Fur seal populations facilitate establishment of exotic vascular plants

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Abstract

The cessation of seal harvesting has prompted a recovery of previously decimated fur seal (*Arctocephalus gazella* and *A. tropicalis*) populations across the Southern Ocean region. Although the associated increase in seal-related soil disturbance is known to impact indigenous vegetation, the effect of increasing fur seal numbers on exotic plant species is not yet clear. Here, we compare plant species composition and cover between 26 sites with

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high fur seal impact paired with nearby control sites on sub-Antarctic Marion Island. Seal-affected sites had a significantly higher number and cover of exotic plants, specifically of the widespread sub-Antarctic invaders, *Poa annua* and *Sagina procumbens*, than control sites. Furthermore, some of the native species, most notably the disturbance-sensitive species, *Blechnum penna-marina*, were significantly less abundant in seal-affected sites compared to controls. We propose that this is a result of both physical trampling, which opens up niches for exotics by damaging natives, and nutrient enrichment of the soils, giving exotic species a competitive advantage over natives. While other studies have noticed associations between exotic plant species and indigenous animal disturbance, this is, to the best of our knowledge, the first study to empirically show that the successful recovery of fur seal populations can have undesirable side-effects such as the enhanced persistence of exotic plant species. We recommend that alien plant management plans specifically include areas of increased animal disturbance into their programmes.

Keywords: exotic plants, fur seals, Marion Island, nutrient enrichment, physical soil disturbance, sub-Antarctic

1. Introduction

Following the cessation of seal harvesting in the early 1900s, successful protection measures have enabled fur seal colonies to repopulate, resulting in the recovery of fur seal numbers at many rookeries across the Southern Ocean (Wilkinson and Bester, 1990;

Goldsworthy et al., 2009; Waluda et al., 2010). For example, on Marion Island (46° 54' S, 37° 45' E) both Antarctic (*Arctocephalus gazella*) and sub-Antarctic (*A. tropicalis*) fur seal numbers have increased steadily between the mid-1990s and early twenty first century at mean rates of approximately 14.8% and 5.3% per annum respectively (Hofmeyr et al., 2006).

Such rapid rates of repopulation can be expected to have both positive and negative consequences for vegetation establishment and survival. On the one hand, high levels of concentrated seal activity on vegetated substrates can increase vegetation productivity due to seal manure fertilisation, especially on nutrient-poor soils (Smith, 1978; Panagis, 1985). On the other hand, seal trampling can create gaps and damage the vegetation layer (Norton et al., 1997), especially when trampling occurs repeatedly or continuously (Bonner, 1985; Gremmen et al., 2003; Hall and Lamont, 2003; Favero-Longo et al., 2011). Moreover, the establishment and dispersal of exotic plant species are often facilitated in areas of increased soil disturbance (MacDougall and Turkington, 2005; Buckley et al., 2007), such as those affected by increasing seal activity.

Exotic plant species commonly display high phenotypic plasticity and are therefore often able to succeed in areas with frequently changing environmental conditions (Daehler, 2003). Furthermore, exotic plant species are often fast-growing and nitrophilous, enabling them to profit from soil enrichment caused by nitrogen-fixing plants (Maron and Connors, 1996) or animal presence (Loydi and Zalba, 2009). Exotic plants therefore often hold a competitive advantage over indigenous species in areas of increased disturbance (Lake and Leishman, 2004).

Although seal-related disturbances, such as trampling and nitrification, affect the indigenous vegetation on sub-Antarctic islands (see e.g. Lewis Smith, 1988; Favero-Longo et al., 2011), our understanding of the effect of seal populations on exotic plant species is incomplete. For example, Ryan et al. (2003) postulated that the rapid spread of *Poa annua*, an exotic grass species, across Prince Edward Island was facilitated by the increased availability of suitable habitat due to increasing numbers of fur seals. Yet in other cases the establishment of exotic species appears to have been hampered by seal-related disturbance. For example, on Marion Island the exotic grass, *Alopecurus geniculatus,* which has not been observed since 1975 (N. Gremmen, pers. communication), possibly disappeared as a result of physical trampling by increasing seal colonies (Gremmen and Smith, 1999). Therefore, although fur seal populations (Hofmeyr et al., 2006) and the abundance and distribution of exotic plants (le Roux et al., 2013) are both increasing in sub-Antarctic ecosystems, the interaction between the two has received little attention thus far.

The aim of this study was to test whether fur seal presence affected the composition and cover of vascular plants (indigenous and exotic) and bryophytes on sub-Antarctic Marion Island. We sampled the vegetation in seal-affected sites across the island, paired with nearby control sites. Since seal density was spatially heterogeneous within seal rookeries, we sampled at two spatial scales: (1) high spatial resolution sampling of high-impact patches within rookeries using a 1 m^2 quadrate, and (2) low spatial resolution sampling across rookeries using transects of up to 50 m in length.
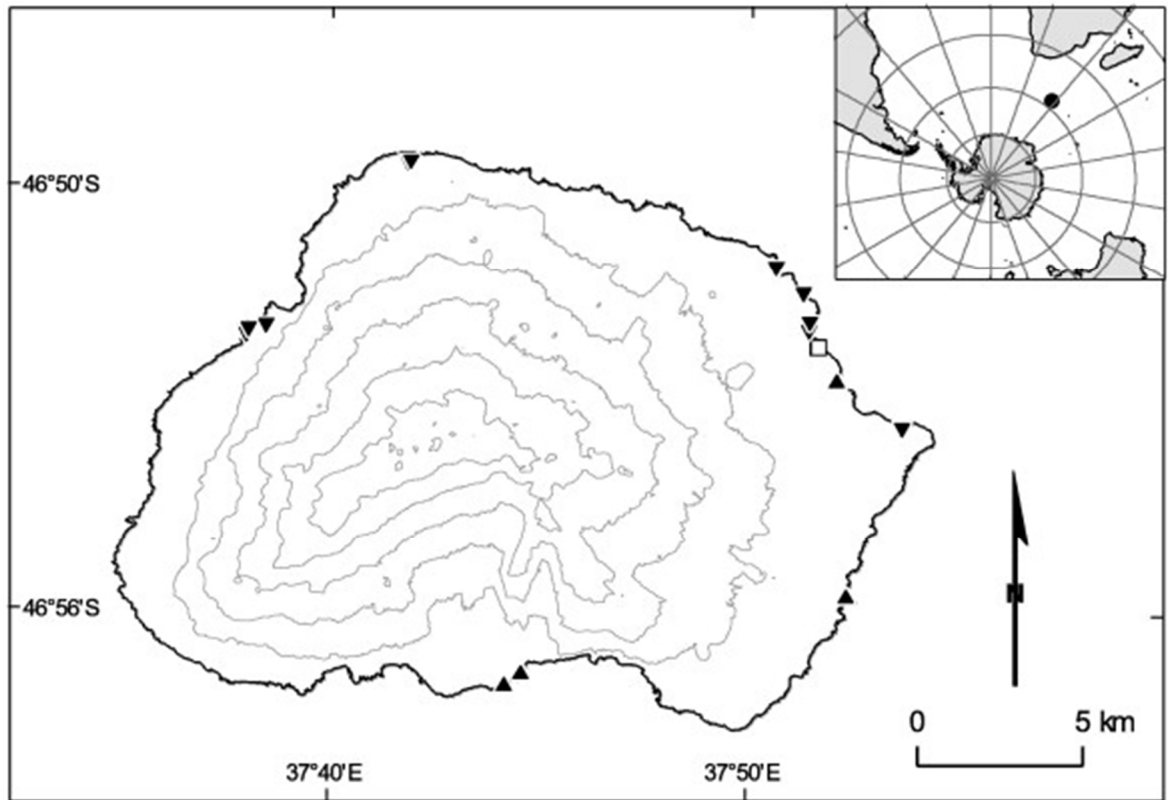
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2. Methods

Figure 1. Distribution of site locations on Marion Island, including the location of the meteorological station (□) and the topological contour lines at 200-m intervals (Transverse Mercator projection). The inset depicts the location of the Prince Edward Islands (PEI, indicated with ●), half-way between Antarctica and Africa (Antarctic polar stereographic geographic projection with a conjugate graticule in 20° intervals). Seal-affected sites were either populated by *Arctocephalus gazella* (n = 9, indicated with ▲) or by *A. tropicalis* (n = 17, indicated with ▼). Note that some locations were in relative close proximity to each other so that some symbols are partially overlapping. The locations of control sites are not presented due to their close proximity to seal-affected sites.

2.1. Study area

The two Prince Edward Islands are located in the southern Indian Ocean, with Marion Island being the greater, covering c. 293 km^2 (Figure 1). This island group experiences an exceptionally maritime climate and strong, predominantly westerly winds (Schulze, 1971). Mean annual temperature is 6° C with little seasonal or diurnal temperature variations and annual precipitation is in the order of 2000 mm (Smith, 2002). Due to its isolated location, the island is relatively species-poor with only 22 native vascular plants, 18 exotic plants, three plant species of unknown status, and an estimated 142 bryophyte and 100 lichen species (Smith and Mucina, 2006). Vascular plants mostly exhibit prostrate, compact growth forms, common to harsh environments, while woody shrubs and trees are completely absent. All known alien plant species are vascular and are found in all habitat types, although they are most common in drainage lines and coastal herbfields (Gremmen and Smith, 2008).

2.2. Study sites

We selected twenty six seal-affected sites based on the current distribution of Antarctic and sub-Antarctic fur seal populations (Figure 1). These sites were known as major breeding sites or as hosting a significant proportion of nursing females (Hofmeyr et al., 2006). Each seal-affected site was paired with a nearby control site. None of these control sites had seals present at the time of sampling, nor were they known to host fur seals during the breeding

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seasons of the two species (McIntyre pers. obs.), presumably as a result of inaccessibility through, for example, the absence of a beach access point. Site pairs were selected based on similar geographic and environmental field characteristics (i.e. elevation, distance from sea, slope angle and aspect).

2.3. Sampling method

Sampling was undertaken in April, during austral autumn, outside of the peak breeding season for both fur seal species on Marion Island (Hofmeyr et al., 2007). Consequently, pups of *Arctocephalus gazella* were mostly weaned and *A. tropicalis* pups approximately 4 months old at the time of sampling, reducing the risk of substantial disturbance to the rookeries during sampling.

2.3.1. Grid level

Quadrates of 1 x 1 m and consisting of 10 x 10 cm cells (Figure 2a) were used to estimate the percentage cover of each species (with a resolution of 0.5% or half a cell). Since seal disturbance was localised and heterogeneously distributed within seal-affected sites (Figure 3a), areas of disturbance could be missed through random or systematic placement of the quadrates. Instead, we placed the quadrates subjectively, in areas with obvious high fur seal impact (identified as areas displaying characteristic flattened or trampled vegetation, as
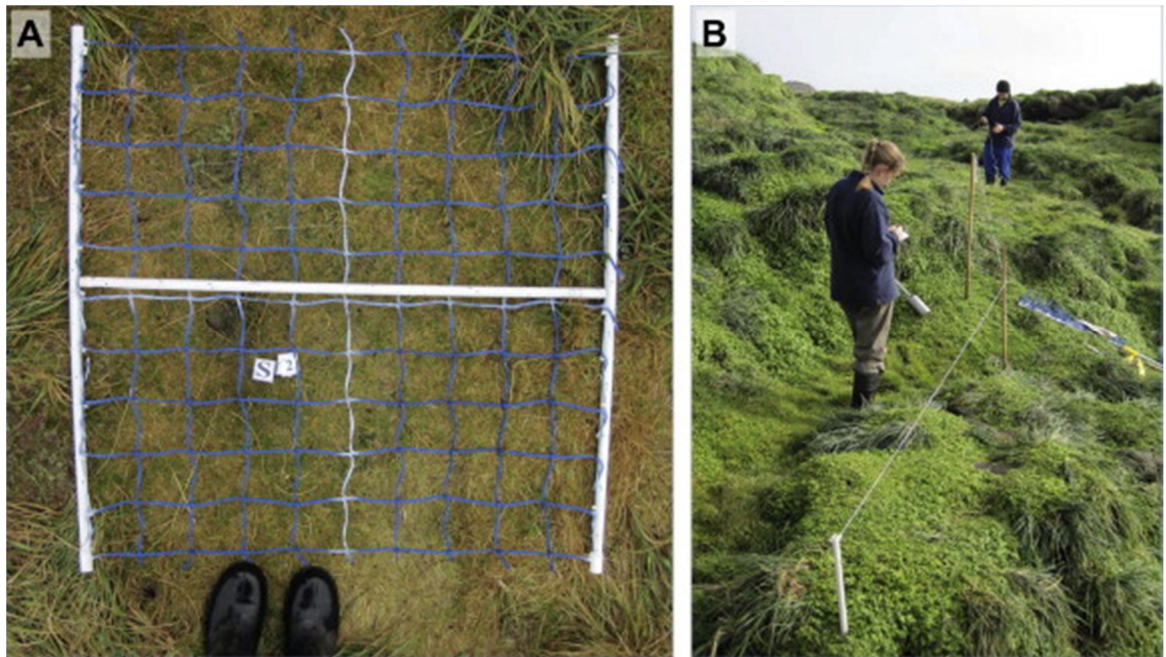
Figure 2. Field sampling method used to estimate plant occurrence (a) at the grid level and (b) at the transect level.

found along regular paths followed upslope by seals). Quadrates therefore measured localised seal impacts and were not considered to be representative of overall site conditions. For site level estimates of seal-related impacts, we additionally undertook transect level surveys (see below). At the control sites the vegetation layer composition was comparatively homogenous (Figure 3b). For consistency we placed quadrates in control sites in between and as close to the centre, of the two transects (see below) as possible. When placing the quadrates, areas where elephant seals or their wallows were present, as well as areas with evident bird and mouse influence (burrows, faeces and feathers) were avoided. Species present, but with a cover of less than 0.5%, were awarded a value of 0.5%.

Figure 3 (a) Seal-affected site, showing *S. procumbens* along a path followed regularly by seals and (b) the paired control site.

When two or more species were found to overlap one another, percentage cover was assigned to the species closest to the soil (Bullock, 1996).

2.3.2. Transect level

In addition to the quadrates, we recorded vegetation composition at a coarser spatial scale using line transects (Figure 2b). At each site two transect lines of up to 25 m were placed parallel to each other in a more or less straight line along an elevational contour, so as to obtain a representative sample of vegetation within the site. Transect lines were placed approximately 1.5 m apart. At each 0.5 m interval point we recorded a list of vascular plant and bryophyte species present. For each species the ratio between number of presences and total number of interval points was calculated as species-specific cover estimation at the transect level.

2.3.3. Environmental data

At the approximate centre of each transect a coordinate reading was taken using a hand-held GPS unit (GPSmap 62, Garmin). These coordinates were used to derive elevation and distance from sea from the most recent Marion Island topographical map (Chief Directorate: Surveys and Mapping, 2001). Slope angle and aspect were measured *in situ* using a clinometer and a field compass. Soil samples were taken using a handheld corer with a 4 cm radius to determine bulk density and soil moisture within the top 10 cm of the soil profile. Finally, at each seal-affected site the presence of seals and seal species were visually confirmed.

2.4. Data analysis

To confirm that seal-affected sites and control sites had similar environmental variables we fitted paired *t*-tests to the variables distance to sea, slope, elevation, bulk density and soil moisture. All variables were normally distributed. To analyse the aspect measurement we calculated the aspect's mean and fitted a Watson-Williams test, using NCSS 8 (NCSS, LLC. Kaysville, Utah). This test provides *F* values similar to an ANOVA analysis, and is suitable to compare circular data (Artes, 2008). All other statistical analyses were done in SPSS 17.0.

   We then used a multivariate analysis to quantify which environmental variables affected the species composition of vascular plants at both grid and transect level, respectively. Specifically, we first used a Detrended Correspondence Analysis on species cover data (in percentage cover) to verify that there was not one single environmental gradient or outlying cluster of plots. We subsequently used a Canonical Correspondence Analysis on species cover data and environmental data (treatment, seal species, latitude, longitude, elevation, gradient, distance to sea, bulk density and soil moisture), with biplot scaling focused on inter-species distances, and using forward selection of environmental variables (Lepš and Šmilauer, 1999). The environmental variables treatment and seal species were analysed as Boolean pseudovariables: treatment or control, and *A. gazella* or *A. tropicalis*. The significance of each environmental variable was quantified using a full model Monte Carlo permutation test with 999 iterations. Results were interpreted using a species-by-environmental-variables biplot in which the distance between nominal variable

centroids and arrow length indicate the relative contribution of that particular variable to the overall model. All multivariate analyses were done in CANOCO 4.5 (ter Braak and Šmilauer, 2002).

We used one-way ANOVA to determine if there was a difference in total plant richness (all vascular plants and bryophytes combined), bryophyte richness, exotic plant richness, proportion of exotic plant richness from total vascular plant richness and proportion covered by exotic plant species between sites occupied by *A. gazella*, *A. tropicalis* and control sites. The significance level between treatments was determined post-hoc using a Bonferroni correction for the degrees of freedom (Quinn and Keough, 2002). We fitted the same model to test for differences in cover of individual vascular plant species between *A. gazella*, *A. tropicalis* and control sites. Calculations were conducted at grid and transect level.

3. Results

Seals were present at all of the seal-affected sites during sampling. Of the 26 seal-affected sites, 9 were categorised as *Arctocephalus gazella* and 17 as *A. tropicalis* sites. We found a total of 12 indigenous and 4 exotic vascular plant species in both grids and transects (Table 1). In addition we observed 14 species of bryophytes at the transect level, but only 11 of these were observed at the grid level (results not shown). Exotic species occurred more frequently in seal-affected sites than in control sites. For example, only one seal-affected site contained no exotic species in either the grid or transect data, whereas ten control sites

Table 1. The percentage of seal-affected and control grids and transects containing each of the observed vascular plant species. Species indicated with an asterisk (*) are exotics.

Plant species	Grid		Transect	
	% Seal-affected	% Control	% Seal-affected	% Control
Acaena magellanica Vahl	19	46	31	73
Agrostis magellanica Lam.	19	35	35	46
Azorella selago Hook.f.	31	42	42	65
Blechnum penna-marina (Poir.) Kuhn	19	85	38	88
Callitriche antarctica Engelm. ex Hegelm.	12	0	19	8
Cotula plumosa (Hook.f.) Hook.f.	42	23	62	27
Crassula moschata G.Forst.	8	8	12	8
Juncus scheuchzerioides Gaudich.	12	23	38	35
Montia fontana L.	12	0	31	0
Poa cookii (Hook.f.) Hook.f.	73	27	81	50
Ranunculus biternatus Smith	12	4	42	15
Uncinia compacta R.Br.	0	15	0	19
Agrostis stolonifera L.*	31	31	46	46
Cerastium fontanum Baumg.*	8	0	15	0
Poa annua L.*	58	4	85	12
Sagina procumbens L.*	31	19	69	35

were free of exotics. Species frequently occurring in seal-affected sites were the exotics

Poa annua (85% of seal transects) and *Sagina procumbens* (69%), as well as the

indigenous species *Cotula plumosa* (62%) and *Poa cookii* (81%). Species occurring most

frequently in control sites were the indigenous species *Acaena magellanica* (73% of control

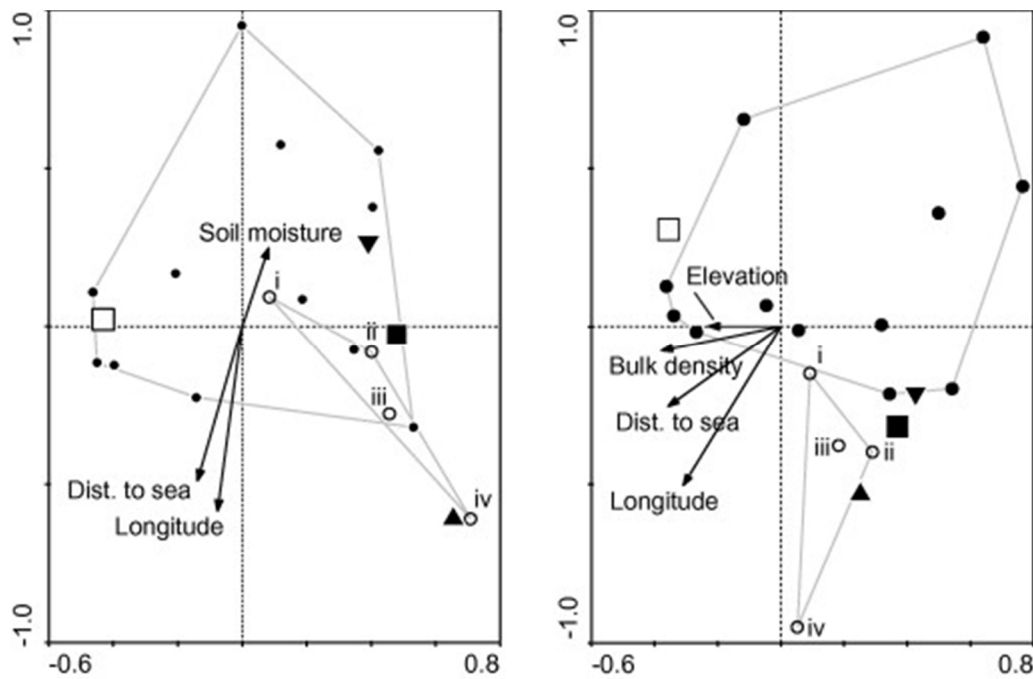transects), *Blechnum penna-marina* (88%) and *Azorella selago* (65%).

Figure 4. Canonical Correspondence Analysis biplots of species and environmental variables against the first two canonical axes for the grid level (left panel) and the transect level (right panel). Only variables that contributed significantly to overall species composition were included in the models: treatment (seal-affected sites: ■; control sites: □), seal species at site (*Arctocephalus gazella*: ▲; *A. tropicalis*: ▼), soil moisture, distance to sea, elevation, and longitude. For the vascular plant species the origin is indicated (indigenous species: ●; exotic species: ○). Exotics species names are as labelled as follows: (i) *Agrostis stolonifera*, (ii) *Poa annua*, (iii) *Sagina procumbens*, and (iv) *Cerastium fontanum*. Distance between centroids of nominal variables or arrow length of continuous variables indicate the relative contribution to overall species composition.

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None of the environmental variables (distance to sea, slope, elevation, bulk density, soil moisture and aspect) differed significantly between seal-affected sites and control sites (all paired t-test: $P > 0.05$; Watson -Williams test: $P > 0.05$, see also Table A.1.), confirming that our control sites were selected appropriately. The DCA analysis showed that variation in species contribution was not along a single axis, justifying the validity of the CCA analysis. Species composition was primarily explained by treatment in both survey levels (Table B.1.). The biplots showed that there was no correlation between treatment and the environmental variables longitude, distance to sea, elevation, and soil moisture (Figure 4). Exotic plant species were distinctly clustered from indigenous species, related with environmental conditions characterised by a longer distance to sea, lower soil moisture content, and located more eastward than indigenous species. Moreover, this cluster of exotics was also more closely associated with the *A. gazella* nominal variable centroid than with the *A. tropicalis* centroid.

At the grid level the ANOVAs showed that the number of exotic species was significantly higher in *A. tropicalis* sites, compared to controls, although both the total number of species and the number of bryophyte species were the same for all treatments (Table 2). This higher number of exotic species also resulted in a higher proportion of exotic richness and cover by exotic plants, but not to the detriment of indigenous vascular plant species. At the transect level, we found a significantly higher number, proportion and cover of exotics at seal-affected sites compared to controls, at the expense of indigenous species cover.

Table 2. Mean values per treatment of the total number of plant species (vascular plants and bryophytes), number of bryophyte species, number of indigenous vascular plant species, number of exotic vascular plant species, proportion of exotic plant species from total number of vascular plant species (%), proportion of indigenous plant cover from total vascular plant cover (%), proportion of exotic plant cover from total vascular plant cover (%), followed by the results of the one-way ANOVA tests. Superscript labeling indicates significant differences between treatments following a Bonferroni posthoc comparison. Analyses were done at grid level and at transect level.

Response variable	Grid					Transect				
	A. gazella	*A. tropicalis*	Control	F	P	*A. gazella*	*A. tropicalis*	Control	F	P
Total species	4.4	5.5	4.9	0.79	0.461	7.8	8.7	7.2	2.97	0.061
Bryophyte species	1.0	1.4	1.2	0.27	0.764	1.3	2.6	2.2	1.93	0.156
Indigenous species	2.3	2.7	3.2	1.18	0.316	4.3	4.0	4.2	0.16	0.850
Exotic species	1.1^{ab}	1.5^{b}	0.5^{a}	6.74	0.003	2.1^{a}	2.1^{a}	0.8^{b}	18.46	< 0.001
Exotics (%)	30.0^{a}	38.2^{a}	10.3^{b}	10. 81	< 0.001	32.8^{a}	35.6^{a}	14.5^{b}	13.55	< 0.001
Indigenous cover (%)	58.7^{a}	38.5^{a}	85.7^{a}	16.64	< 0.001	82.0^{a}	73.2^{a}	120.3^{b}	12.16	< 0.001
Exotics cover (%)	21.7^{a}	46.8^{b}	7.3^{a}	12.60	< 0.001	43.3^{a}	56.9^{a}	9.4^{b}	17.13	< 0.001

Table 3. Results of the species-specific ANOVA models at grid and transect level. Values indicate mean cover (%). Species names in bold and with superscript labeling indicate a significant difference following a Bonferroni correction. Species indicated with an asterisk (*) are exotics.

Plant species	Grid					Transect				
	A. gazella	*A. tropicalis*	Control	*F*	*P*	*A. gazella*	*A. tropicalis*	Control	*F*	*P*
***Acaena magellanica* Vahl**	0.4	0.3	9.7	2.68	0.079	**4.8^{ab}**	**3.0^a**	**16.6^b**	**4.06**	**0.023**
Agrostis magellanica Lam.	0.1	2.9	3.4	0.94	0.399	7.4	2.0	9.4	1.64	0.205
Azorella selago Hook.f.	0.1	6.6	2.6	2.96	0.061	8.4	3.6	8.1	0.80	0.456
***Blechnum penna-marina* (Poir.) Kuhn**	**4.7^a**	**3.0^a**	**50.2^b**	**19.13**	**< 0.001**	**13.5^a**	**5.1^a**	**69.3^b**	**16.25**	**< 0.001**
Callitriche antarctica Engelm. ex Hegelm.	0.0	0.3	0.0	2.55	0.089	0.3	3.1	0.4	2.40	0.101
Cotula plumosa (Hook.f.) Hook.f.	5.3	19.1	12.8	0.77	0.467	11.0	26.0	12.2	1.63	0.207
Crassula moschata G.Forst.	0.0	0.4	0.7	0.40	0.675	0.0	2.9	3.7	0.37	0.691
Juncus scheuchzerioides Gaudich.	1.6	0.1	2.5	0.58	0.561	5.4	6.6	5.2	0.08	0.922
***Montia fontana* L.**	0.1	0.1	0.0	1.60	0.212	**0.5^{ab}**	**2.4^a**	**0.0^b**	**4.32**	**0.019**
***Poa cookii* (Hook.f.) Hook.f.**	**10.3^{ab}**	**24.4^a**	**1.3^b**	**8.82**	**0.001**	**29.4^a**	**15.3^b**	**3.2^c**	**18.29**	**< 0.001**
Ranunculus biternatus Smith	0.9	0.1	< 0.1	3.03	0.058	1.2	3.1	0.9	1.95	0.154

Species										
Uncinia compacta R.Br.	0.0	0.0	2.4	2.32	0.108	0.0	0.0	5.3	1.67	0.200
Agrostis stolonifera* L.	15.2	11.7	6.7	0.82	0.447	**0.3^a**	**22.5^b**	**9.2^{ab}**	**3.59**	**0.035**
Cerastium fontanum Baumg.*	0.0	0.5	0.0	1.34	0.271	4.7	0.2	0.0	2.67	0.079
Poa annua* L.	**36.2^a**	**6.8^b**	**< 0.1^b**	**20.08**	**< 0.001**	**19.3^a**	**25.5^a**	**0.5^b**	**17.08**	**< 0.001**
Sagina procumbens* L.	10.6	6.5	0.6	2.88	0.066	**18.9^a**	**8.8^b**	**1.7^b**	**10.59**	**< 0.001**

Although the species-specific response of vascular plants was generally the same for grids and for transects, it was more prominent at the transect level (Table 3). Species with a relatively low cover such as indigenous *Callitriche antarctica* and exotic *Cerastium fontanum* were mostly not affected by treatment — at least not that we could detect with our sampling method. The opposite was true for abundant species such as *Acaena magellanica* and *B. penna-marina,* with both indigenous species showing a much lower cover in seal-affected sites. Exotic species, such as *P. annua* and *S. procumbens*, mostly had a higher cover in seal-affected sites. Notably, some indigenous species such as *P. cookii* and, albeit to a lesser extent, *Montia fontana*, also had a higher cover in seal-affected sites.

4. Discussion

This study showed that seal-affected sites have a higher number and cover of exotic plant species than nearby control sites. The detrimental effects of introduced mammals on sub-Antarctic vegetation systems are well reviewed (e.g. Chapuis et al., 1994), including facilitation of exotic plant species establishment (e.g. Leader-Williams et al., 1987; Anderson et al., 2006). However, to the best of our knowledge, our study is the first to empirically demonstrate a positive relationship between a recovering indigenous animal species and exotic plant species' establishment and spread in the sub-Antarctic.

Both *P. annua* and *S. procumbens,* the two most commonly occurring exotics in this study, are commonly reported sub-Antarctic invaders, with widespread distributions

(Frenot et al., 2001; Ryan et al., 2003). *Poa annua*'s affinity for biotically influenced sites is well documented (e.g. Smith and Steenkamp, 2001; Ryan et al., 2003; Scott and Kirkpatrick, 2005). It has previously been associated with a reduction in native communities through grazing by introduced reindeer (Leader-Williams et al., 1987), as well as seasonal disturbance by elephant seal wallowing (Frenot et al., 2001; Scott and Kirkpatrick, 2005). Our data on the increased cover of *P. annua* at fur seal rookeries suggest that fur seals also play a facilitative role in the establishment and spread of this species, supporting the suggestion of suitable habitat creation by fur seals (Ryan et al., 2003).

The cushion-forming invader, *S. procumbens*, is widely distributed across Marion Island (Gremmen and Smith, 1999) and has increased rapidly in distribution since first discovered, both on Marion Island (Gremmen and Smith, 1999) and on its more pristine neighbour, Prince Edward Island (Ryan et al., 2003). Unlike *P. annua*, which is outcompeted at sites with no disturbance (Scott and Kirkpatrick, 2005), *S. procumbens* also occurs on sites with little or no animal or human impact (Gremmen and Smith, 1999; Ryan et al., 2003). Nevertheless, our data shows a higher *S. procumbens* cover in seal-affected sites. Furthermore, Gremmen et al. (2003) showed an increased cover associated with trampling along footpaths. Therefore, although disturbance is not the only mechanism by which *S. procumbens* establishes, it seems that it can play a facilitating role. We consequently propose two potential mechanisms by which fur seal disturbance facilitates exotic establishment: 1.) a reduction in less resilient native communities through physical

trampling, creating niches for exotics, and 2.) exotics profiting from increased nutrient loads through seal manure fertilisation.

Physical trampling can reduce less resilient native communities (Bonner, 1985; Lewis Smith, 1988; Gremmen et al., 2003). Most notable in our case was the reduction in cover of the slope species, *B. penna-marina*, in seal-affected sites. This is possibly as a result of increased seal impact along regular routes followed upslope, as graminoid species, such as *P. annua* or *P. cookii*, generally have a higher tolerance towards trampling than ferns or plants with lignified stems, such as *B. penna-marina* or *A. magellanica* (Gremmen et al., 2003). Therefore, by physically damaging natives and opening niches (Favero-Longo et al., 2011), trampling can lead to an increase in exotic species richness (Gremmen et al., 2003).

Nutrient enrichment through fur seal manure probably also plays a role in facilitating the establishment of exotics. In fact, Lake and Leishman (2004) suggest that nutrient enrichment is a prerequisite for exotic species invasion on soils with low fertility, playing a larger role than that of physical trampling. Terrestrial nutrient enrichment has been demonstrated for a variety of pinniped species (see, for example, Fariña et al., 2003 for Galapagos sea lions and Panagis, 1985 for elephant seals), including fur seals (Lewis Smith, 1988; Favero-Longo et al., 2011). This manuring influence of animals in turn plays an important role in the distribution of plant species (Smith and Steenkamp, 2001). On Marion Island, the fertilising effect of fur seal manure along their routes is likely to give nitrophilous exotics such as *P. annua* (Smith and Steenkamp, 2001) a competitive advantage over indigenous species, which, although well-adapted to their environmental

conditions, often lack competing abilities in the Antarctic (Frenot et al., 2005). In addition, seal manure fertilisation is also likely to favour the establishment and growth of nutrient-loving indigenous species. Therefore, as *B. penna-marina* is reduced along these routes through trampling, the slopes are repopulated by a combination of *C. plumosa*, *C. antarctica* and *M. fontanum*, as well as the grass species *P. annua* and *P. cookii*. The clonal grass *A. stolonifera*, however, does not profit as much from nutrient enrichment in competitive environments (Mommer et al., 2012). This is consistent with our finding that the presence and abundance of *A. stolonifera* did not differ between nutrient-enriched seal-affected sites and nutrient-poor control sites.

Whereas increasing scientific and tourist travel form a major contemporary dispersal concern (Chown et al., 2012a), sealing trips to Marion Island are primarily held responsible for the historic introduction of many exotic plant species (Huntley, 1971). All four of the exotic vascular species found in this study, for example, have been present on the island for over 100 years (le Roux et al., 2013) and all except *A. stolonifera* have had sufficient time to colonise available niches on the island. Increasing seal numbers are unlikely to be responsible for the introduction of exotic species. However, seals could potentially transport seeds, which attach to their coats, thereby not only facilitating the establishment of exotics, but possibly also their dispersal. In addition, dispersal from seal rookeries can further be facilitated by bird species, such as Gentoo penguins (*Pygoscelis papua*), Antarctic terns (*Sterna vittata*) and Giant Petrels (*Macronectes* spp), which often frequent vegetated rookeries (T.McIntyre, pers. observation). This increases the risk of

dispersing exotics, such as *P. annua* and *S. procumbens* to uninvaded areas on Marion Island or Prince Edward (Ryan et al., 2003).

The two seal species had slightly different effects on plant species composition and cover. For example, *A. tropicalis* sites tended to be characterised by higher proportions and percentages cover of exotic plant species, compared to *A. gazella* sites. These different effects can potentially be explained through demographic differences. Although *A. gazella* numbers are lower than those of *A. tropicalis* (Hofmeyr et al., 2006) and they have colonised the island more recently (Rand, 1956), their numbers are increasing more rapidly (Hofmeyr et al., 2006). Vegetated areas around *A. tropicalis* rookeries can therefore be expected to have been subjected to more seal-related disturbances over longer time periods than the vegetated rookeries of *A. gazella*. However, *A. gazella* prefer beaches associated with open vegetated areas, whereas *A. tropicalis* are mostly associated with beaches consisting of large boulders (Kerley, 1984). This, combined with the rapid increase of *A. gazella* population numbers, is suggestive of greater expected future increases in vegetation impacts associated with *A. gazella* rookeries.

Although one of the indigenous species, *U. compacta*, was found exclusively in control sites, the majority of the indigenous species do not disappear entirely from seal sites; they merely become much sparser and are therefore not detected as often at the relatively high spatial resolution of 1 m^2 grids. However, combining these data with results from the transects shows a more complete picture of how indigenous species and exotics are distributed within seal-affected sites. These findings therefore emphasize the importance of spatial scale considerations when designing sampling schemes for exotic

plant monitoring programmes, especially in areas where high environmental heterogeneity is expected over relatively small spatial scales.

The negative impacts of exotic introductions in the Antarctic and sub-Antarctic regions are widely recognised (see Frenot et al., 2005 for a review), and the introduction of non-indigenous species is seen as one of the main Antarctic conservation challenges (Chown et al., 2012b). To optimise exotic plant monitoring programmes, we recommend that fur seal rookeries are explicitly included in search efforts. This reduces the risk of overlooking newly established exotics. Such optimised search strategies, which explicitly include areas where animals congregate, is of course not only applicable to fur seal-inhabited systems such as Marion Island, but to any system where the establishment and spread of exotic plant species are potentially facilitated by animal presence.

5. Conclusions

The systematic comparison of seal-affected sites with control sites showed that seal presence facilitates the spread and persistence of exotic plants on Marion Island. This facilitative process is most likely caused by a combination of physical trampling by fur seals on the one hand and by nutrient enrichment of soil on the other. In a nutrient-poor sub-Antarctic ecosystem this combination of disturbances gives fast-growing and nitrophilous exotic species a competitive advantage over indigenous species that are mostly slow-growing. These results have important broader conservation and management implications, as they show that the successful recovery of fur seals can have undesirable

side-effects such as the enhanced persistence of exotic plant species. We therefore recommend that alien plant management plans specifically include areas of increased animal disturbance into their programmes.

Acknowledgements

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