

What affects the probability of biological invasions in Antarctica? Using an expanded conceptual framework to anticipate the risk of alien species expansion

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Abstract Successful alien species invasion depends on many factors studied mostly in post invasion habitats, and subsequently summarized in frameworks tailored to describe the studied invasion. We used an existing expanded framework with three groups of contributing factors: habitat invisibility, system context and species invasiveness, to analyze the probability of alien species invasions in terrestrial communities of Maritime Antarctic in the future. We focused on the first two factor groups. We tested if the expanded framework could be used under a different scenario. We chose Point Thomas Oasis on King George Island to perform our analysis. Strong geographical barrier, low potential bioclimatic suitability and resource availability associated with habitat invisibility significantly reduce the likelihood of biological invasion in Antarctica. An almost full enemy release (low pressure of consumers), the high patchiness of the habitat, and the prevalence of open gaps also associated with habitat invisibility increase the possibility of invasion. The dynamics of functional connectivity, propagule pressure and spatio-temporal patterns of propagule arrival associated with human activity and climate change belonging to the system context contribute to an increase in the threat of invasions. Due to the still low land transport activity migration pathways are limited and will reduce the spread of alien terrestrial organisms by land. An effective way of preventing invasions in Antarctica seems to lie in reducing propagule pressure and eliminating alien populations as early as possible. The expanded

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conceptual framework opens up wider possibilities in analyzing invasions taking place in different systems and with multiple taxa.

Keywords Maritime Antarctic · Alien species · Biodiversity · Biological invasions · Framework · Propagule pressure

Introduction

The dispersal of non-native species in the Antarctic is presently the most challenging issue associated with local human activity (Chwedorzewska et al. 2013; Lee and Chown 2009a; Lityńska-Zajac et al. 2012; Lewis Smith 1996). The intensification of human activity in this zone generates an array of environmental changes that increase the probability of biological invasions (e.g., Frenot et al. 2005; Chwedorzewska 2009; Convey 2010).

In the last few years, numerous papers have focused on understanding the mechanisms and predicting the processes of biological invasions. Among other things, they discuss the traits of the invasive species likely to successfully expand in a new ecosystem (e.g., Kleunen et al. 2010; Moles et al. 2008), predict the effects of climate change (Gilman et al. 2010), or search for links between ecological and evolutionary changes (Facon et al. 2006). These theoretic and conceptual works are also intended to be applicable for developing management (research and conservation) programs, and their theoretical frameworks are “tools to organize research and evaluate the state of a subject area” (Foxcroft et al. 2011; McGeoch et al. 2015; Thomsen et al. 2011). Many models and frameworks, either of a broad nature (e.g., Blackburn et al. 2011; Gilman et al. 2010; Moles et al. 2008; Thomsen et al. 2011), or describing specific species and/or regions (e.g., Facon et al. 2006; Foxcroft et al. 2011; McGeoch et al. 2015) have been proposed by their authors as appropriate for the analysis of other invasions. However, to our knowledge such use has seldom been reported in the literature (Vardien et al. 2012).

Out of these numerous works, “Expanding the conceptual frameworks of plant invasion ecology” (Foxcroft et al. 2011) deserves special attention as this work aims at “identifying the internal features of the receiving site and the nature of the potential invaders”. The framework had been applied to describe two plant species invasions in South Africa region (Foxcroft et al. 2011; Vardien et al. 2012). In order to evaluate if the application of an existing framework in a new context is possible, we assessed the threat of biological invasions in the Maritime Antarctic using the framework of Foxcroft et al. (2011). We do not address a one region to one species relation, but analyze external factors that contributed to the susceptibility of the Maritime Antarctic region to invasions. The novelty in our work lies in evaluating whether such a framework can be used to analyze different invasion scenarios in a different context and with multiple species.

Methods

We analyzed literature on species alien to continental and Maritime Antarctica noted in the vicinity of the H. Arctowski Polish Antarctic Station situated on the western shore of Admiralty Bay on King George Island (hereinafter KGI), South Shetland archipelago, West Antarctica; 62°10'S, 58°28'W. The Arctowski Station lies within the Point Thomas Oasis. This is one of the largest seasonally ice-free areas (approx. 25 km²,

Lityńska-Zajac et al. 2012) in the Maritime Antarctic region with relatively high temperatures during the austral summer (Galera et al. 2015; Kejna et al. 2013) and a constant flow of fresh water (Nędzarek et al. 2014) throughout most of the summer season from December to February, inclusive (Kejna et al. 2013, Braun et al. 2017, Sancho et al. 2017). It is also one of the most environmentally favorable areas in the Maritime Antarctic (Lityńska-Zajac et al. 2012), therefore the most likely location in the whole region for biological invasions. The spatial isolation of this area and well documented logistics of the Polish Antarctic Station located there enabled a detailed assessment of the key driving factors for the probability of a successful invasion in the whole region. Environmental changes on KGI are an example of complicated processes taking place in the Maritime Antarctic region. We compared the reported incidents of alien species appearance with similar problems from other parts of the world, especially on spatially isolated islands.

Our work has been arranged according to the expanded framework by Foxcroft et al. (2011) taking into account three groups of contributing factors: habitat susceptibility (invasibility of the habitat), system context (spatially explicit connectivity between the systems supplying and/or transporting potential invaders and habitat susceptibility to alien organisms), and species invasiveness (traits that predispose a species to be invasive). We considered the probability of biological invasions in Maritime Antarctic with detailed analysis of habitat susceptibility and system context. We do not concentrate on species invasiveness, as we analyze the threat of future invasions not knowing propagules of which species will arrive in the studied region. The sequence of ‘specific mechanisms’ in the Fig. 1 corresponds to the order of sub-chapters in our work.

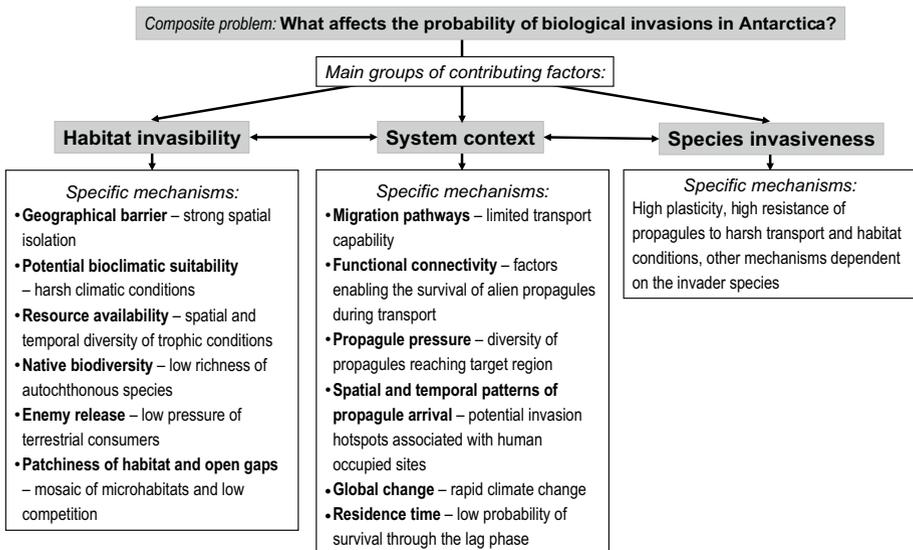


Fig. 1 A framework for the assessment of probability of biological invasions in Antarctica showing factors affecting the likelihood of an invasion. The diagram structure refers to Foxcroft et al. (2011) and Vardien et al. (2012) (slightly changed)

Invasibility of the habitat

It is generally acknowledged that islands are more susceptible to invasion than continental habitats due to prolonged isolation, low competitive capability of the native species, and empty ecological niches (Alpert et al. 2000; Brandes 2008; Trueman et al. 2010). This phenomenon has been studied extensively in tropical oceanic islands (Daehler 2006; Kueffer et al. 2010). On the other hand, a small island well isolated by geographic barriers, for example by specific ocean and air currents, may receive very limited propagule pressure, making it resistant to invasion due to its remoteness. Therefore, an invasion of an open habitat containing resources for the invader is not possible without the existence of dispersal corridors (Grime 2001).

Discrepancies between reports indicate that the relation between the degree of island isolation and target habitat invasibility is not a simple one and in every instance can be governed by different factors (e.g., Daehler 2006; Kueffer et al. 2010; Von Holle and Simberloff 2005). Frenot et al. (2005) stated that cold islands are less susceptible to invasions than warm ones. For insects a similar relationship holds, although indigenous vascular plant richness is also an important correlate of the richness of alien insects. Investigations by Chown et al. (1998) suggested that larger Southern Ocean islands attract more human occupants, increasing the risk of alien organism transfer, while milder climate increases the chance of propagule establishment.

Geographical barrier—strong spatial isolation of Point Thomas Oasis

The Antarctic terrestrial and marine ecosystems are strongly isolated, without any gradual connectivity with those at lower latitudes. The isolation process commenced with the breakup of Gondwana and was maintained by the atmospheric Polar Vortex and oceanic Polar Frontal Zone (e.g., Barnes et al. 2006; Clarke et al. 2005; Convey 2010). Oceanic and atmospheric circulation patterns around the Antarctic significantly restrict the transfer of organisms into this region. Terrestrial ecosystems have developed on the ice-free “environmental islands” restricted to the coastal zones of the Antarctic Peninsula and the associated islands (e.g., Convey 2010; Houghton et al. 2016; Hughes and Convey 2010).

One of such “island-like” enclaves is the Point Thomas Oasis on KGI, located approximately 160 km from the Antarctic Peninsula (Zwolicki et al. 2015). Although the distance from KGI to the nearest continent is relatively short in comparison with other oceanic islands (Kueffer et al. 2010), the nearest continent is Antarctica which is a marginal source of propagules. Therefore, the studied ice-free oasis is one of the most isolated areas on Earth, being separated from other terrestrial communities on the island by permanently glaciated zones (90% of KGI is ice covered year-round; Kejna et al. 2013; Zwolicki et al. 2015). There are over a dozen research stations and refuges located on KGI. Land transport between the stations is highly restricted or non-existent, apart from the U.S.A. Copacabana Field Camp summer station which is situated within walking distance of Arctowski Station (Kejna et al. 2013; Pudelko 2007). Travel between the other stations in the different polar oases is accomplished mainly by sea routes.

Potential bioclimatic suitability—harsh climatic conditions of Point Thomas Oasis

The isolation of Antarctic islands is a result not only of the physical distance to other continents, but also of ecological isolation (Barnes et al. 2006; Clarke et al. 2005). Similarities

in environmental features between potential propagule source areas and the Maritime Antarctic zone are low. Harsh abiotic conditions on KGI are the main selective ecological filter for propagules of terrestrial organisms, diminishing the probability of their establishment. In this way, both spatial and ecological isolation may play the most important role in Antarctic islands invasibility (e.g., Alpert et al. 2000).

The typical polar maritime climate on KGI can be described as extremely inhospitable for terrestrial organisms, especially for alien homeohydric species. Mean monthly temperatures of 2.4 °C in January (warmest month during the austral summer) and −6.7 °C in July (coldest month, data from Admiralty Bay, see Galera et al. 2015) together with high variation in daylight duration (ca 4.5–19.5 h, Kejna et al. 2013) may highly impact the fitness of introduced organisms. The difficult environmental conditions are also shaped by cyclic freezing and melting, humidifying and drying, high intensity of solar radiation in summer, including UVB, lack of light in winter, and the strong winds which act both as a desiccation and an abrasion factor (Giełwanowska et al. 2011). For potential invaders from Europe, the temporal shift between summer seasons in the Northern and Southern Hemispheres (Galera et al. 2015) may also present a problem in adjustment of physiological traits associated with their phenology.

For small terrestrial plants and animals capable of physiological dormancy, the thick snow cover increases the likelihood of survival by providing an insulating blanket of snow where they can remain unaffected by the low temperatures and strong desiccating winds (Ochyra et al. 2008). At the same time the snow cover can extend the cold season by preserving cold temperature close to the soil surface and shortening the growing season (Schroeter et al. 2010 and literature cited therein). In comparison with other Antarctic bioregions the mean yearly precipitation on KGI is relatively high (about 700 mm, Kejna et al. 2013); however, due to prevailing subzero temperatures organisms may still be subject to physiological drought. Nevertheless, the Point Thomas Oasis seems to be one of the most favorable areas for living organisms in the whole of the Maritime Antarctic.

Resource availability—spatial and temporal diversity of trophic conditions of Point Thomas Oasis

The primary production of Maritime Antarctic terrestrial ecosystems is extremely low, making autochthonous resources of biogenic substance minimal (Williams 1994; Hopkins et al. 2014). Vegetation communities in this region depend largely on marine-derived biogenic substances (main vectors—marine birds and pinnipeds, Green et al. 2015). The animal-mediated nutrient deposition creates spatially restricted over-fertilized sites (ornithogenic soils, Tatur et al. 1997). In contrast, deglaciation processes offer sites with a substratum nearly entirely devoid of organic matter. The chemical weathering of rocks, the most important source of nutrients in other climatic zones, is strongly inhibited in severe polar climates (Nędzarek 2008). These contrasting processes make habitats of Point Thomas Oasis very diverse in pH and substratum fertility (Tatur et al. 1997; Zwolicki et al. 2015). Typical for polar coastal oases, the most important limiting environmental factors are water and salinity stress (physiological drought and saline aerosols, Giełwanowska et al. 2011). The Antarctic substratum is characterized by instability due to the exfoliation of rock surfaces and cryoturbation of soil and stones (e.g., Green et al. 2015; Ochyra et al. 2008), together with the presence of permafrost, solifluction or ablation, significantly limiting the development of terrestrial communities (Convey et al. 2009).

Specific Antarctic flora and fauna makes the food resources for potential heterotrophic invaders very different from their habitat of origin. Therefore, trophic resources may be accessible only for organisms capable of changing their diet and feeding behavior. This may present an impenetrable barrier for heterotrophic monophagous species which reach the Maritime Antarctic. For example wood pests recorded in the Arctowski Station (Chwedorzewska et al. 2013; Osyczka et al. 2012). In Antarctica there are no woody plants (e.g., Convey 2010; Hughes and Convey 2014), therefore in the receiving habitat there are no food resources for these organisms. These species are also unable to complete their life cycle without access to wood and bark. All timber in Antarctica is of allochthonous origin, brought in for construction purposes, wooden crates and pallets used for cargo packaging, or driftwood impregnated by seawater (Chwedorzewska et al. 2013). Another example is the problem of accessibility to proper food resources for vagrant bird species, particularly passerines. Gryz et al. (2015) observed that the Austral Negrito *Lessonia rufahasis* was unable to feed on the flightless invertebrates in Antarctica. The species' characteristic feeding behavior, based on catching flying insects, was not successful in this case.

Resource availability has a very high temporal variation, which may be a problem for alien terrestrial organisms. This is connected with the low primary production of palatable plants—potential fodder for grazers. The extended duration of snow cover hampers access to lichens and dead plant biomass. Similarly, the food base for predators is available mainly in the austral summer season during the breeding, molting and/or resting seasons of maritime vertebrates (Ciaputa and Siciński 2006; Jabłoński 1986; Salwicka and Rakusa-Suszczewski 2002; Trivelpiece et al. 1987a). Therefore, according to the fluctuating resource availability theory advanced by Davis et al. (2000), the invasibility of communities at Point Thomas Oasis may be low due to the low levels of unused resources available to an invader and the temporal variation. Nevertheless, this might change with climatic fluctuations, making unused resources available for potential invaders at some future point in time.

Native biodiversity—low richness of autochthonous species in the Maritime Antarctic

Native Antarctic terrestrial communities typically have low species richness and are thought to have low functional redundancy. At the higher taxonomic levels, many groups are missing altogether, no native pteridophytes occur in the Maritime Antarctic. Vascular plants are represented by only two species of flowering plants (e.g., Convey 2010; Hughes and Convey 2014). The poorly developed Antarctic tundra consists mostly of cryptogams. Major components of the terrestrial biota are lichens (294 species on KGI; Olech 2004) and mosses (63 species on KGI, Ochyra et al. 2008). Fauna of true terrestrial animals of the Antarctic region (sub-Antarctic and Antarctica) is limited to small invertebrates (some 520 species of soil animals, but likely underestimated) from the groups: Diptera (only two species), Acari, Collembola, Tardigrada, Nematoda and Rotifera (Houghton et al. 2016).

Apart from the cetaceans, which are fully aquatic, all other Antarctic megafauna species depend on the terrestrial environment to reproduce (Forcada 2008). Species diversity is low and includes 53 species of marine birds (13 breed on KGI) and six species of pinnipeds (five species on KGI; Salwicka and Rakusa-Suszczewski 2002). Most of those animals form large breeding colonies and resting concentrations on shore which remain very patchy and strongly depend on accessibility to the shore (e.g., Shirihai 2008; Sierakowski et al. 2017; Trivelpiece et al. 1987a).

It is widely claimed that the more isolated oceanic islands should be less resistant to invasion than the less isolated ones, because endemic species of isolated oceanic islands are weak competitors (Caujape-Castells et al. 2010, but see comments by Kueffer et al. 2010). Hughes and Convey (2014) argue that the long history of evolutionary isolation of Antarctic biota is evidenced by high levels of endemism across most groups of organisms. In fact, the high percentage of endemics refer to the biota of lichens (151 endemic species—39% of biota of lichens of the Maritime and Continental Antarctic, Ochyra et al. 2008). Approximately 170 animal soil species are endemic (about 33% of terrestrial invertebrates fauna of the sub-Antarctic and Antarctic, e.g., Houghton et al. 2016). Almost or entirely all Nematoda fauna is endemic, despite the fact that generally nematode worms are highly capable of long-distance dispersal (Convey 2010). In contrast, the flora of bryophytes is characterized by a low level of endemism—no endemic taxa occur in the flora of liverworts, and the relatively rich flora of mosses contains only 6% strict Antarctic endemics (Ochyra et al. 2008).

The correlation between native species richness and the invasibility of a habitat has been discussed by many authors (e.g., Kueffer et al. 2010; Thuiller et al. 2007). It has been shown that the relationship between species richness and ecosystem invasibility is scale-dependent (Kühn and Klotz 2007; Richardson and Pyšek 2006). However, it seems that the number of the native species, including endemic species, is less important for invasibility than, for example, the presence or absence of a species that may interact with the potential invader (Borges et al. 2006). Therefore, as stated by Crawley et al. (1999), the characteristics of the dominant native species may be more important for habitat invasibility than the overall species richness.

Enemy release—low pressure of terrestrial consumers in Antarctica

The trophic complexity of the Antarctic terrestrial ecosystems is thought to be generally simple and mostly relies on marine resources. The different trophic levels are represented by singular species or not represented at all (Convey 2010; Frenot et al. 2005). All vertebrates (marine birds and pinnipeds) rely on marine resources for food (Hughes and Convey 2014); there are no terrestrial herbivores in the Antarctic region (Olech et al. 2011). Predators that could present pressure for alien terrestrial animals are primarily skuas *Stercorarius* spp. and the southern giant petrel *Macronectes giganteus*, which are intelligent generalists with a diverse diet and the ability to quickly change their food preferences (e.g., Carneiro et al. 2015; Malzof and Quintana 2008). The similar abundant and highly successful avian predator, the kelp gull *Larus dominicanus*, is characterized by its dietary breadth, wide-ranging foraging strategies, and acclimation to modified landscapes (Gallagher et al. 2015). Among the pinnipeds, the fur seal species *Arctocephalus* spp. could potentially present pressure for alien animals. Some incidents of predation on various birds species have been recorded in the Antarctic (e.g., Ciaputa and Siciński 2006; Visser et al. 2008).

The absence of terrestrial mammalian herbivores (Olech et al. 2011) and predators may present an advantage for alien species under the enemy release hypothesis. This may promote higher susceptibility of native biota to the introduction of any heterotrophic organisms, which may remain without control by predators (Frenot et al. 2005). This characteristic of Antarctic habitats leaves open ground for unobstructed development of any potential newcomer according to the enemy release hypothesis (Blossey 2011; Keane and Crawley 2002).

Patchiness of habitat and open gaps—mosaic of microhabitats and low competition in the Maritime Antarctic

Antarctic ice-free areas are a mosaic of microhabitats (see section *Resource availability*), clearly differentiated by abiotic features, e.g., water conditions, salinity and/or nutrient content of substratum. This patchiness also shapes the distribution of microorganisms in Maritime Antarctic, making the interactions involved more limited in space and different from species-rich environments (Bölter et al. 1997). Harsh environmental conditions impact the poor development of vegetation and loose vegetation cover (see Wilson et al. 2007 and sections *The possibilities of bioclimatic suitability* and *Native biodiversity* in this article). This type of open habitat leaves potential for ecological niches to be filled by newcomers and presents the possibility for establishment of novel trophic functions in the ecosystem (Hughes and Convey 2014).

Due to the severe environmental conditions native Antarctic biota is characterized by a predominant life history of poor competitive ability and vulnerability to invasion by more effective competitors (Convey 2010; Hughes and Convey 2014). On one hand, this relaxed competitive ability of indigenous organisms is promoted by the harsh environmental conditions in Antarctica, and on the other by the spatial isolation of the islands (Kühn and Klotz 2007), enhancing the high invasibility of this region. The underlying assumption is that an invading species will benefit in a community where it does not encounter intense competition for resources (Alpert et al. 2000).

System context

In the case of spatially isolated habitats, the breaking of geographic barriers is of major importance for the system context (spatial and temporal influence arising outside the habitat that might be invaded; Foxcroft et al. 2011). The breaking of a geographic barrier has been mostly achieved through deliberate introduction and cultivation of economic (especially ornamental) plants. This general principle is pertinent in the majority of oceanic island plant invasions (e.g., Keller et al. 2011; Kueffer et al. 2010). In contrast, the propagule pressure on Antarctic islands is mainly mediated through inadvertent introductions. Strict phytosanitary regulations are aimed at reducing the likelihood of the introduction of alien propagules by this vector (Chown et al. 2012a; Hughes and Convey 2014). Due to the strict spatial and ecological isolation of the Point Thomas Oasis (chapter *Geographical barrier*), humans are the only vector of alien propagule dispersal. This is true for long distance transportation (transoceanic), as well as for local propagule dispersal within the Antarctic between islands and ice-free oases. Transport duration and conditions have to meet propagule survival requirements to enable their establishment in the target environment. The route and mode of transport are key aspects for the probability of invasion success.

The natural fine scale vectors are wind and birds, including vagrant species (birds found far outside their expected range). There are several potential mechanisms by which vagrant individuals arrive in the Antarctic. They may have either drifted off course from their normal migration routes by austral gales (e.g., Lazo and Yañez 1989), traveling on errant headings (e.g., Lees and Gilroy 2009), or may represent the vanguard of individuals pioneering new migration routes—“pseudo-vagrants” sensu Gilroy and Lees (Gilroy and Lees 2003; Korczak-Abshire et al. 2011a). They may be potential diaspore migration agents.

Migration pathways—limited transport capability in the Maritime Antarctic

Antarctica has received a rapid increase in tourism over the last two decades (e.g., Chwedorzewska 2009; Chwedorzewska and Korczak 2010). Tourist airplane flights over the Antarctic continent started in the 1950s and were soon followed by cruises to the South Shetland Islands (Frenot et al. 2005). In comparison with other areas of the World (Hulme 2009), the intensity of these visits remains small. The main means of transport of alien species into Antarctica are tourist and expedition ships, despite the quarantine inspections and fumigation at cargo facilities (Houghton et al. 2016). The number of cruise ship visits at Arctowski Station during each of the last seven austral summers has ranged from 7 to 29, with 350 to even 5700 persons landing per season (Chwedorzewska et al. 2015, Fig. 2). Most tourists are from Europe, North America and Japan (Chwedorzewska 2009). Above all, ships (touristic, research, fishing and military vessels) can be accompanied by vagrant birds (Gryz et al. 2015; Korczak-Abshire et al. 2011b), capable of bringing alien propagules to the Antarctic. Ship—assisting vagrant birds transported to South Shetland Islands have been reported by Couve and Vidal (2003) and Shirihai (2008).

The abundance of propagules of alien species was found to be pathway dependent (Houghton et al. 2016). The majority of tourist ships depart from Ushuaia or Punta Arenas and participate in multi-site tours. The sequence of sites visited over the short time period is from warmer areas of higher biodiversity (Tierra del Fuego and sub-Antarctic islands) to the cooler highly pristine sites in Maritime Antarctica and the Antarctic continent (Chwedorzewska 2009). For most ships, the Polish Station is the first place visited after departure from South America. Furthermore, the same ships commonly visit high-latitude polar regions in the Northern Hemisphere within 6 months of departing for Antarctica (Chwedorzewska and Korczak 2010). Also the supply ship of the Polish Antarctic Station operates as a tourist ship in the Arctic during the boreal summer (Chwedorzewska 2009). This can increase the probability of introduction of non-native species with pre-adaptations to survive in polar conditions.



Fig. 2 Tourists visiting Arctowski Station in the austral summer. Photo by M. Wódkiewicz

Despite the huge number of landing people, tourism seems to contribute only a minor proportion of alien propagule traffic. The main reasons are strict phytosanitary regulations (www.iaato.org) and the short visit time—tourists are responsible for only 5% of total person days spent on land in Antarctica (Jabour 2009). In contrast the equipment and clothes of station personnel do not undergo such strict inspection. Station staff constitute a smaller group of people visiting the Antarctic (Frenot et al. 2005), however their stay is considerably longer and therefore creates a greater impact on the environment (e.g., Lee and Chown 2009a, b). It is estimated that about 75 Antarctic research stations are inhabited by around 4000 employees in austral summer while approximately 1000 people stay for the winter (Hughes and Convey 2014). In the last seven seasons the number of expeditioners working at Arctowski Station has ranged from 6 to 8 wintering persons (staying at the station at least 12 months) and 5–33 persons staying only for the austral summer (from 2 to 6 months, Arctowski Station logbook).

For the Polish Antarctic Station the main means of transportation is by ship and helicopter. Air transportation is not frequent and of marginal importance for Arctowski Station (small number of passengers and volume of cargo). While the transport of alien animals into Antarctica by air has been reported in literature (Frenot et al. 2005), the probability of an invasion mediated by air traffic in Point Thomas Oasis still seems to be low.

Functional connectivity—factors enabling the survival of alien propagules during transport to Point Thomas Oasis

The main introduction routes are associated with polar station provisioning. Alien organisms might be accidentally transported on packaging materials, vehicles, scientific equipment, construction materials. Fresh food products and staff personal items including clothes, boots and luggage all have the increased probability of propagule carryover (Chwedorzewska et al. 2013; Chown et al. 2012b; Lityńska-Zajac et al. 2012). The Polish Station is usually provisioned once a year, with small amounts of fresh products resupplied from South America several times during the summer season. The majority of cargo destined to Arctowski Station originates in Poland, but some fresh fruit, vegetables and eggs are supplied from Argentina. The produce are transported at 4 °C for approximately 40 days from Poland and 7 days from Argentina. These conditions may prolong the longevity of a wide spectrum of living organisms. The rest of the cargo (on average 30 tonnes per year), excluding frozen items, are kept in the ship's hold, where conditions may also promote survival of many propagules (Chwedorzewska et al. 2013).

Transportation conditions may on the other hand limit the successful arrival of propagules to the target environment. In the case of animals with a short life cycle, long duration transport presents a major barrier as the life of some invertebrates is too short to survive the passage to King George Island where they could potentially close their life cycle (Chwedorzewska et al. 2013).

Propagule pressure—diversity of propagules reaching Point Thomas Oasis

Due to the distinct spatial isolation of Antarctica, direct observations of alien propagule migration to the Polish Antarctic Station were possible. Due to strict control of potential vectors (compare sections *Geographical barrier* and *Migration pathways*) this presents a unique possibility to perform a direct study of propagule pressure.

Altogether 103 alien species were found to arrive to Point Thomas Oasis (Electronic Supplementary Material A1). During three summer seasons, 148 generative diaspores belonging to 45 species of flowering plants alien to the Maritime Antarctic were found on personnel field clothing, gear and equipment (Lityńska-Zajac et al. 2012). *Juncus bufonius* has not been physically observed in Antarctica, but its diaspores capable of germination were found in soil samples collected in the vicinity of Arctowski Station (Cuba-Díaz et al. 2013). A total of 45 specimens of non-indigenous lichens belonging to 24 species alien to the Antarctic biota were found on the cargo of one of the expeditions (mostly on wooden pallets and cases; Osyczka 2010). Also nine species of macrofungi were discovered on timber brought for one of the expeditions (Osyczka et al. 2012). In the cargo of three expeditions, altogether 271 live specimens of 24 species of invertebrates were found, mostly among the fresh fruits and vegetables (Chwedorzewska et al. 2013). Additionally, four specimens of insects belonging to two species were noted on timber materials for one of the expeditions (Osyczka et al. 2012). Only a Barn swallow (*Hirundo rustica*) individual observed in Point Thomas Oasis (Korczak-Abshire et al. 2011b) could be considered as an alien vertebrate species transported to Antarctica by a human vector as individuals of this species have been observed on vessels visiting Antarctica (e.g., Shirihai 2008; Couve and Vidal 2003; Joseph Charles Abshire, the captain of RV Laurence M. Gould, also observed a juvenile Barn swallow on board off shore of Livingston Island in South Shetlands archipelago on 6th Nov 2011).

The relatively large propagule pressure in Antarctica, however unexpected it may seem at first, has also been confirmed by other authors (Hughes and Pertierra 2016; Houghton et al. 2016 and literature cited therein). Around 10 alien plant species have survived the Antarctic environmental conditions (sometimes their identification was ambiguous; Hughes and Pertierra 2016). Some alien species function only in artificial manmade habitats and are not observed in the outside environment, such as *Trichocera maculipennis* and *Lycoriella ingenua* (Hughes et al. 2005; Houghton et al. 2016; Hughes and Pertierra 2016) or populations of *Drosophila melanogaster* and *Ctenosciara hyalipennis* found almost every year in the vegetable warehouse at Arctowski Station (Chwedorzewska et al. 2013). All these findings indirectly confirm propagule pressure. Despite the relatively high species diversity of propagules reaching Arctowski Station (Electronic Supplementary Material A1) only one species (*Poa annua*) has penetrated the survival (Olech 1996), reproduction (Wódkiewicz et al. 2013), as well as dispersal and environmental barriers (Olech and Chwedorzewska 2011; Galera et al. 2017).

Spatial and temporal patterns of propagule arrival—potential invasion hotspots associated with human occupied sites in Antarctic stations

In the context of the framework, it has been proposed that the spatial arrangement of habitats subject to different kinds and levels of anthropopressure (e.g., areas strongly transformed by man vs. relatively undisturbed natural habitats) “provides essential context that will influence the functional connectivity and transfer of propagules between patches” (Foxcroft et al. 2011). Simberloff (2009) also indicates that the spatial and temporal patterns of propagule arrival are an important component. It is typical that the areas of highest human-generated disturbance neighbor logistics cargo hubs (e.g., railway areas—Brandes 1983, 2005; Wiłkomirski et al. 2012; inland ports—Brandes 1989; airports and seaports—Tatem et al. 2006). A similar phenomenon can be observed in the Antarctic.

Human activities in the Antarctic are concentrated mainly in small, scattered, ice-free coastal zones. Most of the research stations are also located at these coastal areas which are at the same time favorable to development of biological communities (e.g., Hughes and Convey 2014; Hughes et al. 2011). Moreover, the sites most likely visited by tourists coincide with the locations of most scientific bases and high wildlife concentration. Due to the interaction of the comparatively favorable microclimate and expanding human interest in the vicinity of research stations, the likelihood of encroachment by alien organisms increases. Areas near polar research stations generally receive frequent visits (station staff and some of the stations also tourists). The consequences may be visible immediately, but are often cumulative and may only become apparent over a longer time (Chwedorzewska and Korczak 2010). The construction and utilization of the Antarctic research station infrastructure results in irreversible environmental impacts (Hughes and Convey 2014; Frenot et al. 2005). Thus, all known introductions of terrestrial alien species have been found in the vicinity of the research stations (Hughes and Worland 2010; Hughes et al. 2012; Olech 1996). The majority of activities associated with the functioning of the stations are performed during the austral summer. This presents a high probability of alien propagules reaching potentially invulnerable sites and become established, in comparison with the winter season when the area is covered by snow and conditions disable life development.

Tourists are attracted mainly to sites of high/medium biological diversity (Frenot et al. 2005 and literature cited therein), and their visits concentrate on small coastal areas rather than on inland ice (Bölter and Stonehouse 2002). The standard pattern of visits during the 1980s and 1990s was simply to land on beaches and observe any immediately accessible wildlife, but the options now include extensive walks, kayaking, skiing, and even a marathon (see www.marathontour.com). Currently, over 30,000 ship-based tourists visit the Antarctic region each year (Chown et al. 2012b), making use of the over 150 landing sites. While some locations receive only a few visits per decade, the most popular may be visited three times weekly throughout the summer season (even 430 landings per site, see iaato.org).

Arctowski Station is one of the most attractive Antarctic research stations for tourists. Here, visitors have good access to such attractions as a penguin rookery, gathering places of pinnipeds, relics of the whaling industry (e.g., harpoons, whale bones), valuable plant communities, and a visit to the main station building (Zwolicki et al. 2015).

Global change—rapid climate change on King George Island

Earlier studies indicated that the climate of Antarctica is closely linked with other parts of the global climate system (Summerhayes 2009; Turner et al. 2014). However recently Turner et al. (2016) contradicted these findings stating that the local changes “are not primarily associated with the drivers of global temperature change but, rather, reflect the extreme natural internal variability of the regional atmospheric circulation”. Numerous authors showed that the climatic conditions of the Antarctic Peninsula region show the largest warming trend in the whole Antarctic (e.g., Nielsen and Wall 2013; Turner 2009; Turner et al. 2014). Data from 1948 to 2011 from nine meteorological stations located on KGI and on Deception Island, 120 km away from KGI (Kejna et al. 2013) indicate that an increase in air temperature has occurred, reaching 0.19 °C/10 years. In summer, the warming was more than twice as high as in wintertime (Kejna et al. 2013). However the latest data of Braun et al. (2017) indicate that the summer warming trend that persisted on KGI until the end of 20st century has collapsed. Data from the last years indicate that

the climate in the Antarctic Peninsula region is more variable in space and time than previously expected (Turner et al. 2016; Braun et al. 2017; Sancho et al. 2017). Such rapid changes of weather conditions may disturb the ecosystem balance what may increase its susceptibility to invasions.

In contrast to changes in mean monthly air temperature, the precipitation level on KGI has only changed minimally (Braun et al. 2017). In the Maritime Antarctic, summer precipitation increasingly occurs as rain rather than snow (Chwedorzewska 2009). This increases liquid water availability during the vegetation season. The water availability is still increased by seasonal snow and glacial melt (Turner 2009; Turner et al. 2014). The melting of ice banks not only increases water resources but also uncovers large areas from under the ice cover (Chwedorzewska 2009). The most spectacular changes in polar regions are colonization and primary succession on glacier forefields recently denuded of ice (e.g., Chwedorzewska 2009; Olech et al. 2011). The process of climate warming in this region (even if local and temporal) will enable the survival and spread of alien species once introduced (e.g., Frenot et al. 2005; Olech and Chwedorzewska 2011) should they possess the strategy of soil seed bank formation. This poses the risk that Antarctic taxa, well adapted to cold environments, will come eventually under pressure and may be pushed out of their natural environments by newcomers (Chwedorzewska 2009; Convey 2003; Frenot et al. 2005; Hughes and Convey 2014). If climate change follows a warming trend, the consequences may be expected to include increased diversity, biomass and trophic complexity, all of which contribute to the development of a more complex terrestrial ecosystem structure (Convey 2006). Climate warming may alter the natural distribution limits for species or even whole communities (Convey 2003; Convey and Lewis Smith 1993). Consequences at ecosystem level may be wide-ranging, rather than being restricted to just the directly impacted taxa (Chwedorzewska 2008; Olech 1996).

Providing a further climate warming the related factors, such as altered depth and extent of snow cover, permafrost melt, recession of glaciers, freeze–thaw cycles, and potential increase in the frequency and magnitude of extreme events, may influence plant and animal communities (see overview by Nielsen and Wall 2013). For example the white-rumped sandpiper *Calidris fuscicollis* with only sporadic visits has become more frequent on KGI and can be the first example of a natural species range shift (Korczak-Abshire et al. 2011a; Trivelpiece et al. 1987b). This trend could be the result of short term and longer term variations in weather and climate conditions during the austral spring and summer months, when this species is observed. In addition however, a higher air temperature, which is a result of predominant northerly winds bringing relatively warm and moist air, would probably result in habitats more suitable for settlement and better food resources that would allow the birds to persist or survive. Such precedent has already taken place in Point Thomas Oasis area. Individuals of a non-native bird species *Calidris fuscicollis* have been seen feeding on accumulations of macroalgae remains after storms and exposed seaweed flora during warmer summer seasons (Korczak-Abshire et al. 2011a).

The ozone hole has increased the penetration of UV-B radiation in Antarctica to levels similar as in moderate climate zone (Frenot et al. 2005; Robinson et al. 2003). The UV-B radiation varies throughout the year with elevated levels coinciding with the time of plant emergence from winter dormancy and melting of the protective snow cover (Robinson et al. 2003). While alien species that come from other climatic zones may be preadapted to higher UV-B levels, native Antarctic organisms may have had relatively little time for evolutionary adjustment and acclimation to new conditions (Robinson et al. 2003). However some Antarctic mosses have been found to quickly deploy sufficient UV protection (News-ham et al. 2002; Green et al. 2005). Negative effects of UV-B can be reduced by various

defense mechanisms (Robinson et al. 2003; Turnbull et al. 2009). However, their launch is associated with the additional costs, which may prove to be too large, especially for organisms living at the physiological limits of survival.

The potential changes in species distribution due to climatic changes have been addressed by many authors (Thuiller et al. 2007; in city environment—e.g., Neil and Wu 2006; Sukopp and Wurzel 2003, and literature cited therein). However, the patterns observed in the Arctic or alpine zones representing a spatial continuum within a continent (Nielsen and Wall 2013), may not apply to the Maritime Antarctic due to a lack in spatial connectivity between regions differing in climatic conditions.

Residence time—low probability of survival through the lag phase in the Antarctic

In other regions under favorable conditions a long residence time is one of the most cited factors preceding a successful invasion (Houghton et al. 2016; Richardson and Pyšek 2006; Wilson et al. 2007) and has almost exclusively been studied *post factum*. In contrast, due to harsh weather conditions in the Maritime Antarctic, the factors promoting plant growth are met for only a short time during the year. Moreover, in some years they may not be reached at all. This would induce the residence time to be extended in comparison with the temperate regions. Also the stochastic occurrence of extreme conditions and any possible human caused disturbance of the newly established population of an alien species may decrease the probability of alien species survival. These factors may break the residence time required for a species to accomplish a successful invasion. A good example is the dispersal of *P. annua* on Deception Island interrupted by a volcanic eruption (Chwedorzewska et al. 2015).

Species invasiveness

The characteristic of invasive species has already been analyzed by many authors (Keller et al. 2011; Kueffer et al. 2010; Moles et al. 2008; Pyšek and Richardson 2007). Treating functional traits of a potential invaders as a prerequisite for successful invasion is often criticized. During the last few years a debate has focused on genetic diversity and phenotypic plasticity in alien populations of invasive species (Colautti et al. 2017; Espeland 2013). These phenomena restrict the possibility to fully study species invasiveness only to *post factum* situations—during an ongoing invasion. The assessment of risk associated with alien organisms while they are still in the lag time and before they enter the phase of expansion is therefore highly limited.

In the case of invasions in Antarctica local climatic conditions may favor the invasion of poikilothermic and poikilohydric organisms, with a broad capacity to tolerate extreme conditions, notably low and rapidly fluctuating temperatures and tissue water content. Only a few flowering plants possess such traits. The transplantation experiments showed that Antarctic conditions prevent the survival and spread of intentionally introduced terrestrial plants. It is worth highlighting that these experiments resulted in accidental introduction of *P. pratensis* at Cierva Point (Danco Coast, Antarctic Peninsula; Pertierra et al. 2017).

A successful invasion is more probable when conditions in the target community parallel those in the native range of the invader. This especially pertains to similar climatic zones. Therefore, Arctic and alpine species originating from the coldest parts of the globe

may be especially fit for the particularly harsh Antarctic conditions. Arctic and alpine organisms may possess the necessary life history features making them resistant to unfavorable abiotic conditions, and similarly to Antarctic organisms may be of low competitive ability. However the probability of unintended exchange of propagules between these areas is extremely low (except potentially by transport in a tourist vessel operating both in the Arctic and Antarctic). This further diminishes the probability of invasion. The lack of any Arctic or alpine species in a list of 15 worst invasive alien plants in broader Antarctic (McGeoch et al. 2015) seems to confirm this hypothesis.

Edaphic conditions prevailing in the Antarctic may favor the spread of species tolerating high soil salinity and unfavorable mechanic properties. This hypothesis has been confirmed under Maritime Antarctic conditions. For example, the only successful alien flowering plant *P. annua* exhibits a high tolerance to saline, poorly aerated, and compacted soils (e.g., Chwedorzewska et al. 2015; Gielwanowska et al. 2011). A population of this species existing at Point Thomas Oasis for over 30 years displays specific traits that enabled its successful invasion (Wódkiewicz et al. 2014, 2018; Galera et al. 2015, 2017). High phenotypic plasticity of this species may be a key driving factor.

Conclusions

Our work should be seen not as a direct comparison of South African (Foxcroft et al. 2011; Vardien et al. 2012) and Antarctic systems. The expanded conceptual framework opens up wider possibilities in analyzing invasions taking place in different systems. In such a way we may be able to refine our ideas instead of multiplying the number “disposable” tools such as theoretical frameworks. Moreover, the expanded conceptual framework used in this study enables an assessment of the threat of alien organisms belonging to different taxa. We have invoked additional mechanisms specific to the Antarctic region. However, we did not fully address one element of expanded framework—species invasiveness (Fig. 1), due to the goal of predicting invasions of undefined organisms, that is not belonging to a specific taxa.

The Arctowski Station system presented a unique opportunity to analyze relationships between system context and specific characteristics of the Antarctic habitat influencing the susceptibility of the region to invasion. The isolation and simple trophic complexity of the Antarctic terrestrial ecosystems, the legal obligation to enforce control over Polar Station functioning, relatively low penetration of Point Thomas Oasis by tourists, have all enabled a detailed analysis of factors influencing the probability of biological invasion of this area. The most important factors presenting a barrier to the encroachment of alien species are the harsh environmental conditions and high isolation of Antarctica. The pressure of autochthonous competitors and consumers may be seen as a less obstructive factor for the establishment of alien organisms.

Our analysis indicates that Antarctica is threatened by invasions due to the complexity of factors belonging to the system context (Fig. 1). It is almost impossible to stop climate changes from increasing the habitat susceptibility of this region. Therefore, an effective way of preventing biological invasions in Antarctica seems to lie in reducing propagule pressure and eliminating alien populations as early as possible.

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