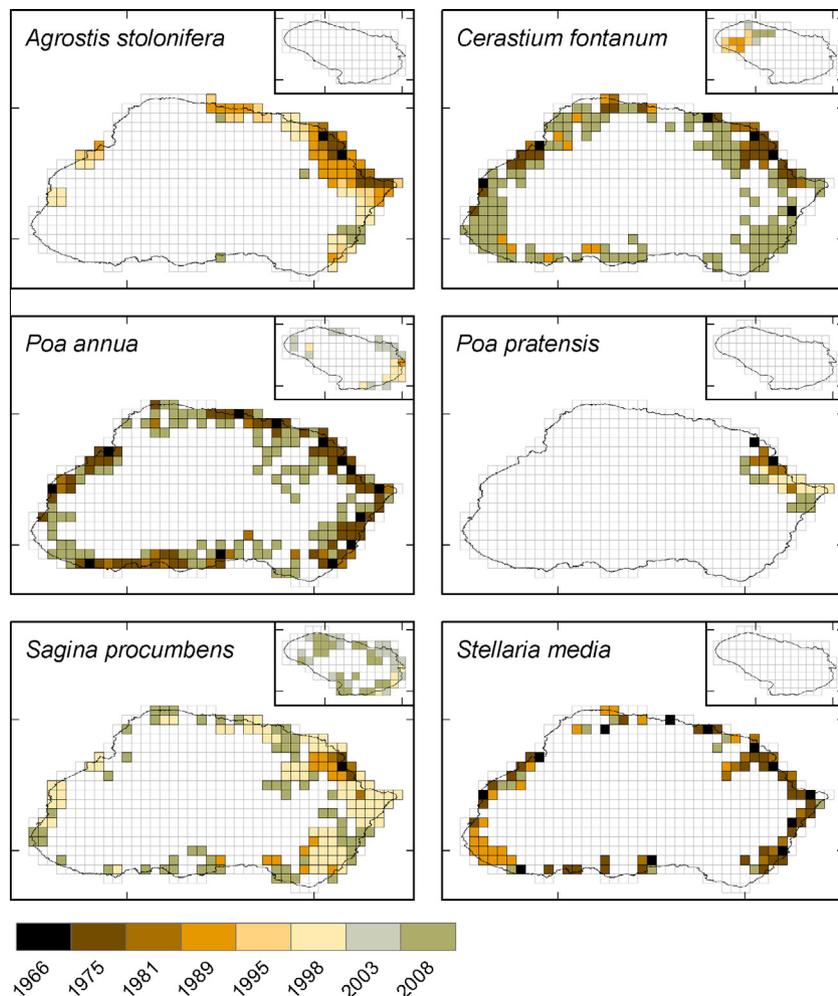

Fig. 2. Distribution of the six widespread alien vascular plant species on Marion Island (main figure) and Prince Edward Island (inset). Occupied half-minute grid cells are colored to indicate the year when the species was first recorded (see Table A1 for the details of previous surveys).
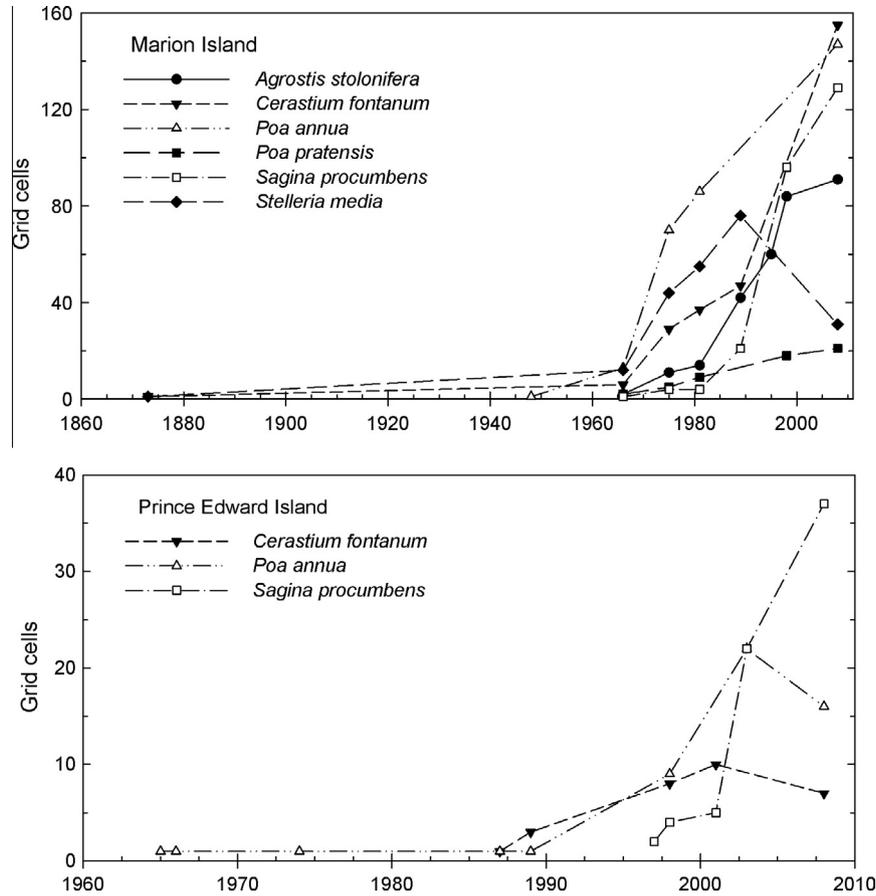
Fig. 3. Spread of the six widespread invasive alien species on Marion Island and Prince Edward Island. The number of occupied half-minute grid cells was set to one (i.e. 0.589 km²) for the date of first recording (unless the first record indicated otherwise), although the species may well have been present before then and at the time of first recording may have been more widespread. Note that the lag phases of the species in common to the two islands are different in duration.

Table 2
Best fit generalized linear (GLM) and estimating equations (GEEs) models for the presence/absence of the six widespread alien vascular plant species on the Prince Edward Islands (see also Tables A5 and A6). The Akaike weight (AIC$_w$, or GEE equivalent, the QIC$_w$), adjusted D^2 (or equivalent measure of explained deviance for GEE models, the adjusted R^2) are shown for each model, together with the estimates of the coefficients of all the predictors retained in the best fit model. Coefficients differing significantly from zero are shown in bold.

Marion Island Species	Model	AIC$_w$ (QIC$_w$)	Adj. D^2 (Adj. R^2)	n	Coefficient estimates					
					Intercept	Altitude	Altitude^2	NCP[a]	Base	Min. hut
A. stolonifera	GLM	0.37	0.61	1207	**1.745**	**−0.019**		**−6.226**		
	GEE	0.42	0.60	1207	**1.926**	**−0.021**		**−5.490**	−0.034	
C. fontanum	GLM	0.40	0.50	1227	**2.697**		**−0.00001**	**−5.319**		**−0.190**
	GEE	0.51	0.57	1227	**2.193**		**−0.00001**	**−4.949**	0.003	−0.104
P. annua	GLM	0.47	0.54	1165	**3.362**		**−0.00001**	**−5.824**	**−0.045**	**−0.217**
	GEE	0.55	0.62	1165	**2.962**		**−0.00001**	**−5.586**	−0.042	−0.150
P. pratensis	GLM	0.27	0.67	447	8.586		−0.00006	**−5.437**	**−0.405**	**−0.883**
	GEE	0.70	0.69	447	3.968		−0.00005	**−3.851**	−0.184	−0.347
S. procumbens	GLM	0.40	0.52	1580	**2.02**	**−0.004**		**−5.933**		
	GEE	0.53	0.61	1580	**1.68**	−0.001		**−6.033**		
S. media	GLM	0.19	0.43	906	0.188		−0.00003	**−2.062**		
	GEE	0.18	0.37	906	0.766	**−0.008**		**−2.072**		−0.084
					Intercept	Altitude	Altitude^2	NCP[a]	Kent Crater	Cave Bay
Prince Edward Island										
C. fontanum	GLM	0.20	0.79	1100	**4.724**			**−11.064**	**−0.949**	
	GEE	0.20	0.68	1100	5.491	0.009		**−10.918**	−0.805	−0.272
P. annua	GLM	0.29	0.60	1081	**1.403**			**−30.936**		**0.395**
	GEE	0.31	0.48	1081	1.287		**<0.001**	**−32.717**		0.456
S. procumbens	GLM	0.69	0.51	1120	**4.175**		**<0.001**	**−10.876**	**−0.527**	
	GEE	0.69	0.47	1120	−0.765	**0.009**		**−9.022**		0.409

[a] NCP = distance to nearest conspecific population, Base = distance to the research station, Min. hut = distance to the closest field research hut or the research station, Kent crater = distance to Kent Crater, Cave Bay = distance to Cave Bay (all measured in km).

area. The models typically explained more than 50% of the variation in the occupancy of the species, except for *S. media* where the explanatory power was lower. Differences between the GLM and GEEs in predictors included, variance explained, and the size and direction of the estimates were small.

Inclusion of slope, aspect, lava type and vegetation type data in the more restricted data set did not lead to large increases in the percentage deviance explained by the models (Table A3). Typically, the variables shared between this analysis and the previous one had the same sign and size. Although the additional variables often entered the best models, they frequently were not significant or had small effect sizes. Notable exceptions were for vegetation type in the case of *C. fontanum*, indicating a strong avoidance of salt-spray habitats and a preference for herbfield and mires, and for *Poa annua*, which avoids fellfield.

On Prince Edward Island, the species with the longest known history is *P. annua*, (Table 1). The occupancy of this species does not seem to have increased dramatically since 1966, and inter-survey variation likely reflects the extent to which the plant was actively sought by observers. In the models, distance to nearest conspecific population had significant negative effects, with a high proportion of the variance explained (48–60%; Table 2). For *S. procumbens c.* 50% of the variance in the data could be explained, with nearest conspecific population and altitude entering the models significantly. Curiously, a positive relationship with distance from Cave Bay (an area designated for camping) was found, reflecting the fact that the species was first found distant from this site and is still not associated with it. This species is spreading the most rapidly on the island (Table 1, Fig. 3). *C. fontanum* is also spreading rapidly, and distance from Kent Crater (the original site of colonization) and the presence of conspecifics are both significant and strong contributors to the *c.* 70% of the variance explained by the models. The decline in 2010 (Fig. 3) reflects lower sampling coverage of the inaccessible western side of the island than in previous years.

3.3. Effect of residence time and predictions of future spread

A significant positive relationship between residence time and area of occupancy exists for the established alien species on Marion Island (RMA: slope (and 95% CI) = 2.1 (0.85–5.24), $n = 14$, $R^2 = 0.26$, $p = 0.038$ based on 999 permutations, Fig. A3).

Based on their current upper altitudinal limits and habitat preferences (Tables A2 and A4), the six most widespread alien plant species on MI could be expected to occur over at least 30–74% of the island given sufficient time for propagule transport (and an even larger proportion of PEI; Table 3). If the widespread alien species expand upslope for the next 50 years at the same rate as indigenous species have for the last 40 years, owing to climate change, then these invasives could potentially occupy 51–86% of the island by 2060 (Table 3).

3.4. Species richness

Alien species richness on MI is highest in the proximity of the research station and certain coastal field huts (Fig. 1b). The best fit models included terms for altitude, altitudinal variability (GEE only), area, number of localities sampled, distance to hut and research station, and alien richness in surrounding grid cells. Of these, neighboring alien richness was strongest (explaining 30–43% of variation alone). Both GLM and GEE models explained a similar proportion of variability in species richness (62–63%; Table 4). On PEI, mean altitude, range of altitude, number of presence records, and average and maximum surrounding alien richness were important predictors in both GEE (28% variance explained) and GLM (49% variance explained) models (Table 4; Fig. 1b). However, the spatially explicit model also included terms for altitudinal variability, number of localities sampled and distance to Kent Crater.

4. Discussion

Of the 17 non-indigenous vascular plant species currently established on the Prince Edward Islands, six have spread rapidly since their introduction, and can now be considered widespread. An early statistical generalization suggested that about 10% of established species spread to become problematic, acknowledging that variance about the relationship is to be expected (Williamson and Fitter, 1996). To date, the transition on MI has taken place in about 35% of the established species, much higher than the earlier

Table 3
The current and potential future ranges of the six most widespread alien plant species on the Prince Edward Islands, expressed as percentage of total island area. Three scenarios of species range expansion in response to further climate change (+50 years) were calculated, using two estimates of species current upper altitudinal range limits; the 95th percentile and the maximum altitude of species' observations. Three species occurring on Marion Island are currently absent (or very rare; Table A2) in fellfield and scoria vegetation types, and therefore calculations were repeated only for the portion of the island that is currently covered by suitable habitat types.

Island	Species	Current distribution[a]	Scenarios for future altitudinal range expansion[b]					
			No expansion		Conservative expansion		Liberal expansion	
			95th percentile	Maximum	95th percentile	Maximum	95th percentile	Maximum
Marion Island (293 km²)								
	Agrostis stolonifera	7.2	17.0	37.9	31.3	47.9	41.9	57.1
	Cerastium fontanum	27.8	50.0	61.1	58.9	68.9	67.1	75.6
	Poa annua	26.4	45.7	69.4	55.0	76.1	63.5	82.2
	Poa pratensis	3.8	14.1	30.1	29.9	40.9	40.7	50.7
	Sagina procumbens	23.2	31.6	74.0	42.4	80.3	51.9	85.6
	Stellaria media	5.6	31.6	34.5	42.4	45.2	51.9	54.3
Prince Edward Island (45 km²)								
	Cerastium fontanum	7.0	51.1	55.1	61.9	65.7	72.9	75.8
	Poa annua	16.0	39.5	55.7	53.3	66.3	63.4	76.6
	Sagina procumbens	18.0	51.9	73.2	62.2	83.3	73.1	94.5
Marion Island excluding fellfield, scoria cones and polar desert (suitable habitat: 70 km²)								
	Agrostis stolonifera	49.1	94.7	82.6	99.9	98.3	100	
	Poa pratensis	41.2	80.2	79.8	97.6	97.5	100	
	Stellaria media	83.2	88.7	98.6	99.4	100	100	

[a] Calculated at a resolution of half-minute grid cells.

[b] Calculated from the DEM (i.e. resolution of 20 m for Marion Island and 30 m for Prince Edward Island). No expansion = in-filling of present altitudinal range only; Conservative expansion = upper altitudinal limit increases by 1.7 m/year; Liberal expansion = altitudinal limit increases by 3.4 m/year. Altitudinal range expansion scenarios are based on observed upslope expansion by indigenous vascular plant species on Marion Island (le Roux and McGeoch 2008).

Table 4
Best fit models explaining alien vascular plant species richness on the Prince Edward Islands (see also Table A7). The Akaike weight (AIC$_w$, or its GEE equivalent, the QIC$_w$), adjusted D^2 (or the equivalent measure of explained deviance for GEE models, the adjusted R^2) are shown for each model, together with estimates of the co-efficients of all the predictors retained in the best fit model. Coefficients differing significantly from zero are shown in bold.

Island	Model	AIC$_W$ (QIC$_W$)	Adj. D^2 (Adj. R^2)	n	Terms included	Coefficient estimate
Marion	GLM	0.054	0.62	401	Intercept	−0.350
					Minimum altitude of grid cell	**−0.005**
					Grid cell size	**0.0001**
					Number of localities sampled	**0.011**
					Mean alien plant richness in surrounding cells	**0.348**
	GEE	0.047	0.63	401	Intercept	−0.424
					Minimum altitude of grid cell	**−0.005**
					Mean topographic roughness index	0.015
					Grid cell size	**<0.001**
					Co-efficient of variation of altitude	−0.412
					Number of localities sampled with alien species present	**0.011**
					Distance to nearest hut	−0.016
					Distance to research station	0.004
					Mean alien plant richness in surrounding cells	**0.401**
Prince Edward	GLM	0.011	0.49	61	Intercept	**−1.016**
					Minimum altitude of grid cell	**−0.005**
					Number of localities sampled with alien species present	**0.065**
					Max. alien plant richness in surrounding cells	**0.472**
	GEE	0.004	0.28	61	Intercept	**−1.562**
					Minimum altitude of grid cell	−0.004
					Altitudinal range	−0.0004
					Mean topographic roughness index	0.008
					Grid cell size	0.000
					Co-efficient of variation of altitude	0.641
					Number of localities sampled	−0.011
					Number of localities sampled with alien species present	**0.089**
					Mean alien plant richness in surrounding cells	0.012
					Max. alien plant richness in surrounding cells	0.329
					Distance to Cave Bay	−0.030

generalization (see also Richardson and Pyšek, 2006). Elsewhere, residence time plays a role in the proportion of species that are likely to spread and become problematic (Wilson et al., 2007). This appears to be the case also for MI despite the short residence time of most species (probably since the establishment of the scientific station in 1947; Huntley, 1971; Gremmen, 1981). However, because spread has also been rapid at Prince Edward Island (where *S. procumbens* and *C. fontanum* have only recently established; Table 1), residence time may not be the only mechanism determining the current extent of alien species distributions.

Rather, the islands' ecosystems may provide ready opportunity for the transition between establishment and invasion. Why this might be the case is not clear. Several works have suggested that islands are not more invasible relative to mainland areas (Lonsdale, 1999; Sol, 2000). By contrast, others have shown that islands house more invasive alien species than mainland areas (Sax and Gaines, 2008; McGeoch et al., 2010), suggesting that the transition from established species to invasive might be commonly made on islands. Across the SOIS, a positive relationship exists between indigenous and alien plant richness (Chown et al., 1998), implying little role for biotic resistance. On islands elsewhere, a disturbance mechanism (such as habitat alteration) might plausibly be responsible for the success of invasive species (e.g. Case, 1996). By contrast, at the Prince Edward Islands, human disturbance is low, although disturbance by birds and seals (Chown and Froneman, 2008) is common. Nonetheless, our analyses suggest that human intervention may well play a role in the local spread of the species.

Among the correlates of occupancy for all of the species, nearest conspecific presence contributed significantly in all species, emphasizing the significance of propagule pressure, in keeping with many other studies (e.g. Lonsdale, 1999; Richardson and Pyšek, 2006; Lockwood et al., 2009; Spear et al., 2013). However,

distance to a site of human activity, such as the research station or field huts on MI, was either significant or included in the best fit models for most of the species too. Thus, the colonization of typically undisturbed areas of the islands (i.e. the transition from established to invasive) has likely been facilitated by human activity. Human activity on MI is limited largely to movement on paths among field huts (Chown and Froneman, 2008). No other form of anthropogenic habitat disturbance takes place except in the immediate vicinity of the research station and to a much smaller extent at the field huts on MI. Thus, human influences appear largely to have been in the form of additional propagule pressure, especially given high human activity during the cat eradication programme on MI between 1986 and 1991 (Bester et al., 2002). At this time, activity during the summer months was more than double the average. In addition to the usual overwintering team (10–16 personnel), hunting teams of *c.* 16 persons, deployed in groups of two from the field huts and scientific station, operated continuously and traversed the island actively hunting, trapping and baiting cats (Bester et al., 2002). Such activity might easily have led to the dispersal of several of the alien species, especially given their propensity for adhering to clothing or becoming lodged in bags (Lee and Chown, 2009).

Potentially confounding this explanation is the fact that average annual temperature has increased and total annual precipitation declined at the island since the 1950s (le Roux and McGeoch, 2008). More significantly, the increase in temperature has been especially pronounced since the late 1970s. Warmer temperatures may have improved the probability of species establishing and reproducing successfully, leading to what appears to be a change in rate of spread in the 1980s. That species are also spreading rapidly on PEI, where human activity is virtually non-existent (Chown and Froneman, 2008), provides further support for this idea. In all likelihood, both mechanisms are operating.

Irrespective of the causes of the transition from established to widespread, it is clear that *A. stolonifera*, *C. fontanum*, *P. annua*, *P. pratensis*, and *S. procumbens* are all widespread and likely to spread further, both assuming a constant climate and factoring in on-going climate change. Indeed, with the latter it can be assumed that more than 50% of the islands' vegetated areas will support one or more of these species by 2060. These forecasts are in keeping with the assumption that weedy species will take up the diversity capacity made available by increasing temperatures in non-water-limited systems (Woodward and Kelly, 2008; Chown et al., 2012b), especially given that, on isolated islands, natural colonization rates are exceptionally low. A curious exception on MI is *S. media*, the only species showing a decline in range. Given its wide global distribution in temperate areas it might be expected to have continued spreading on MI. The only plausible explanation for its decline is that since the 1995 ban on the delivery of fresh produce to the island (de Villiers et al., 2005), it has been widely sought by the scientific teams as an edible fresh green vegetable. Its disappearance from much of the east coast close to the research station, but on-going presence on the more distant, and less visited west (Fig. 2), provides support for this explanation.

The current distributions of the alien species, and the rapid spread of some of them, suggest that management actions to limit further impacts should first focus on the single species that is now starting to spread rapidly, *Luzula* cf. *multiflora*. Eradication of the eight species that have not spread (Table 1), but could plausibly do so given their histories elsewhere (e.g. *Elymus repens* and *Rumex acetosella*, Holm et al., 1977), is also a priority. Eradication of the more widespread species may cause more disturbance than no action at all, given that human movement has been implicated in this study as a cause of spread.

In addition, surveillance for new species should be undertaken routinely, and prompt action taken following discovery (see Hughes and Convey, 2012 for an assessment procedure). Surveillance for new species arrivals on the less impacted Prince Edward Island should be accompanied by an anticipatory management plan. Whilst visits to Prince Edward Island have frequently included surveillance for new alien species (e.g. Ryan et al., 2003), where these have been found no immediate action has been taken, leading to a situation where the species are now too widespread for effective control.

More generally, our results suggest that *A. stolonifera*, *C. fontanum*, *Luzula* cf. *multiflora*, *P. annua*, *P. pratensis*, and *S. procumbens* are likely to become widespread on other Southern Ocean Islands, and/or Antarctica were they to be introduced there. *P. annua* is already known to have done so on many of the islands, is the most widespread plant invader in the region (Frenot et al., 2005), and has also now started spreading on the Antarctic continent (Chown et al., 2012a; Molina-Montenegro et al., 2012). On Possession Island (Crozet archipelago) and Amsterdam Island, several of these species have also spread extensively (Frenot et al., 2001). Their seeds also routinely appear as propagules in the clothing and gear of those visiting these islands and Antarctica (Chown et al., 2012a). These species should therefore be targeted for surveillance, especially in rapidly warming areas of the continent. Thus, active and ongoing screening of clothing, equipment and cargo is important. Indeed, given the efficacy of such procedures in locating and reducing propagule loads (Lee and Chown, 2009; Chown et al., 2012a), management interventions should focus on these surveillance and prevention activities, coupled with rapid response action plans. Protocols for such action in the Antarctic Treaty area have already been set out (Hughes and Convey, 2012). They now need to be developed into action plans that are accepted by the various bodies such as national conservation agencies and the Committee for Environmental Protection of the Antarctic Treaty, that are jointly responsible for the conservation of the region.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.02.005.

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