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Aliens in Antarctica: Assessing transfer of plant propagules by human visitors to reduce invasion risk

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ABSTRACT

Despite considerable research on biological invasions, key areas remain poorly explored, especially ways to reduce unintentional propagule transfer. The Antarctic represents a microcosm of the situation, with the numbers of established non-native species growing. Information to help reduce potential impacts is therefore critical. We measured the propagule load of seeds, and fragments of bryophytes and lichens (the number of other plant or animal fragments was too low to draw any conclusions) carried in the clothing and gear of visitors to the Antarctic, during the 2007/08 austral summer. Samples were collected from different categories of visitors associated with national research programs and tourism and different categories of clothing and gear, new as well as used. We also collected information about the timing of travel and the regions visitors had travelled to prior to Antarctic travel. Seeds were found in 20% and 45% of tourist and science visitor samples, respectively. For bryophyte and lichen fragments the proportions were 11% and 20%, respectively. Footwear, trousers and bags belonging to field scientists were the highest risk items, especially of those personnel which had previously visited protected areas, parklands/botanic gardens or alpine areas. Tourists who visited rural/agricultural areas prior to travel, and/or travel with national programs or on smaller tourist vessels had the highest probability of transferring plant propagules. Travel either during the boreal or austral autumn months increased the probability of propagule presence. Our assessment is applicable to other areas given evidence of propagule transfer patterns in those areas that are broadly similar to those documented here.

The current work provides a sound evidence base for both self-regulation (e.g. taking care of personal equipment) and organization-based regulation (e.g. issuing guidelines and holding regular inspections) to reduce propagule transfer of plants to the Antarctic.

1. Introduction

Biological invasions are major agents of environmental change. They are capable of altering the functioning of ecosystems, causing local population extinction and are among the major sources of hazard to many of the world's threatened species (Blackburn et al., 2004; Asner and Vitousek, 2005; McGeoch et al., 2010). Early appreciation of these impacts led to the development of research on the pathways for and impacts of biological invasions that has grown significantly in scope (e.g. Mack et al., 2000; Pyšek and Richardson, 2010; Blackburn et al., 2011; McGeoch et al., 2012). Nonetheless, significant areas remain relatively poorly understood. These include pathways for inadvertent introduction (Puth and Post, 2005; Hulme et al., 2008), the ways in which the impacts of invasions play out in different parts of the world (Sax and Gaines,

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2008; Pyšek et al., 2008, 2012), and the way the current evidence base can be used to more effectively manage the problem (Simberloff et al., 2013). The latter constitutes further recognition of the need to narrow the gap between knowledge and implementation in many areas of conservation (Fischer and Van der Wal, 2007; Shanley and Lopez, 2009).

The Antarctic continent and its surrounding islands (hereafter the Antarctic) can serve as model of the above-mentioned problems around the introduction of non-native species. The potential conservation threat of biological invasions was appreciated early on (Carrick, 1964), and much work has since been done to understand the correlates of invasion, the identity, distribution and species richness of the region's non-indigenous and invasive biota, and the impacts of invasion (e.g. Gremmen, 1975; Chapuis et al., 1994; Chown et al., 1998; Gremmen et al., 1998; Gaston et al., 2003; Frenot et al., 2005; Lebouvier et al., 2011; Molina-Montenegro et al., 2012; Lecomte et al., 2013; le Roux et al., 2013). Moreover, it is only recently that the specific role of human visitors to the Antarctic, and especially to the continent, in inadvertently transferring propagules has been fully investigated (Whinam et al., 2005; Lee and Chown, 2009a; Chown et al., 2012a).

While the studies referred to above have demonstrated which categories of visitors (e.g. tourists, scientists, science support personnel) carry the highest propagule loads, and also indicated what personal clothing items produce a relatively high risk, it remains devoid of specific analysis within these categories. Evidence to provide detailed advice to visitors and conservation managers on what patterns of behavior prior to travel to the region may elevate the likelihood of propagule transfer is still lacking. Such information is especially important for enabling self-assessment of the threat by visitors to the region, so aiding sustainable management of the problem. Self-assessment and correction form part of the social pillar for sustainable management of biological invasions (Daab and Flint, 2010; Larson et al., 2011). Thus, rather than a single assessment of personal items being made by managers en route to the continent, as is often now the case, self-assessment would result in multiple screenings becoming the norm. High risk individuals would be aware that their risks are elevated and so likely to pay greater attention to the problem (Daab and Flint, 2010; Root and O'Reilly, 2012). Improving public perception may also help reduce weak links in formal governance (Peters and Lodge, 2009) that might compromise existing regulations in the region to reduce propagule transfer (CEP, 2011).

In this study we therefore provide the specific evidence base for mitigation of propagule transfer to the Antarctic. In previous work we identified the areas of the Antarctic continent most likely to be at risk from the establishment of non-indigenous species based on the vascular plant propagule (seed) loads of visitors, patterns of visitation, and identity of the propagules (Chown et al., 2012a). Here we explore in greater depth these data to provide specific conservation management advice to reduce plant propagule transfer to the region. While our work has an Antarctic focus, it has clear relevance to management of ecotourism risks elsewhere, given similar patterns of propagule transfer (e.g. Ware et al., 2012).

2. Methods

2.1. Propagule surveys and visitor information

The number and identity of propagules transported by visitors to the Antarctic were determined by sampling visitors to the region during the first austral summer (2007/2008) of the 4th International Polar Year using vacuum cleaners (Philips FC 9154 Performer Animal Care vacuum cleaners, Eindhoven, The Netherlands) (description in Supplementary Methods and in Chown et al., 2012a).

Different categories of Antarctic visitors were distinguished: ships' or aircraft crew, tourists, tourist support personnel, and national program personnel subdivided as: field-based scientists, station- and ship-based scientists, field-based national program support personnel, and station- and ship-based national program support personnel. These visitors were travelling by different means of transport: aircraft, national program vessels, small tourist ships (40–80 passengers, medium-sized tourist ships (81–200 passengers), large tourist ships (>200 passengers). The visitors travelled along different routes: departing from South America, South Africa, Australia and New Zealand, or in two occasions from elsewhere. Visitors were sampled over 5 months (November–March), with an additional sample (10 visitors) from a single voyage in early September. Five to ten people per visitor category (if available) per individual voyage were sampled. In total 853 people, travelling on 27 different ships or aircraft, representing 55 different voyages were sampled.

Using a questionnaire, additional data were collected on visitor class, geographical areas and major ecosystems visited previously by the sampled visitors, and on previous use of the sampled items of clothing and other gear. We highlighted alpine, Arctic and sub-Antarctic regions because of a likely match in climate to parts of the Antarctic (Chown et al., 2012a). Additional information on the date and port of departure, and the type of transport used was likewise recorded for each visitor.

The questionnaire used in the visitor sampling work was also distributed to additional Antarctic visitors in the 2007/2008 austral summer season (except for the questions on individual items of clothing and equipment). Questionnaires and an accompanying information leaflet were available in 10 different languages. 5024 of these general visitor survey (GVS) questionnaires were returned. Including questionnaires from the propagule survey, this brought the total number of questionnaires up to 5869. Questionnaires were read electronically, including their unique bar code, and the data compiled in spreadsheets, with some adjustments where answers were inconsistent (51 cases, Supplementary material).

All samples were then returned to our laboratories (Supplementary material). Here the samples were weighed (on digital balances with a 0.1 g precision), after air drying for at least 14 days. The samples were then sorted into vascular plant seeds, other plant propagules (entire leaves or larger fragments of moss and hepatics and identifiable lichen fragments), invertebrate animal remains, and other material. The plant seeds per sample were counted, and sorted into morphologically similar groups (generally corresponding to different species). Identification of the seeds was undertaken by comparing the seeds with photographs of seeds in seed-atlases and Internet databases (Supplementary material Table S1). Damaged seeds, seeds assumed to have come from processed foodstuffs (e.g. sesame seeds), and items not clearly identifiable as seeds were excluded. Identifications were made independently by NJMG, JEL, DMB and CW. Subsequently, differences in identification were checked and discussed, until consensus was reached. A confidence level on a four-point scale was given for each identification (Supplementary material Table S2). Bryophyte and lichen fragments were sorted per sample into morphotypes, but were not identified.

2.2. Data analysis

Proportions of visitors with seeds, seed numbers and species numbers were compared among different visitor categories or different item categories using their mean, and bias-corrected, accelerated (BCa) bootstrap estimates (1000 resamples) of the 95% and 99% confidence interval of the differences between these means (Efron and Tibshirani, 1993). Where these confidence intervals did not include zero, the difference was inferred to be significant at $p < 0.05$ and $p < 0.01$, respectively. Because factors affecting the presence of propagules may be different from factors influencing the number of propagules or species, the presence/absence of propagules was analyzed separately from the number of propagules and the number of species in the samples with propagules. For groups with only a few samples, bootstrap samples under-represent real variation making results unreliable (Chernick, 2008). Therefore groups with fewer than 10 observations were omitted from analysis. Proportions with propagules among visitor categories were also compared using a two-sided Fisher's exact test (Sokal and Rohlf, 1995).

The effect of visitor characteristics on the presence of propagules was analyzed using logit regression, while the relationship between visitor characteristics and number of propagules was analyzed by linear regression. For the regression analyses propagule numbers were log-transformed. For the analysis of sample data at visitor level we summed the data from personal gear items sampled separately per visitor. Similar analyses were undertaken for bryophyte and lichen fragments collectively. The relationship between date and seed incidence was analyzed by logit regression. Because the proportion of tourists and national program personnel was not constant over the field season, with most tourist visits concentrated in December and January, this was done separately for tourists and for national program personnel. The latter travelled to the Antarctic mainly in November and December, but reasonable numbers (>30) were also available for January and March. In February only 8 national program visitors were sampled, while 10 were sampled in early September. Because of the nearly two month gap in time between the early September samples and the next ones, the analysis of the national program visitors was done with and without the September samples. All statistical analyses were undertaken in Genstat 13 (VSN International, 2010).

To predict the number of additional species expected in the total propagule population given increased sampling effort, the program SPADE (Chao and Shen, 2010) was used. A Poisson model was assumed (Chao and Shen, 2004), and predictions made for surveys including up to 10 times as many samples (Chao and Shen, 2010). Presence/absence data of morphotypes, rather than the numbers of seeds, were used to reduce possible bias associated with non-independent entrainment of seeds (e.g. through seed pod entrainment of multiple propagules). The analyses were undertaken separately for tourists and for national program personnel because the proportions of visitors sampled for each of these groups were different.

3. Results

3.1. Proportions of visitors carrying propagules

Tourists and crew were significantly less likely to carry plant seeds than all other visitor categories (Table S3). Within national program personnel, field scientists were more likely to carry seeds than station support personnel (Table S3). Tourists were also less prone to carrying bryophyte and/or lichen fragments than other categories of visitors (Fig. 1 and Table S4), except for ships' crew, station-based scientists, and station-support personnel. By contrast, tourist support and field science support personnel were most likely to carry fragments of bryophytes or lichens.

Using habitats visited (national parks/nature reserves, rural/agricultural areas, parklands/botanical gardens, Arctic areas, high altitude areas, and sub-Antarctic/Antarctic areas) as explanatory variables, regression with stepwise selection revealed that national program personnel who had visited national parks/nature reserves, and/or parklands/botanical gardens carried plant seeds significantly more often than those that had not visited these habitats (58% against 23% respectively, bootstrap test of differences, $p < 0.05$). National program visitors to the Antarctic who visited rural/agricultural and/or alpine/high altitude areas also carried bryophyte and/or lichen fragments more often than visitors who had not been to these habitats (29% against 9% respectively, bootstrap test of differences, $p < 0.05$). In the case of tourist visitors, no significant relationship between habitats visited and the proportion of visitors carrying plant seeds was found, although tourists who had visited rural/agricultural areas in the year before coming to the Antarctic were significantly more likely to have carried bryophyte and/or lichen fragments than those who had not (15% against 5% respectively (bootstrap test of differences, $p < 0.05$)).

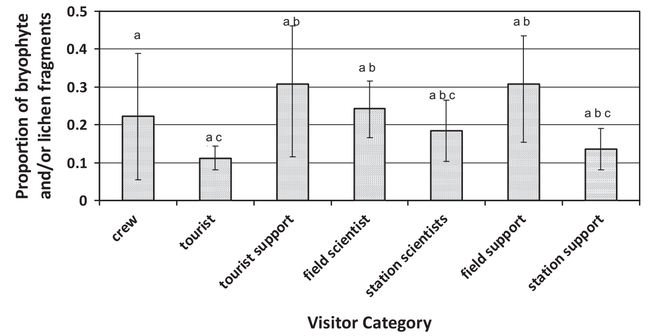

Fig. 1. Proportion of sampled visitors carrying bryophyte and/or lichen fragments for each visitor category. The vertical bars represent the 95% confidence interval for this proportion. Similar letters indicate non-significant differences ($p > 0.05$). The number of observations and the significance of differences are given in Table S4.

Tourists travelling on aircraft or national program ships were more likely to carry seeds than those on tourist ships, while the proportion of tourists carrying seeds was significantly lower on medium or large vessels than on small vessels (Fig. 2 and Table S5). A similar pattern was found for bryophyte and/or lichen fragments (small:medium:large vessels' proportion = 0.208:0.063:0.029, bootstrap test of differences, $p < 0.01$).

Logit regression with day number from 1 September 2007 and the squared day number as explanatory variables, revealed the same general pattern for analyses both including and excluding September data for national program personnel: in the southern spring and autumn the proportion of national program visitors carrying plant seeds was significantly higher (*ca.* 0.7, $p < 0.01$) than in mid-summer (*ca.* 0.3–0.4, $p < 0.01$) (Fig. S1). Tourists and their support personnel visit the Antarctic predominantly in December and January, with low numbers in spring, the second half of the austral

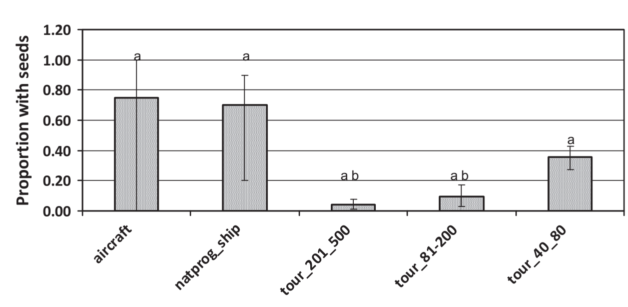

Fig. 2. Proportion of tourists carrying plant seeds for each transport category. The vertical bars represent the 95% confidence interval for this proportion. Similar letters indicate non-significant differences ($p > 0.05$). The number of observations and the significance of differences are given in Table S5.

summer, and autumn. The proportion of tourist visitors carrying plant seeds was not significantly different in the different parts of the summer season.

3.2. Propagule numbers per visitor

The only significant differences in seed numbers per visitor were observed between tourists and field support personnel, and between tourist support personnel and field support personnel (Table S6). However, comparing tourists to all national program personnel (field scientists, station scientists, field support personnel, and station support personnel) together showed a significantly higher number of seeds per visitor for the latter group. With respect to the number of bryophyte and/or lichen fragments per visitor, for people carrying such fragments, we found no significant differences between the separate visitor classes (Fig. 3 and Table S7), but the difference between tourists and all national program personnel taken together was significant.

3.3. Propagule distribution among clothing and gear items

For 349 visitors various items of clothing and other gear were sampled individually. Samples for single items were obtained for 1857 items. Of these items, 1113 were used, 498 were new, and for 246 items the use was unknown. The proportion of items with seeds, and the number of seeds and other propagules were calculated for used items only (assuming new items are propagule free). Large differences in the proportion of items with seeds were found. Footwear and packs/bags showed significantly larger proportions with plant seeds than nearly all other item types (Fig. 4 and Table S8). Bryophyte and/or lichen fragments were most often found in footwear and trousers, and least often in gloves and headwear (Fig. 5 and Table S9).

The mean number of seeds per item ranged from 11.7 for footwear to 1.7 for insulation layer items (Table S8), but only the differences between footwear vs. trousers and insulation layer, and between packs/bags vs. hand and insulation layers were significant. The mean number of bryophyte and lichen fragments per item ranged from 5.1 for packs and bags, to 1.6 for insulation layer items, but the only significant difference was between footwear and insulation layer (Table S9).

3.4. Overall seed number and diversity

Of the 853 visitors sampled, 33% (281 visitors) were carrying a total of 2686 seeds, representing 530 morphotypes, while 16% of visitors carried in total 535 bryophyte and/or lichen fragments. Of these seeds, we identified 114 morphotypes to species level, although not all of these with complete confidence (Table S2). An additional 129 morphotypes were identified to genus level, and another 115 to family level (again with varying levels of confidence, Table S2). The remainder of the seed morphotypes (172) remained unidentified. In 4.7% of the samples more than 10 seeds were found. The highest number of seeds found on a single visitor was 472, representing 86 different species. The number of species (morphotypes) of seeds per sample was 5 or less per visitor sampled in 96.2% of the cases. The number of morphotypes of bryophytes and/or lichens per sample was less than 5 in 99% of all cases with a maximum value of 33. In addition, in a few samples, marine diatoms (of the genera *Grammatophora*, *Rhabdonema*, and *Cocconeis*, amongst others), sporulating fern fronds (*Gleichenia dicarpa* R. Br.), some (presumably marine) algae, and a few sclerotia of the fungus *Claviceps* sp. were found. Many samples contained fragments of grass leaves with other fungal infections.

The tourists sampled carried 314 seeds of 93 species, while national program personnel carried 1814 seeds of 426 species. Among the other visitors (tourist support personnel, ship's crew, and visitors that did not give their status) seeds of 76 species were found. Based on the total number of visitors to the Antarctic in the 2007/2008 season (33,054 tourists and tour guides, and 7085 national program personnel; Chown et al., 2012a), we estimated the total number of plant seeds transported to the Antarctic by all visitors together as 74,148 (95% confidence interval 52,261–101,284), and the number of bryophyte and lichen fragments as 17,468 (95% c.i. 12,240–23,114).

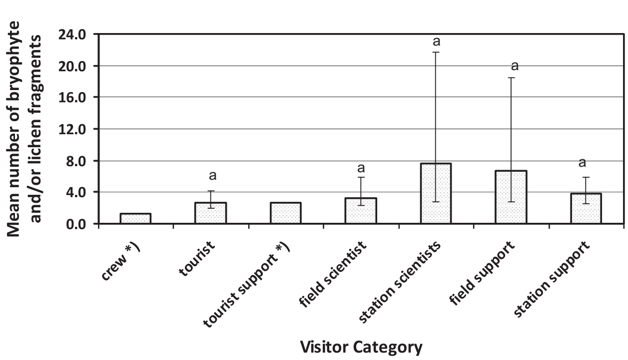

Fig. 3. The mean number of bryophyte and/or lichen fragments carried per visitor for each visitor category. The vertical bars represent the 95% confidence interval for these means. Similar letters indicate non-significant differences ($p > 0.05$). Only visitors carrying such fragments were included. The number of observations and the significance of differences are given in Table S7. (*) for ship's crew ($n = 4$) and tourist support personnel ($n = 8$) no reliable confidence interval could be estimated.

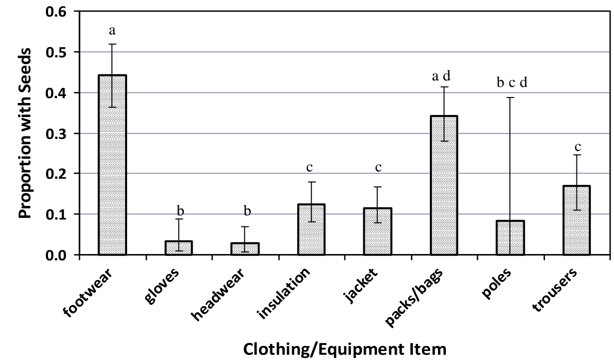

Fig. 4. Proportion of sampled items carrying plant seeds for each item category. The vertical bars indicate the 95% confidence interval for this proportion. Similar letters indicate non-significant differences ($p > 0.05$). The number of observations and the significance of differences are given in Table S8.

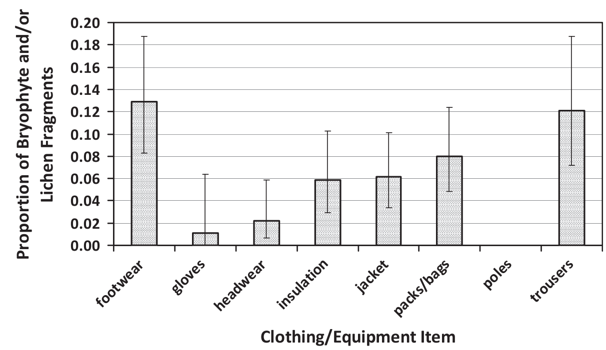

Fig. 5. Proportion of sampled items carrying bryophyte and/or lichen fragments for each visitor category. The vertical bars represent the 95% confidence interval for this proportion. Similar letters indicate non-significant differences ($p > 0.05$). The number of observations and the significance of differences are given in Table S9.

The total number of species estimated by the Chao1index was 493 (95% c.i. = 274–976) for tourists, and 2010 (1509–2744) for national program personnel. However because of the relatively small proportion of visitors sampled and the large number of singletons (ca. 75% of the species were represented by a single seed only), the estimates should be treated with caution (Colwell et al., 2012).

4. Discussion

Although the Antarctic is one of the most biologically isolated regions of the planet, increasing numbers of human visits since the 19th century have largely disrupted that isolation. There have been a growing number of successful inadvertent introductions of terrestrial species, many of which have established and are invasive (Frenot et al., 2005; Olech and Chwedorzewska, 2011; Molina-Montenegro et al., 2012; Cuba-Díaz et al., 2013; Volonterio et al., 2013). The pathways and vectors for introductions are now well understood, comprising a small subset of those known globally (Hulme et al., 2008; Chown et al., 2012a) and involving various vehicles, station construction material, supplies and food, and direct visitor-mediated introduction for terrestrial species (Whinam et al., 2005; Hughes et al., 2005, Hughes et al., 2010, 2011; Lee and Chown, 2009a,b; Tsujimoto and Imura, 2012).

At least for terrestrial systems, our study during the 4th International Polar Year summer, the results of which we report here and elsewhere (Chown et al., 2012a), indicates that direct visitor-mediated introductions are the most significant (*contra* Hughes et al., 2010). What is known of the other pathways suggests that station construction contributes c. 2000–3000 seeds per station per year (Lee and Chown, 2009b), with six stations under reconstruction during the 4th International Polar Year, while routine cargo handling appears to contribute only small numbers of seed per item (Lee and Chown, 2009a), and even an astonishingly high occasional load found on construction machinery (40,000 seeds–Hughes et al., 2010) do not match the >70,000 seeds estimated to have been transported to the region by visitors. Besides seeds, moss and lichen fragments are shown to be carried in substantial numbers too. Since mosses and lichens are the major components of the Antarctic flora (Lewis Smith, 1984) and even fragments of those may stand a better chance to propagate and establish in the area than seeds (Longton, 2009), transport thereof may represent a greater risk than transport of vascular plant seeds. In consequence, although the mitigation of transfer across all pathways is important, management of the visitor pathway is likely to be one of the most significant interventions that could be applied, especially given that visitor numbers are forecast to continue growing (Chown et al., 2012b).

The in-depth exploration of the entrainment data presented here (we did not estimate drop-off, but both drop-off and seed viability following transport can be high – Lee and Chown, 2009a; Wichmann et al., 2009) provides clear evidence for the development of mitigation protocols for visitors which complement those of the broader, spatially explicit assessment we undertook previously identifying sites of high risk (Chown et al., 2012a). Among national program personnel, the footwear, trousers and the bags of field scientists are the highest risk items, with the risk being most pronounced if those personnel have visited protected areas, parklands/botanic gardens or alpine areas prior to travelling to the Antarctic. For tourists, those who have visited rural/agricultural areas prior to travel, and/or whom travel with national programs or on smaller tourist vessels have the highest probability of transferring plant propagules.

The causes of these patterns cannot be firmly elucidated without a much more detailed sampling effort including the sampling of visitors prior to their travel to the region. Nonetheless, they fit with our experience that visitors tend to have a limited stock of cold-weather clothing and field gear that is used in multiple areas, and that this behavioral pattern tends to be most prevalent in field personnel and tourist-support personnel who routinely travel to remote areas, including alpine, Arctic, and Antarctic sites (Whinam et al., 2005), tend to interact more closely with the vegetation, and are therefore more likely to inadvertently collect plant propagules. Tourists who travel on smaller ships also seem more likely to prefer more frequent and closer encounters with natural systems than those who travel on large vessels (Lamers et al., 2008; Haase et al., 2009). Travel either during the boreal or austral autumn months also increases the probability of propagule transfer, which is in keeping with the common pattern of autumn seed dispersal (post summer seed production). Antarctic mid-summer is a period with comparatively little travel. National program personnel arrive usually early in the season and tourists do not pose a high risk, as it is the boreal winter, with few seeds available or the austral summer when the seed load is also low.

Irrespective of the causes of the patterns found here, the management implications are clear. Field scientists and national program personnel who routinely travel to protected areas and parklands should be encouraged to undertake the most rigorous assessments of their gear. Although their travel to alpine/Arctic/Antarctic sites did not seem to have an influence on seeds as propagules, the influence on bryophytes and lichens was clear, showing that thorough assessments following visits to these sites are important because a considerable number of the seeds sampled are from these areas and climate matching would suggest an elevated probability of establishment were propagules to be introduced to the Antarctic environment (Chown et al., 2012a). Similarly, the most rigorous assessments should be applied when travelling with national operators and on small vessels. Moreover, it is not only the visitors that should be expected to be most vigilant in advance of such travel, but vessel operators and managers of national programs should also take these differences in risk category into account and apply additional scrutiny to that already implemented. Although a range of treatments is available to reduce propagule load or viability (Lee and Chown, 2009a), it appears that the most effective measure is for new clothing and gear to be used for each trip to the continent. If the provision of new clothing and gear is not possible, issued outer clothing and gear could be reserved for use in the Antarctic only and distributed either en route to (post aircraft or ship departure) or in the region, serving to substantially limit the potential for contamination. By contrast, vacuuming, washing and other techniques are less effective, but still more efficacious than no treatment at all (Lee and Chown, 2009a). Nonetheless, it should also be recognized that in a region as biogeographically diverse as the Antarctic continent and its surrounding islands (e.g. Lewis Smith, 1984; Terauds et al., 2012), intra-regional propagule transfer also poses a substantial biodiversity risk, given that entrainment of propagules from the region is common (Hughes and Convey, 2010; Lee and Chown, 2011). In this case, taking separate sets of clothing, or cleaning of clothing and gear in advance of transfer between major biogeographic regions (islands and island groups or the Antarctic Conservation Biogeographic Regions – Terauds et al., 2012) seems to be the most practicable solutions,

While interventions to reduce propagule transfer into the Antarctic and among regions within it have implications in terms of personnel time, tourist experience, and investments in clothing and gear, by comparison with the total cost of Antarctic operations these interventions are likely to be relatively inexpensive. For example the US Office of Polar Programs 2013 Antarctic budget request was c. US$ 308 million (http://www.nsf.gov/about/budget/fy2013/pdf/13-OPP_fy2013.pdf). The South Korean Antarctic budget for 2010 was c. US$ 30 million (Brady and Kim, 2012), and the expenditure of Antarctic New Zealand for 2011/12 was *c*. NZ$ 14.6 million (*ca*. 11.4 US$) (Antarctica NZ Annual Report, 2012). Clearly, variety among other nations and tour operators means that a range of financial scenarios apply to Antarctic operations. However, as is the case with conservation more generally, the costs relative to the benefits, and relative to expenditure in other areas of the economy are likely to be low (e.g. James et al., 2001; Simberloff et al., 2013).

In conclusion, the current work provides a sound evidence base for both self-regulation and organization-based regulation to reduce propagule transfer of plants to the Antarctic. Given similarities with findings for other remote regions (e.g. Ware et al., 2012) they are likely also to be more broadly applicable.

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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.2014.01.038.

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