10. BIOLOGICAL INVASIONS

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Introduction

At first sight, and certainly in comparison with most other land areas worldwide, Antarctica appears exceptionally well protected against the dangers of invasion by

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non-indigenous (alien) species. It is geographically isolated from other Southern Hemisphere continents and smaller landmasses, historically lacks indigenous human populations or contact, and presents extreme environmental challenges that must be survived both during any transfer process and after establishment at an Antarctic location. Despite this, it is clear that biological invasions have taken place, and have led to serious impacts on indigenous biota, ecosystems, and ecosystem functions, posing a serious risk to the Antarctic region (Dingwall 1995, Smith 1996, Chown et al. 2001, Greenslade 2002, Frenot et al. 2005).

In common with elsewhere, parts of the Antarctic have been experiencing a period of very rapid environmental change, relating to a number of significant variables, over the last 50 or more years (Huiskes et al. this volume, Convey this volume, Lyons et al. this volume). In addition to confirming the significant influence of some existing biological invasions, Frenot et al. (2005) have identified that rapid climate change, in combination with increased human activity, is likely to increase the frequency and significance of future invasions, and increase the impacts of alien biota that are already established.

Worldwide, biological invasions are one of the most important threats to biodiversity (McKinney and Lockwood 1999, Sala et al. 2000, Courchamp et al. 2003) and ecosystem processes (Heywood 1989, d'Antonio and Dudley 1995, Mack et al. 2000). In an Antarctic context, these threats are serious. The subantarctic islands, continental margin, packice and surrounding seas are home to spectacular concentrations of marine megafauna, including a large proportion of the world's seabird species and marine mammals. Life on land, while species poor and less visually spectacular (Gressitt 1970, Chown et al. 1998, Vernon et al. 1998, Convey 2001) is no less significant, and terrestrial biotas often include a particularly high proportion of endemic taxa (as illustrated by lichens, liverworts, flowering plants, arthropods and nematodes).

Antarctic terrestrial habitats are typified by low species richness and the absence of many functional groups that are present elsewhere. This itself may be sufficient to render the sub- and maritime Antarctic islands, and the ice-free islands of exposed land on the continent, susceptible to alien invasion (Bergstrom and Chown 1999, Chown et al. 2000). Furthermore, island biotas may be more susceptible to invasion as indigenous species are less able to cope with the associated change (d'Antonio and Dudley 1995, Vermeij 1996, Williamson 1996, Bowen and van Vuren 1997).

Although human contact with the Antarctic has occurred only over the last two centuries, our influence has increased rapidly. Initially, effort was almost exclusively focused on economic activity. On land, this related to the support requirements that were necessary to allow the excessive commercial exploitation of marine resources (whales, seals, penguins) from the Southern Ocean. In parallel, some farming, social and recreational development also occurred, resulting in many of the introductions of grazing and predatory vertebrates that remain on most of the subantarctic islands today. Throughout this period, concerns over human impact on indigenous Antarctic biota received scant attention, even in the context of the virtual extermination of successive target industrial species.

The second phase of human impact in the Antarctic became apparent through the importance attached to scientific research as being integral to the expeditions of the 'heroic age' of exploration of the early 20th Century. The initially piecemeal and competitive development of scientific activities eventually led to a large and coordinated Antarctic contribution to the International Geophysical Year (1958) and, soon after, to the development of the Antarctic Treaty System (Hull and Bergstrom 2006). Subsequently, research stations have been established by over 30 nations across the Antarctic and approximately 45 are now signatories to the Treaty. In recognition of the need to protect the Antarctic environment in a comprehensive and legally binding form, in 1991 the Madrid Protocol was established. Within the protocol, in the context of this paper, are included the prohibition of introduction of fauna or flora and the establishment of protected areas in Antarctica.

A third phase of human impact on the continent – tourism – developed during the latter decades of the 20th Century, with tourists (mostly arriving on specially designed cruise ships) now numerically outnumbering the scientific and associated logistical operations of national operators by a factor of four to five, and numbers continuing to increase rapidly (Frenot et al. 2005). In the austral summer season of 2004/05 just under 50 000 people (tourists and crew) visited the region with 27 950 tourists on expeditions that included a landing component (http://www.IAATO.org).

Current significance of invasive species in the Antarctic

Chown et al. (1998) studied the correlates of successful invasions on Southern Ocean islands by investigating the relationships among several abiotic and biotic variables and the richness of alien vascular plants, insects, birds and mammals. Their data were subsequently re-analysed by Selmi and Boulinier (2001) to take into account spatial auto-correlations, resulting in similar conclusions. Island size was a significant contributing factor, with larger islands having more alien vascular plants because of both greater habitat heterogeneity and human populations. Temperature was also important, with cold islands being less susceptible than warm ones. Similar relationships were found for insects, with the additional contributing factor of indigenous plant species richness. Human occupancy and temperature were the main correlates for alien mammals. Studies on Marion Island (Chown et al. 1998, Gabriel et al. 2001) suggest that the interactions of alien invertebrates with indigenous biota are less important to the success of the invasion process than the direct impacts of local (micro) climate. These findings support the proposal that climate matching rather than biotic resistance (competition) (Lee 2002) is a major determinant of invasion success, although this remains a subject of considerable debate.

Frenot et al. (2005) provide an up-to-date and comprehensive review and literature resource of the current status of invasive species across the Antarctic continent and subantarctic islands. Here, we do not seek simply to repeat the detail of this review, rather drawing upon it to provide a concise overview of the current and likely future significance of biological invasions in this region (Table 1).

Table 1. Total number of alien species currently established on the main subantarctic islands. 'nd' indicates no data available

Island	Plants	Invertebrates	Vertebrates:		
			mammals	fishes	birds
Iles Crozet:					
Cochons 46.10°S 50.23°E	nd	nd	3	0	0
Possession 46.42°S 51.50°E	59	14	1	2	0
Est 46.43°S 52.20°E	nd	nd	1	0	0
Pingouins 46.50°S 50.40°E	0	0	0	0	0
Prince Edward I 46.63°S 37.95°E	3	1	0	0	0
Marion I 46.90°S 36.75°E	12	18	1	0	0
Iles Kerguelen 49.37°S 69.50°E	69	30	7	5	0
McDonald I 53.03°S 72.60°E	0	0	0	0	0
Heard I 53.10°S 73.50°E	1	3	0	0	0
South Georgia 54.25°S 37.00°W	33	12	3	0	0
Macquarie I 54.62°S 158.90°E	3	28	3	0	3

PLANTS

Virtually all non-indigenous plant species known in the Antarctic are found on the subantarctic islands (Table 1, Fig. 1a, b). To date, all are higher plants, with no confirmed examples of cryptogams (bryophytes, lichens), despite these being the dominant native vegetation type across most of Antarctica, including large parts of some subantarctic islands. This dichotomy is unlikely to reflect the true situation, rather being a function of the focus of past scientific research efforts - partly through poor knowledge of the worldwide distribution for many species, while Antarctic data are also patchy. Little is known about invasive bryophytes, diatoms and other lower plant groups. Thus, there is insufficient basis to assess whether an occurrence on a single island is a true disjunctive distribution, indicating the possibility of introduction, or simply the first record in a very incompletely surveyed area. Furthermore, the local (within-island) distribution patterns of most Antarctic cryptogams are also hardly known. A distribution centering on a locality of human occupation and spreading out from there can be interpreted as a strong indication of introduction, but such data are generally lacking. Lindsay (1973) considered a number of lichens on South Georgia to be probably introduced and Ochyra et al. (2003) suggest that the moss *Thuidium delicatulum* (Hedw.) Schimp. may have been introduced to Marion Island.

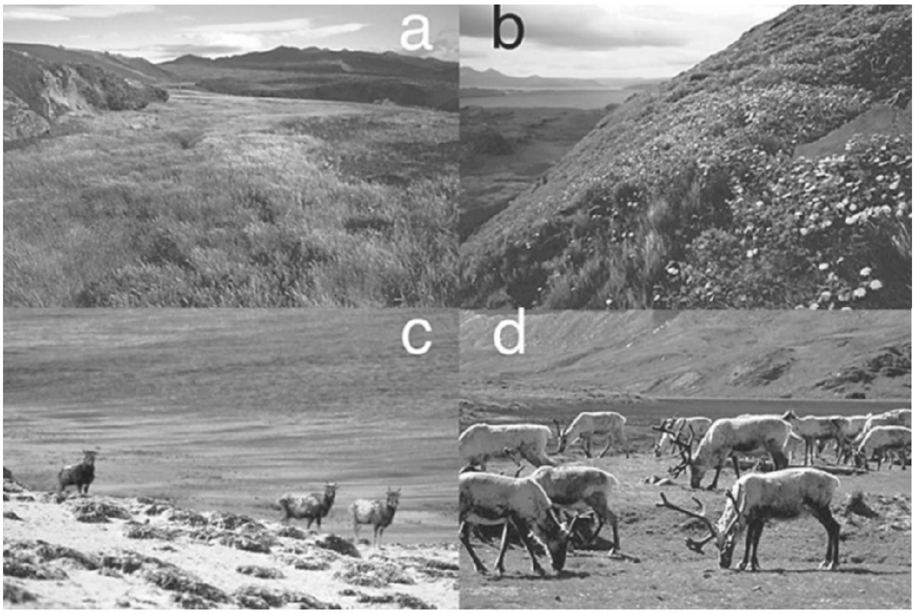

Figure 1. Examples of highly visible invasive plants and vertebrates on the subantarctic islands. (a) Large stand of the alien grass Agrostis stolonifera *in an area originally covered by* Acaena magellanica *dominated vegetation, Marion Island, 1998 (photo: N. Gremmen), (b) Well-drained slope on Ile Australia, Golfe du Morbihan, Iles Kerguelen, invaded by* Taraxacum spp. *and* Senecio vulgaris*, January 2004 (photo: N. Gremmen), (c) Mouflon on Ile Haute, Iles Kerguelen, during winter 1991 (photo: D. Réale), (d) Reindeer grazing on a sward of the introduced grass* Poa annua*, South Georgia (Photo: D. Bone).*

Frenot et al. (2005) list 108 species of non-indigenous vascular plant currently present in the subantarctic, providing a striking comparison with the two species known from single locations in the maritime zone (Smith 1996) and none from the continental Antarctic (although in the late 1990s, a flowering grass and a daisy were found growing and removed from the vicinity of Progress Station, in addition to seeds of many angiosperm species being found within the station, M. Riddle, pers. comm.). It is clear that a range of plants from lower southern latitudes, and from the Northern Hemisphere, can survive and in some cases reproduce under the conditions of the sub- and even maritime Antarctic and that the challenges of long-distance dispersal and establishment are greater than survival alone.

Most of the higher plants established in the Antarctic belong to common and widely distributed families that are often invasive at a global scale (Pyšek 1998). These include Poaceae (39 species), Asteraceae (20), Brassicaceae (8) and Juncaceae (7) (Frenot et al. 2005). In terms of simple species numbers, alien plants contribute a considerable proportion of the contemporary biodiversity on some subantarctic islands – approaching 50% on South Georgia and 70% on Iles Kerguelen. However, there is little commonality at the species level among the different islands, with only one species (the grass *Poa annua*) present on all major islands, and a further five with wide distributions. Indeed, most alien plant species are found only on one or at most two islands.

The contemporary impacts of most species are also small, as they can be classified as persistent rather than invasive (as defined by Frenot et al. 2005), with very restricted distributions (in some cases even limited to single plants). For instance, only 7/69 alien species on Iles Kerguelen and 7/59 on Possession are invasive and more widely distributed away from sites of human activity (Frenot et al. 2001). The impact of these low numbers of species can be severe, with native species being displaced (Fig. 1).

Established alien species are generally long-lived, with 75% of species being perennial. Possession of obligate annual or biennial life cycles may not be a viable strategy for plants with the opportunity of colonising the subantarctic, with data indicating that two-thirds of transient species recorded on Iles Kerguelen and Possession were of this type (Frenot et al. 2001). Even the normally annual *Poa annua* can adopt a perennial life cycle in certain habitats or circumstances in the subantarctic (Frenot and Gloaguen 1994, Smith and Steenkamp 2001).

VERTEBRATES

No alien vertebrates (other than the permanent human presence) have become established in the maritime or continental Antarctic. Historically, commercial concerns, research stations and exploring expeditions have imported a range of mammals and birds for logistic (dogs, ponies), food (cattle, reindeer, mouflon, pigs, rabbits, hens) or companionship or pest control (cats) purposes. Such activities are no longer permitted on the continent or Antarctic Peninsula under the terms of the Madrid Protocol. Alien mammals have received considerable study on several of the subantarctic islands and receive the highest profile in public awareness. It is important to realise that a unique feature of Antarctic terrestrial ecosystems is that they naturally lack terrestrial mammalian herbivores or carnivores. Various introductions of these groups (both deliberate and accidental) clearly have had and continue to have considerable impacts on native ecosystems (Bonner 1984, Leader-Williams 1988, Chapuis et al. 1994, Bester et al. 2002). Large and visible vertebrates that are present in spatially defined locations are, in principle at least, potential targets for effective eradication measures and some such have been attempted or completed (Micol and Jouventin 1995, Myers et al. 2000, Bester et al. 2002, Chapuis et al. 2001, Copson and Whinam 2001, Whinam et al. this volume).

Eight invasive mammals are currently established on subantarctic islands (Frenot et al. 2005) (Table 1, Fig. 1c, d). Other than rodents, the remainder were originally deliberately introduced by humans. The Iles Kerguelen hosts the highest number of alien mammals (7), and a number of alien freshwater fish. Mice and rats are the most widespread species (Cumpston 1968, Chapuis et al. 1994, Pye et al. 1999). The selective herbivorous nature of rabbits has resulted in significant ecosystem modification on all islands where they have been released (Copson and Whinam 2001). However, alien predators have had the greatest impacts on the native fauna – cats are responsible for drastic reductions in some seabird populations and local extinctions of several species (Pascal 1980, van Aarde 1980, Bonner 1984, Brothers 1984), while rats have also had major impacts on burrow-nesting bird species (Jouventin et al. 1984) and the endemic South Georgia pipit (Pye and Bonner 1980), the only passerine occurring naturally anywhere in the Antarctic. Rats and mice also have considerable impacts on endemic invertebrate (Pye and Bonner 1980, Chown and Smith 1993, Smith et al. 2002) and plant populations (Shaw et al. 2005). Cats have been the target of successful eradication programmes on Marion and Macquarie Islands (Copson and Whinam 2001, Bester et al. 2002). No concerted efforts have yet been attempted to eradicate rats from any large subantarctic island, although trials have commenced on some small coastal islets off South Georgia in addition to on two islands of Iles Kerguelen. Successful eradication of rodents has been achieved on some of the more northerly cold temperate Southern Ocean Islands including St Paul Island (Micol and Jouventin 2002), and Campbell and Enderby Islands (Torr 2002, see also http://www.doc.govt.nz/Conservation/Offshore-Islands/Campbell-Island-Rat-Eradication.asp).

Few alien birds are established on the subantarctic islands (Table 1) and little is known about their biology and impact. None are established on the continent. Those in the subantarctic are representatives of families with the highest success of introduction globally (Lockwood 1999) and include the Palaearctic mallard (*Anas platyrhynchos*), redpoll (*Carduelis flammea*) and starling (*Sturnus vulgaris*) on Macquarie Island. Species such as the starling (originally of European origin) can probably reach the subantarctic relatively frequently, and without human assistance, from southern temperate locations where they have been long established. Indeed, the subantarctic islands and more southerly locations record vagrant birds regularly (eg Burger et al. 1980, Gauthier-Clerc et al. 2002). Humans did however introduce wekas (*Gallirallus australis scotti*), flightless birds native to New Zealand, as a food source on Macquarie Island in the 1870s (Copson and Whinam 2001). Taylor (1979) credited the extinction of the endemic subspecies of the Macquarie Island rail (*Rallus phillipensis macquariensis*) and the Macquarie Island parakeet (*Cyanoramphus novaezelandiae erythrotis*) to predation from both wekas and cats. Wekas have subsequently died out on Macquarie Island, partly resulting from the efforts of an eradication program, but more importantly through increased predation by cats, a secondary impact of a rabbit eradication program (Copson and Whinam 2001).

INVERTEBRATES

Our ability to provide an overview of the current status or impacts of non-indigenous invertebrates in the Antarctic is compromised by considerable variation in the level of knowledge available, both among taxonomic groups and across locations. The highest numbers (Table 1) are known from the subantarctic Iles Kerguelen (30 species) and Macquarie Island (28 species) (Frenot et al. 2005). Some islands, notably McDonald, Pingouins and Apôtres Islands, are largely non-impacted, while Macquarie, Iles Kerguelen, Possession, Marion Islands and South Georgia are those with the highest numbers. However, even on these much larger islands, the distribution of alien species is very patchy, with sometimes considerable areas (eg between glaciers, offshore islands) currently remaining pristine. Only two species of invertebrate (a dipteran and an enchytraeid worm) are confirmed to have established and remain persistent in the maritime Antarctic, with both introductions associated with human activity on Signy Island in the South Orkney Islands (Block et al. 1984) and none are proved to be resident in the continental Antarctic. A small fly (*Lycoriella* sp.) has been known from within station buildings at the continental station Casey (Hughes et al. 2005), illustrating a frequently observed feature of alien species being able to co-exist synanthropically but (currently at least) unable to expand beyond the confines of such situations. An eradication program on this fly was conducted at Casey station in April 2005, and at the beginning of 2006 appeared to have been successful.

Most studies of alien invertebrates in the Antarctic have focused on the physically larger groups of molluscs and arthropods, with little attention yet paid to smaller microscopic groups or the soil fauna. For instance, the tardigrade, rotifer and nematode species known from subantarctic islands generally are thought to have cosmopolitan distributions, but both detailed taxonomic studies and distributional data are lacking.

Most aliens are drawn from three groups of insects - Diptera, Hemiptera and Coleoptera. It is no coincidence that the two most widely distributed species are both capable of parthenogenetic reproduction (see Crafford et al. 1986) and very commonly associated with horticultural activities and food transport, these being *Psychoda parthenogenetica* (Diptera, Psychodidae) and *Rhopalosiphum padi* (Hemiptera, Aphididae). Indeed, many of the alien invertebrates recorded both as being established on subantarctic islands (Frenot et al. 2005) and anecdotally from maritime and continental Antarctic research stations (Hughes et al. 2005) are known to have been imported amongst general and food stores. As concluded by Pugh (1994) for mites (Acari), many species introduced to the region will have been imported with live vegetation, litter or soil.

Even though well documented for some islands (eg Ile de la Possession and Iles Kerguelen, Bouché 1982, Frenot 1985), some large and visible groups such as earthworms have not been well surveyed elsewhere. Likewise, although alien species of slug are known from three subantarctic islands (Iles Kerguelen, Macquarie Island, Marion Island), little is known of their biology or impacts. Other groups, such as non-marine Crustacea, while small in representation, have the potential for considerable impacts. The single species established on Marion Island (*Porcelio scaber*) is also already an invasive species on the South Atlantic cold temperate Gough Island (Jones et al. 2003). If the same situation were to develop on Marion Island the species could substantially alter nutrient cycling by reducing the bottleneck currently imposed by native lepidopteran larvae and earthworms (Slabber and Chown 2002, see Smith and Steenkamp 1992a,b).

Alien springtails (Collembola) are known from several subantarctic islands. The only major island from which none are known is Heard Island, and the group contributes 10% of the springtail fauna on South Georgia, >15% on Macquarie, 17% on Iles Kerguelen, 21% on Iles Crozet and 38% on Marion Island (Frenot et al. 2005). The alien faunas include several widespread invasives, particularly in the genus *Hypogastrura*. A member of this genus, *Hypogastrura viatica*, has been reported from the northern maritime Antarctic South Shetland Islands (Wise 1971) and from Léonie Island in the southern maritime Antarctic (Greenslade 1995), although the current status at either location is unconfirmed. Also in the South Shetland Islands, the presence of geothermal activity and heated ground on Deception Island may provide assistance for any alien species accidentally imported, such as the records of *Folsomia candida* and *Protaphorura* sp. reported by Greenslade and Wise (1984). Extensive geothermal activity on the maritime Antarctic South Sandwich Islands is also proposed to explain the presence of a range of subantarctic bryophytes and arthropods (Convey et al. 2000a,b), although human influence at this most isolated and extreme of locations remains so minimal that no evidence of anthropogenic introductions has been suggested.

MICROBIAL GROUPS

In much of the world, and despite the recognition that soil communities are key to the overall maintenance of ecosystem processes, remarkably little attention has been paid to their understanding. This is particularly true of the Antarctic, where many soils are relatively barren of both multicellular autotrophs and metazoans (Freckman and Virginia 1997, Convey and McInnes 2005), while decomposition pathways dominate nutrient and energy flows. Little is known about levels of endemism in most of the microbial flora (Lawley et al. 2004) or, alternatively, cosmopolitanism, although the algal flora is thought to be largely cosmopolitan (Broady 1996). However, if the ‘global ubiquity hypothesis’ (Finlay and Clarke 1999) does apply even in part to the Antarctic microbial flora, it is clear that the constraints to microbial dispersal and biodiversity will be fundamentally different to those applying to multicellular organisms.

There are virtually no data available on the presence of alien microbial species in the Antarctic, with the exception of a number of yeasts, fungi (see Wynn-Williams 1996a, Downes 2003) and algae (Broady and Smith 1994). The lack of detailed Antarctic studies is further complicated by a lack of comparable data from elsewhere including, in contemporary molecular studies, a lack of both Antarctic and non-Antarctic sequence data. However, there is evidence for at least some of the Antarctic prokaryote and eukaryote microbial floras being distinct (Franzmann 1996, Lawley et al. 2004).

Notwithstanding the overall lack of knowledge, the risk of importation into the Antarctic has been recognised (Smith 1996, Wynn-Williams 1996b). It is already clear, as with the macroscopic biota discussed above, that human-mediated imports play a significant role. Examples include the discovery of spores of a *Penicillium* species at Mt. Howe, of human pathogens in soil close to McMurdo station (Wynn-Williams 1996b), the isolation of fungi from historic sites on Ross Island (Minasaki et al. 2001) and, in the subantarctic, the infection of stands of *Pringlea antiscorbutica* by *Botryotinia fuckeliana* on Marion Island (Kloppers and Smith 1998) and *Albugo candida* on Iles Kerguelen (Y. Frenot and F. Hennion unpubl. data, Fig. 2a), both fungus species probably transferred from fresh vegetables. Circumstantial evidence of human introduction is also provided by diversity studies that report a proportion of taxa restricted to sites of human activity, as found by Azmi and Seppelt (1998) near Casey Station in the Windmill Islands and Kerry (1990) in the Vestfold Hills and Mac.Robertson Land.

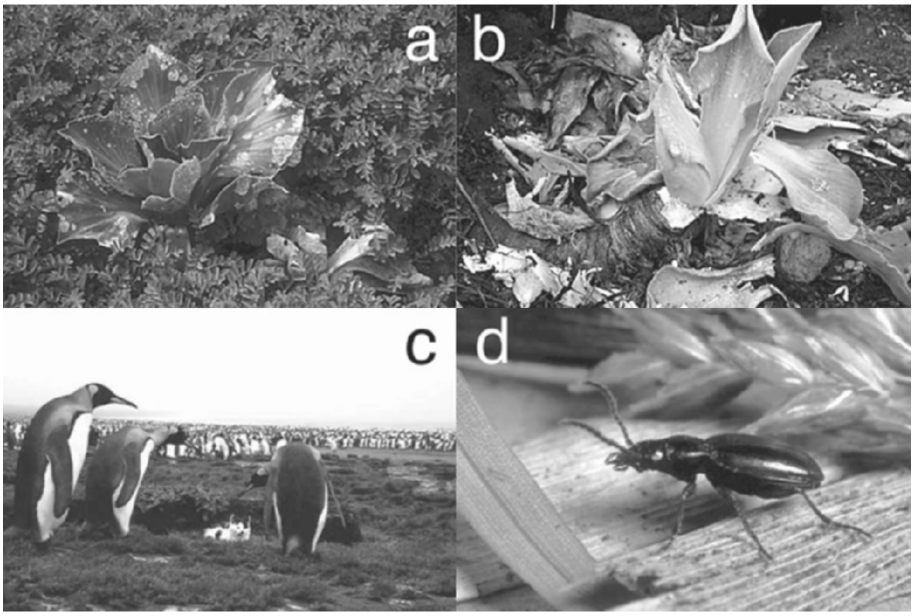

Figure 2. Consequential impacts of some invasive species. (a) Infection of Pringlea antiscorbutica *by the fungus* Albugo candida *on Ile Australia, Iles Kerguelen, February 2000 (Photo: Y. Frenot), (b) Damage to* P. antiscorbutica *caused by rats on Ilôt Colbeck, Iles Kerguelen (Photo: J.-L. Chapuis), (c) Cat in a king penguin colony, Iles Kerguelen (Photo: J.-L. Chapuis), (d) The predatory carabid beetle* Trechisibus antarcticus *introduced to South Georgia (Photo: P. Bucktrout/British Antarctic Survey).*

A potentially significant, and certainly widely publicised, risk associated with human activity in Antarctica lies in the potential introduction or activation of diseases to which regional wildlife are susceptible (Kerry et al. 1999). Although the risk is clear, such a causal link has yet to be documented, and categorical proof is confounded by the fact that many Antarctic birds and mammals interact with humans well beyond the boundaries of the region. Nevertheless, there is considerable evidence of exposure to various pathogens (see reviews by Clarke and Kerry 1993, Kerry et al. 1999, Frenot et al. 2005). Furthermore, mass mortality events, such as the deaths of hundreds of chinstrap penguins from what is believed to be avian cholera (*Pasturella multocida*) at a tourist visitation locality on South Georgia, have now been reported (S. Harvey pers. comm. http://www.sgisland.org/pages/main/news16.htm).

Some human activities carry with them a virtual certainty of some form of contamination of the Antarctic environment which, while they can be controlled by reasonable measures (eg Hughes and Blenkharn 2003), could realistically only be removed completely by ending human contact with the continent. One such is the introduction of microorganisms associated with sewage. Although, again, few detailed studies have been completed, these organisms have been located in the marine and sea-ice environments near to McMurdo Station (Ross Sea) (Smith and McFeters 1999, Edwards et al. 1998) and in nearshore and coastal locations near to Rothera Station (Adelaide Island) (Hughes 2003a,b), in the continental and maritime Antarctic, respectively. Smith and McFeters (1999) further identified a risk that indigenous microbiota may be susceptible to the transfer of harmful genetic features from pathogenic microorganisms in untreated sewage, with potential knock-on consequences for other wildlife.

FRESHWATER AND MARINE HABITATS

There have been no reports of non-indigenous species in freshwater habitats (lakes, pools, streams) of the continental and maritime Antarctic. Pugh et al. (2002) conclude that anthropogenic dispersal is a likely explanation for at least some records of non-marine (ie terrestrial and freshwater) Crustacea on subantarctic islands. However, their suggestion that the presence of the copepod *Boeckella poppei* in Beaver Lake and adjacent lakes (Amery Oasis, continental Antarctica) is linked with human transfer is now known to be incorrect, as the species is found in sediment cores from these lakes dating back at least several thousand years (see Gibson et al. this volume).

Antarctica has no native freshwater fish. Several salmonids were introduced and survive on the subantarctic Iles Kerguelen and Iles Crozet (Davaine and Beall 1997), but their current status has not been researched in detail. Brown trout introduced to Marion Island were restricted to a single river system and are now considered to be extinct (Cooper et al. 1992), as are rainbow trout introduced to some pools. Although these probably have had substantial local impact on invertebrate populations no detailed studies are available. Trout were also introduced to some lakes on South Georgia near to occupied whaling stations (Headland 1984), but have long been extinct, with no information available on any impacts on these ecosystems. The subantarctic islands also have few native freshwater birds, these being restricted to two species of duck on South Georgia and Iles Kerguelen.

Palaearctic mallard (*Anas platyrhynchos*) is a non-indigenous species of duck first recorded on Macquarie Island in 1950s. The species is to be expected to have impacted the freshwater ecosystems of this island, though no specific data appear to exist.

Although marine ecosystems do not fall within the scope of this volume, brief mention is warranted given the acknowledged significance of human activity in dispersal and alien colonisation in marine habitats worldwide. Despite this attention, there are few studies or even anecdotal observations of alien marine taxa in the Antarctic region. Two clear records have been published, both from the South Shetland Islands. Mats of a non-indigenous green alga (*Enteromorpha intestinalis*) have been found in the intertidal zone at Half Moon Island (62°37'W 59°57'S), which Clayton et al. (1997) suggested may have been introduced on the hulls of ships or yachts. Most recently, Tavares and de Melo (2004) reported a North Atlantic species of spider crab from a trawl collection off the Antarctic Peninsula, to date the only record of a non-indigenous marine species in Antarctic seas.

Human activity again presents clear opportunities for transport of alien marine species into the Antarctic. The most direct route (Lewis et al. 2003) involves the ships used in Antarctic science and tourism activities, with opportunities presented by the transport of ballast water and by hull fouling assemblages. Lewis et al. (in press) reported how a barge loaded onto a supply ship had the potential to introduce an entire temperate epibenthic community to Macquarie Island (the barge's deployment was stopped once the biosecurity hazard had been identified). A second, more indirect, route exists through the potential for transfer on anthropogenic marine debris (Barnes 2002, Barnes and Fraser 2003), a route that also may provide opportunities for transfer of terrestrial and intertidal taxa (Hughes et al. this volume).

Case studies

PLANT COMMUNITIES

Prince Edward Islands

The recorded vascular flora of Marion Island consists of 23 native, 18 alien and three species of uncertain status. Of the 18 introductions, six have died out or have been eradicated. Despite the imposition of strict quarantine measures, even in recent years new species have reached the islands, with four becoming established the 1990s (Gremmen and Smith 1999). Several of the alien species introduced to Marion Island at the time of construction of the weather station in 1948 have spread rapidly. Gremmen and Smith (1999) and Ryan et al. (2003) estimated continuous rates of spread of 200 - 600 m.year^{-1}. These rates exclude occasional 'jumps' of several kilometres by some species. Of the alien species that have become established on Marion Island, two (*Cerastium fontanum* and *Sagina procumbens*) have subsequently spread to Prince Edward Island without apparent human assistance (Bergstrom and Smith 1990, Gremmen and Smith 1999, Ryan et al. 2003).

Of the 12 alien species presently occurring on Marion Island, eight are grasses. Nine species are able to become dominant in the communities they invade, of which seven are grasses (Gremmen 1997, Gremmen and Smith 1999, Fig. 1a). One other species, *Rumex acetosella*, may locally also become dominant, but not in the sense that it crowds out many native species. Six species are presently widespread, three of which are grasses, and at least one other grass, the recently introduced *Agrostis gigantea*, is expected to become widespread if unchecked. A program to eradicate this latter species is presently underway.

The impact of *Agrostis stolonifera*, which now dominates many plant communities of slope drainage lines and riverbanks, has been studied in detail by Gremmen et al. (1998). This species has invaded 19 of 22 major plant communities on Marion Island, and in seven of these, it has become dominant, at least locally. In the drainage line communities it has invaded, vegetation structure and community species composition and species richness have been significantly affected. The vegetation has changed from a deciduous *Acaena magellanica* dwarf-shrub dominated community into a permanent dense sward of high grass. Total standing crop has not changed significantly, but the percentage of bryophyte matter in the standing crop has diminished from 15% to 1%, and the total number of native plant species (vascular plants and bryophytes) from 7.4 to 3.6 per $4m^2$ sample plot. A comparison of estimated total species richness of all invaded *vs.* unaffected drainage lines led to a prediction of a reduction in total species richness in this habitat by some 20%, once *A. stolonifera* has spread throughout the island. The impacts of *A. stolonifera* also extended to soil macro- and meso-invertebrates, with significant consequences detected in terms of overall species composition and population densities of individual species. Changes of a similar magnitude are also associated with invasion by a number of other alien species, including *Poa annua*, *Poa pratensis* and *Sagina procumbens*, although rigorous studies have not been completed (Gremmen 1997). On South Georgia, the different nutritional qualities of alien (*P. annua*) over native grasses have been shown to impact the biology of endemic herbivorous/detritivorous beetles (Chown and Block 1997).

The impacts of alien plants on their host indigenous plant communities appears to be related to their ability to spread vegetatively, thus forming dense colonies, rather than simply to their ability to disperse rapidly. For instance, some grasses with a very restricted distribution on Marion Island have a massive impact on the original communities of the sites they have invaded. Examples include *Agropyron repens* (1 site) and *Festuca rubra* (2 sites), both of which have almost totally replaced the native species at the locations they have invaded. The impact of alien species can be measured in different ways. In addition, as above, to quantifying the changes introduced in individual invaded communities, an alternative or complementary approach is to consider the total invaded area. A combination of both approaches can then be used to provide a better overall assessment of impacts. Following this approach it can be seen that, although several alien plants on Marion and Prince Edward Islands have large impacts at a local scale, it is also the case that, at present, only a low percentage of the total area of the islands has been invaded. Most alien plants are patchily distributed, relating to their mode of reproduction and dispersal (often vegetative) and to the patchiness of occurrence of suitable habitats. This contrasts markedly with distribution patterns of some invasive animals (eg mice), which rapidly become much more ubiquitous.

Heard Island

On Heard Island until recently, only a single alien vascular species was known to occur, *Poa annua*, with the first report in 1987. Subsequent to this, the species' density and abundance have increased (Scott and Kirkpatrick 2005). Its mode of introduction or arrival is unknown, and its centre of distribution is not related to the main areas of human activities on the island, although the fact that it is a Northern Hemisphere species, widely introduced to most of the Southern Hemisphere, makes its alien status unequivocal. On Heard Island, *P. annua* is most common in open communities on moraine soils, where it usually achieves low cover but can reach 75% over small areas (measured in $1m^2$ sample plots). It is not clear if *P. annua* simply occupies open space in these communities, or replaces any of the native species, as the total native species richness of sample plots in invaded areas is identical to comparable, non-invaded areas (N.J.M. Gremmen unpubl. data). Quadrat survey data obtained in February 2001 indicated an average density of 18 908 ± 880 $plants.m^{-2}$ and a mean of 10 502 ± 825 $inflorescences.m^{-2}$ (D.M. Bergstrom unpubl. data).

Iles Kerguelen

A number of alien vascular plants are widespread on Iles Kerguelen and locally reach dominance in the vegetation. In a study of islands in the Golfe du Morbihan, aliens were found to invade mainly well-drained lowland slopes and other well-drained lowland habitats (Fig. 1b). Again, some grasses reach local dominance, spreading vegetatively and replacing most of the native plants in the areas they invade. Several non-graminoid species, however, notably *Taraxacum officinale*, *T. erythrophyllum* and *Senecio vulgaris*, also reach high cover values, assisted by the abundant production of wind-borne seeds. In general, sites in which alien species have reached high cover values contain fewer native species than comparable pristine sites (N. Gremmen unpubl. data).

One of the notable ecosystem interactions of alien plant species on islands of the Iles Kerguelen is that with native seabirds and alien rats. On Ile Australia, rats have had a negative impact on burrowing bird populations. The stature and cover of alien plant species such as *Poa pratensis*, *Vulpia bromoides* and *Taraxacum officinale* is substantially less on Ile Australia than on the rat free Ile Mayes, which thus supports substantial burrowing bird populations. It is believed that the alien plants are responding to increased levels of nutrient input from bird guano on Ile Mayes, although further research to substantiate this hypothesis is needed.

Pattern of colonisation along tracks on Iles Crozet

On Possession Island, the last six years have been marked by significant increases in the distribution of the dominant alien plant species established away from the immediate vicinity of the research station (M. Lebouvier and Y. Frenot, unpubl.

data). *Sagina procumbens*, for example, was first recorded in 1978 at Alfred Faure Station. By the mid 1990s, it was present in the vicinity of all the field huts on the island and, by 2002, its distribution had expanded considerably, not only around sites of most human activity, but also along the tracks linking these sites. Similar trends are apparent in *Taraxacum erythrospermum*, a species located only at the research station until 1996. These two examples demonstrate the obvious role of humans in the spread of alien species in the subantarctic islands and the significance of tracks used by walkers in assisting alien establishment and spread.

VERTEBRATES

The house mouse (*Mus musculus domesticus*) is the most widespread alien vertebrate species, introduced to several subantarctic islands. On Iles Kerguelen (Le Roux et al. 2002) and Marion Island (Smith et al. 2002) this opportunistic rodent includes a variety of items in its diet: earthworms, larvae of a flightless and endemic moth, weevil adults and larvae, seeds of grasses and *Acaena magellanica* and floral parts of the alien dandelion (*Taraxacum officinale*). At Iles Kerguelen, Le Roux et al. (2002) showed that mice had a marked preference for plants in the summer months (January and February), whereas invertebrates formed nearly 100% of the prey items taken in winter (July). Pye and Bonner (1980) reported analogous sequential changes in dietary composition of rats (plant material, invertebrates, vertebrates) over the seasonal cycle on South Georgia. On Marion Island mice have a significant impact on *Azorella* cushions, which they destroy by burrowing into them, often eating through the main roots. Mice also selectively collect *Uncinia compacta* seedheads. As a result, ripe *Uncinia* seeds are now rarely seen on Marion Island, in contrast with the situation on Prince Edward Island, which is mouse-free and where ripe seeds are produced in abundance (Smith and Steenkamp 1990). Rats were seen to destroy *Azorella* cushions in a similar fashion on Ile Australia and Iles Kerguelen (D.M. Bergstrom, pers. obs., Fig. 2b). It is clear that alien rodents can affect several different components of subantarctic terrestrial food webs. Furthermore, on Marion Island Huyser et al. (2000) identified mice as playing an important role in the decrease in lesser sheathbill (*Chionis minor*) populations, an indigenous bird that relies on terrestrial invertebrates for winter survival.

The cat is the only mammalian predator present on some subantarctic islands, introduced as a pet or for the control of alien rodent populations. Food sources include other alien mammals (rats, mice and rabbits) and native birds. Say et al. (2002) estimated that the population of cats at Iles Kerguelen approached 7000 individuals on the main island, while Pontier et al. (2002) showed that the diet of feral cats varied markedly among different sites. Rabbits were the most common dietary item (about 90% throughout the year) in sites remote from bird colonies, whereas near a king penguin colony (Fig. 2c) and a large black-browed albatross colony rabbits, mice and birds were similarly represented (about 30%). These results contrast strongly with those of an earlier study (Derenne 1976): in 1976, 66.3% of stomachs examined contained birds and 35.0% contained rabbits whereas in 1998/99, scats consisted of 7.3% bird remains and 84.2% rabbits. While the methodologies used differed, it is known that rabbit populations did not fluctuate significantly between the two studies and, therefore, the large difference is interpreted as strongly suggesting that bird availability is now lower than in 1976 and that cats have had a major impact on the Kerguelen avifauna over a time period of less than 50 years (Pontier et al. 2002).

The impact of rabbits has been disastrous for most of the sensitive subantarctic islands to which the species has been introduced, causing soil erosion and rapid decreases in the native vegetation. At Iles Kerguelen, some plant species normally dominant in native communities, such as the Kerguelen cabbage *Pringlea antiscorbutica* and the cushion plant *Azorella selago* have became rare, replaced by almost monospecific communities of *Acaena magellanica* (Chapuis et al. 1994). Changes in plant cover have indirect consequential impacts on invertebrate communities (Chapuis et al. 1991) and the breeding potential of some burrow-nesting birds (Weimerskirch et al. 1989). Rabbits were also the main winter food resource for cats and ensured their survival during the less favourable months (Chapuis et al. 2004). Consequently, the rabbit can now be considered as a keystone species at Iles Kerguelen.

Similar ecosystem damage and impacts have occurred on Macquarie Island, where rabbits have demonstrated selective grazing of approximately 50% of native vascular plant species as well altering habitat for burrowing birds (Copson and Whinam 1998). Modifications to the plant communities and bird habitats may also have impacted on the invertebrate fauna and caused alterations to edaphic processes (Copson and Whinam 2001). Recent analysis of native plant species with restricted populations on the island suggests that rabbits may be limiting the potential expansion of the tussock grass *Poa littorosa*, with grazing observed at all four known populations. Rabbits may therefore be affecting ecosystem evolution (Bergstrom et al. in press).

Norwegian reindeer were introduced to South Georgia on three occasions between 1911 and 1925, in the vicinity of whaling stations. Archival information is summarized by Leader-Williams (1988). There are currently two genetic stocks and the total number of reindeer is estimated to about 2 - 4000. Population densities are far greater than those typical for the source locations in Scandinavia. Ten animals from Sweden were introduced to Iles Kerguelen in 1955/56 (Lésel 1967). In 1972, Pascal (1982) estimated the population at 2000 and there is no indication of any subsequent decrease (J.-L. Chapuis, pers. comm.). Reindeer on the Iles Kerguelen are restricted to Grande Terre, with the reported presence on the pristine Ile Foch (Chapuis et al. 1994) now appearing doubtful. On South Georgia (Leader-Williams 1988), snow cover limits the choice of forage available for reindeer to tussock grass (*Paradiochloa flabellata*) for up to three months of winter and other forage species (*Deschampsia antarctica, Acaena magellanica*) remain unavailable for up to six months. This dependence upon a single grass species in winter is mainly responsible for the overgrazing of the tussock grassland and to a lesser extent, of mesic meadow, dwarf-shrub sward and dry meadow. Overgrazing has also resulted in soil erosion. In addition to altering the structure and composition of plant communities (Leader-Williams et al. 1987), a further consequence of the activities of reindeer on South

Georgia lies in their assisting the rapid spread of the alien grass *Poa annua* (Fig. 1d), whose nutritional characteristics are different to those of native grasses, leading to impacts on invertebrate communities (Vogel et al. 1984, Chown and Block 1997). No accurate study on the impact of reindeer on the vegetation of Iles Kerguelen has been carried out but some effects are obvious, for example, many cushions of *Azorella selago* are turned over (Chapuis et al. 1994) and trampling causes severe damage in wet areas (Y. Frenot, pers. obs.).

The eradication of alien vertebrates is likely to be practicable, at least for the larger mammals. At first sight, such action provides a visible and probably useful response limiting or mitigating the damage caused by certain alien species. However, management approaches must be carefully planned and executed and require a multidisciplinary approach. There is no doubt that eradication campaigns removing rabbits from Macquarie Island (Copson and Whinam 2001) or cats from Marion Island (Bloomer and Bester 1991) have been successful and have led to positive consequences for native ecosystems. However, several examples are available in the literature demonstrating that undesirable cascade or consequential effects may ensue. For instance, van Aarde et al. (1996) pointed out the significance of the regulatory role of cats on mouse populations on Marion Island. Similarly, eradication of rats on St. Paul Island led to a large increase in the abundance of mice, most probably with an increase in their impact on native invertebrate communities. The eradication of rabbits on three islands of the Iles Kerguelen also produced unexpected results. Chapuis et al. (2004) observed a consequential decrease in cover of some plant species (primarily *A. magellanica*) and an increase in the abundance of other alien species such as *Taraxacum officinale*. While this trend is most closely linked to the removal of grazing, recent changes in climatic conditions (warming and increased drought stress) are also influential in the decrease or slow recovery of native species and the success of alien species (Convey this volume). In these contexts, the decisions over whether to attempt eradication are not trivial and, as emphasized by Myers et al. (2000), alternative approaches may be preferable.

INVERTEBRATES

In comparison with vertebrates, the consequences of most invertebrate introductions have received scant attention, indeed it is likely that many more examples exist than are currently recognised, at least on the subantarctic islands. Where terrestrial vertebrates are lacking, invertebrates play a correspondingly greater role in ecosystem processes. Ecosystems of the subantarctic and more extreme Antarctic regions are also simple in terms of both biodiversity and trophic complexity, featuring reduction in the number of higher taxonomic groups and trophic levels present. In the maritime and continental Antarctic, it is doubtful whether true herbivory is currently sustainable on energetic grounds and a large majority of the invertebrates present are regarded as detrivores or microbivores. While some predatory invertebrates are present (mites, springtails, nematodes, tardigrades), their impact currently appears to be low or undetectable (Lister et al. 1988, Convey

1996a), although few studies have been attempted. The two invertebrates known to have been introduced to the maritime Antarctic by human activity (Block et al. 1984) are both detritivores. Although they have local distributions that are gradually expanding, they have not been the subjects of detailed investigation and any impacts on indigenous communities remain unknown.

Some invertebrates introduced to the subantarctic islands have the potential to markedly accelerate the rate at which ecological processes related to nutrient cycling can take place. Thus, on Marion Island, the woodlouse *Porcelio scaber* may in future remove a bottleneck in decomposition processes as discussed above (Slabber and Chown 2002). On the same island, the alien midge *Limnophyes minimus* may have comparable trophic impact as an indigenous and endemic lepidopteran (Hänel and Chown 1998). Others, such as the fly *Calliphora vicina* introduced to Iles Kerguelen, are thought likely to compete strongly with native dipterans (in this example, *Anatalanta aptera*) (Chevrier et al. 1997).

Particularly significant introductions are likely to be those that involve new feeding guilds or trophic levels. In this context, the introductions of two predatory carabid beetles (*Trechisibus antarcticus* and *Oopterus soledadinus*) to South Georgia and one (*O. soledadinus*) to Iles Kerguelen have been studied in detail (Ernsting 1993, Ernsting et al. 1995, 1999, Todd 1996, Chevrier et al. 1997, Brandjes et al. 1999) (Fig. 2d). These introductions are relatively unusual, involving Southern Hemisphere species and most likely taking place during the mid to late 20th Century (Ernsting 1993, Chevrier et al. 1997) and provide an illustration of the potentially rapid consequential changes experienced in ecosystems. They also provide a form of 'natural experiment' that would otherwise be impossible elsewhere in the world, in which fundamental ecological questions and theories can be tested relating to the consequences of introducing new trophic levels into pre-existing natural ecosystems. On South Georgia, where the most detailed studies have been completed, major consequences include considerable reductions in populations of endemic herbivorous perimylopid beetles, whose larvae form a major prey item, combined with accelerated rates of development of prey larvae permitting a less vulnerable size to be reached more rapidly. On both islands, the two carabids are also thought to be restricted (to different extents) by the low temperatures of their habitats and hence to be sensitive to any increase in availability of thermal energy brought about by climate warming.

The introduction of alien earthworms to many of the major subantarctic islands provides a further example of the potential impacts of a new functional group within an existing ecosystem. The native earthworms of the subantarctic islands belong to the family Acanthodrilisae and the genus *Microscolex*. However, earthworms of the family Lumbricidae originating from the Northern Hemisphere are now present. Their introduction is generally related to the importation of soil for use in glasshouses or to the rinsing of water barrels by sealers during the 19th Century. Until recently, all alien Lumbricidae known from the subantarctic were epigeous and humus feeders, as are the native *Microscolex* species. The most widespread alien species, *Dendrodrilus rubidus tenuis*, has similar digestive capabilities to the indigenous *M. kerguelensis* (Prat et al. 2002), characterized by a low cellulose decomposition capacity, a feature that largely reduces their role to the fragmentation of soil organic matter. In February 2004, a new lumbricid species (*Allolobophora chlorotica chlorotica*, albinic form) was found at Iles Kerguelen, in a location close to the glasshouses at Port-aux-Français (M. Lebouvier and Y. Frenot unpubl. data). This observation is significant because this species shares ecological characteristics of the anecic and endogeous earthworms (as defined by Bouché 1972), meaning that *A. chlorotica chlorotica* is not only detritivorous and a litter feeder, but also geophagous. It contributes, therefore, to the burying of organic matter in soil and its presence in a subantarctic location could drastically alter the processes of pedogenesis in this region.

Future scenarios

The term 'climate change' is often equated with 'climatic amelioration' – thereby carrying an implicit assumption that change will automatically lead to less stressful and hence 'better' conditions for biota. This is a particularly tempting assumption in the context of Antarctic biology, where change is often perceived simply as an increase in temperature, hence in availability of thermal energy and a reduction in the risks and costs of freezing stress. In many locations and circumstances, this simplistic interpretation does carry some weight, but it is also clear that patterns and consequences of climate change are far more complex and, particularly if changes in patterns of water availability are seen, can result in considerable increases in stress (Kennedy 1995, Block and Convey 2001, Convey et al. 2002, Convey this volume).

Where climate amelioration occurs, it is likely to enhance the ability of both natural long-distance colonists and human-assisted aliens to complete successfully the two key stages of long distance transport and establishment, particularly in the subantarctic (Kennedy 1995, Bergstrom and Chown 1999, Frenot et al. 2005). Whinam et al. (2005) has identified transport routes for propagules in association with national logistic programs. However, to date there are only a few documented instances of long-distance colonization of new sites within the Antarctic even by indigenous species and no new records of alien species that can be linked clearly with climate amelioration as distinct from direct human intervention. Founder populations of four flowering plant species (two species on each island) have been identified as being less that 200 years old on subantarctic Macquarie and Heard Islands (Bergstrom et al. in press) and another single plant found on Heard Island in 2004 (*Leptinella plumosa*) provides a very recent possible example (Turner et al. 2006). Local colonisation and rapid population expansion has been well documented in the two native plant species in the maritime Antarctic (Fowbert and Smith 1994, Smith 1994) and linked with regional climate warming. Similar effects might be predicted for plant species across the Antarctic, but no rigorous studies of other species over time have yet been attempted.

In the subantarctic, where many alien plant and animal species are already established, climatic amelioration is likely to have two main effects. First, species already established but only of persistent status may be able to switch to a more aggressively invasive status. Recent changes in status of some alien plants on Marion Island (Gremmen and Smith 1999) might already illustrate such a response. In this context, it has also been proposed that indigenous subantarctic invertebrates have inherently slower life cycles and less ability to respond to temperature increase than their alien competitors (Barendse and Chown 2000). However, some indigenous species may be able to respond more rapidly. This seems to be true across the region. The diving beetle *Lancetes angusticollis* is the top predator in lake ecosystems on South Georgia. It currently undergoes a typically biennial life cycle, with its development limited by the thermal energy currently available in its habitats and the possession of a temperature mediated larval diapause stage (Nicolai and Droste 1984). This species may show a very rapid response to warming, with an increase of only 1°C in lake temperature providing enough additional thermal energy to allow development to be completed on an annual rather than a biennial timescale. Such a change in population dynamics of the top predator is likely to have considerable impacts on the trophic dynamics of these lake food webs (Arnold and Convey 1998).

Changes in colonisation patterns may also be facilitated by alterations in the relative success of asexual and sexual reproduction. Studies of the two native maritime Antarctic flowering plants have indicated a greater frequency of successful seed maturation with climate warming (Convey 1996b), leading to greater opportunities for more rapid and distant dispersal. Such a process may also allow an established alien species to colonize nearby locations by natural means, as appears to have occurred at the carefully protected Prince Edward Islands (Gremmen and Smith 1999). A general consequence of increasing success in sexual reproduction will be to generate increased genetic diversity, with the attendant possibility of offspring better capable of surviving the environmental extremes of Antarctic habitats. Although untested, such an explanation may underpin the success of the invasive microlepidopteran *Plutella xylostella* on Marion Island (Chown and Avenant 1992, Chown and Language 1994), as wider literature on this otherwise cosmopolitan pest species suggests it does not possess appropriate ecophysiological abilities to survive the subantarctic climate (Convey 2005).

Summary

A wide range of non-indigenous plants, invertebrates and vertebrates occur on most of the subantarctic islands and on some much more restricted parts of the Antarctic continent. The same is likely to hold true for microbial groups, although as yet there are few explicit demonstrations or even ongoing studies. Their arrival in the Antarctic region has been closely linked with human activity, which commenced only two centuries ago and exerts ever increasing pressure today. To date, despite the Southern Hemisphere location of the Antarctic, a large majority of the alien species known are European in origin. Their impacts on the functioning of Antarctic terrestrial ecosystems are diverse, but include examples of substantial loss of local biodiversity and changes to ecosystem processes.

Human activity essentially circumvents one of the key stages required for successful colonisation of Antarctic terrestrial habitats by biota from lower latitudes – that of long distance transport of organisms or propagules from source locations and the associated requirement for survival of the stresses experienced *en route.* Given this assistance, it is already known that a range of biota possess appropriate life history and ecophysiological capabilities to allow longer term establishment in the Antarctic. On their own, the rapid climate changes that are occurring in some parts of Antarctica are likely to reduce the barriers to successful survival of long distance transport by propagules and to increase the chance of successful establishment on arrival at an Antarctic location. However, such natural colonisation events are likely to be far outweighed in frequency by instances of human-assisted transport. Thus, climate change and human assistance in tandem are expected to result in an elevated frequency of introduction and establishment events.

Consequent increases in impacts on ecosystems are hard to forecast in detail, or for specific locations. The large majority of examples existing today are drawn from the subantarctic, where most islands already host a range of non-indigenous species. The most obvious impacts of these include (i) extensive habitat modification or destruction by grazing vertebrates, (ii) local population reduction or extinction of indigenous bird species by alien predatory vertebrates, (iii) the introduction of new trophic levels (vertebrate and invertebrate predators) into invertebrate communities where they were previously not present, with consequential impacts on prey, and (iv) alterations in the levels of competition faced in plant and invertebrate communities. Of course, the true picture is far more complex, with many direct, indirect and synergistic effects implicated across different communities and ecosystems.

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