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REVIEW PAPER

The impacts of non-native species on the invertebrates of Southern Ocean Islands

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Abstract
Isolation and climate have protected Southern Ocean Islands from non-native species. Relatively recent introductions have had wide-ranging, sometimes devastating, impacts across a range of species and ecosystems, including invertebrates, which are the main terrestrial fauna. In our comprehensive review, we found that despite the high abundance of non-native plants across the region, their impacts on native invertebrates are not well-studied and remain largely unknown. We highlight that non-native invertebrates are numerous and continue to arrive. Their impacts are multi-directional, including changing nutrient cycling regimes, establishing new functional guilds, out-competing native species, and mutually assisting spread of other non-native species. Non-native herbivorous and omnivorous vertebrates have caused declines in invertebrate habitat, but data that quantifies implications for invertebrates are rare. Predatory mammals not only indirectly effect invertebrates through predation of ecosystem engineers such as seabirds, but also directly shape community assemblages through invertebrate diet preferences and size-selective feeding. We found that research bias is not only skewed towards investigating impacts of mice, but is also focused more intensely on some islands, such as Marion Island, and towards some taxa, such as beetles and moths. The results of our review support and build on previous assessments of non-native species in the Antarctic region—that the responses of invertebrate fauna on these islands are under-reported and often poorly understood. Given the importance of invertebrates as indicators of environmental change, and their potential utility in quantifying change associated with island restoration projects (such as eradications), these knowledge gaps need to be urgently addressed.

Keywords Invasive species · Island conservation · Sub-Antarctic · Ecosystem impacts · Monitoring

Introduction

Invasive species are the greatest driver of global biodiversity loss and ecosystem disruption on islands (Mack et al. 2000; McCreless et al. 2016). Although islands comprise only 5% of the world's landmass, their level of endemism is a magnitude higher than for continents, and many global biodiversity hotspots are islands and archipelagos (Kier et al. 2009; Bellard et al. 2014; Courchamp et al. 2014). Thus, island ecosystems have proportionally high biodiversity, and often host näive indigenous species that lack competitive traits and are highly adapted (Bowen and van Vuren 1997; Convey et al. 2006a; Smith 2007).

Sub-Antarctic and cool-temperate islands of the Southern Ocean are some of the most remote environments in the world, yet their ecosystems are susceptible to invasion by non-native species (Frenot et al. 2005; Convey et al. 2006b; Shaw 2013; McGeoch et al. 2015). Low temperature, remoteness and associated low human visitation to these

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islands have historically been an important limiting factor in the establishment of non-native species (Smith and Steenkamp 1990; Chown et al. 1998, 2005; Gabriel et al. 2001). However, increasing human visitation has intensified opportunities for new introductions (Whinam et al. 2005; Convey et al. 2006b; Chown et al. 2012), and relatively recent climatic changes are likely to further reduce physical barriers to invasion and enhance colonisation success (Walther et al. 2009; Janion et al. 2010; Chown and Convey 2016; Laparie and Renault 2016). The relatively simple ecosystems found on Southern Ocean Islands (SOI) provide a unique opportunity to understand the processes of colonisation, establishment and impacts of non-native species.

Most of the 560 non-native species documented for the Antarctic and Southern Ocean region are established on SOI (McGeoch et al. 2015). The majority are plants and invertebrates inadvertently introduced through human activity (Frenot et al. 2005). Although some non-native invertebrates and plant species have been studied individually (e.g. Convey et al. 2010; Laparie et al. 2010; Williams et al. 2016), their broader ecosystem impacts remain largely unknown. Vertebrates such as house mice (*Mus musculus*), black rats (*Rattus rattus*) and brown rats (*Rattus norvegicus*) were introduced unintentionally, but others such as rabbits (*Oryctolagus cuniculus*), cats (*Felis catus)*, sheep (*Ovis aries)*, mouflon (*Ovis ammon musiman*), cattle (*Bos Taurus)*, goats (*Capra hircus*), pigs (*Sus Scrofa*), reindeer (*Rangifer tarandus*), weka (*Gallirallus australis*), and trout (*Salmo trutta*) were purposefully released as companions, food or game (Headland 2012; McGeoch et al. 2015). As has occurred globally, non-native mammals have transformed SOI ecosystems through habitat destruction, causing extinctions and altering ecosystem processes (e.g. Courchamp et al.2003; Campbell and Donlan 2005; Frenot et al. 2005; Wanless et al. 2007; Jones et al. 2008; Nogales et al. 2013; McGeoch et al. 2015; McCreless et al. 2016).

The impact of species invasions on islands has typically been determined through monitoring the responses of iconic or charismatic species, like albatrosses (Towns et al. 2006; Towns 2009; Angel et al. 2009; St. Clair 2011; Jones et al. 2016). On SOI, this translates to extensive research on the impacts of non-native vertebrates on seabirds and vegetation (e.g. Copson and Whinam 1998; Cuthbert and Hilton 2004; Scott and Kirkpatrick 2008). Impacts on invertebrates have been less comprehensively studied. This is despite the fact that invertebrates comprise most of the terrestrial fauna on SOI and perform a variety of critical ecosystem functions such as soil nutrient cycling (Convey et al. 2006a; Smith 2008; Chown and Convey 2016). In consequence, their suppression or extinction by invasive species has a range of important implications (Fukami et al. 2006; St Clair 2011; Collen et al. 2012). Furthermore, because of their diversity, invertebrates are important biological indicators of environmental change, and can be useful for conservation planning and monitoring (Kremen et al. 1993; Gerlach et al. 2013). Comprehensive understanding of the interactions between invasive species and invertebrates is therefore critical for future SOI conservation and management (Chown et al. 2008). Non-native vertebrates, invertebrates and plants threaten native SOI invertebrates through predation, competition, and loss of habitat, but our understanding of these interactions is limited compared to other threatened taxa (McGeoch et al. 2015). Here we review the current state of knowledge of non-native species interactions with, and impacts on, native invertebrates on SOI and discuss the consequences and ramifications for these ecosystems.

Terminology

Greenslade and Convey (2012) outline terminology around invasive species that we follow here, including for the terms 'invasive', 'introduced', 'exotic', 'naturalised', 'native', and 'endemic'. Taxa that we refer to as 'non-native' are synonymous with 'introduced' in Greenslade and Convey (2012), and are those which have clearly been transported to a novel locality, directly or indirectly, by human activities. Taxa that we refer to as 'invasive' are those that have followed the invasion pathway, i.e. they been introduced to a new location, colonised, reproduced and spread, causing disruption to the pre-existing ecosystem (Williamson and Fitter 1996).

The study area

Southern Ocean Islands

Southern Ocean Islands (SOI) comprise a series of relatively small, isolated, oceanic islands and archipelagos located on either side of the Antarctic Polar Frontal Zone (APFZ) between 37°S and 55°S (Fig. 1) (Shaw 2013). They are known for their cool, wet, windy but equable climates (Bergstrom and Chown 1999; Huiskes et al. 2006; Pendlebury and Barnes-Keoghan 2007). Almost all are designated as protected areas (Shaw 2013). Despite similarities in their contemporary climate, SOI have significantly different climatic histories, glaciations, geological origins and ages that have influenced natural (ie not mediated by humans) colonisation by terrestrial biota, speciation, and species turnover (Bergstrom and Chown 1999; Shaw et al. 2010; Shaw 2013). Most SOI have no resident human settlements (except for the Falkland Islands and Tristan da Cunha), but some island groups are visited by tourists, and most are either regularly visited by research expeditions or have permanent research stations (de Villiers et al. 2006).

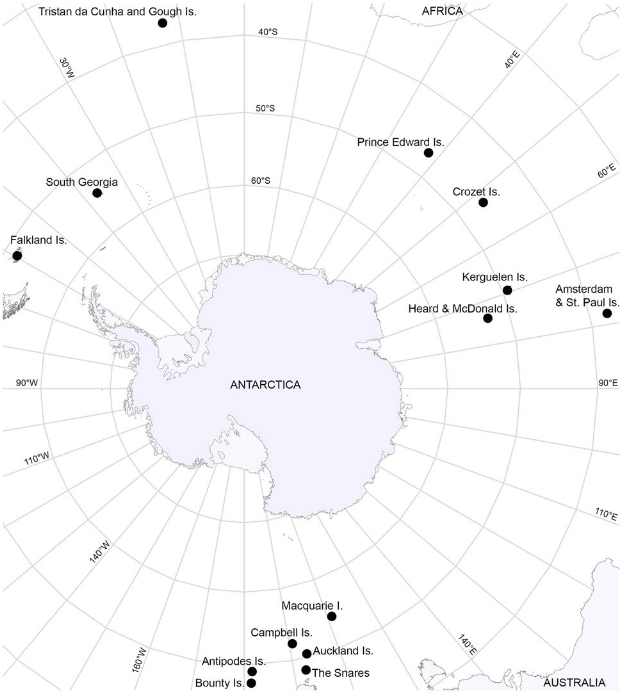

Fig. 1 Map of the biogeographic region referred to as the Southern Ocean Islands, between 37°S and 55°S

Ecosystems

A significant component of the fauna of Southern Ocean Islands are the millions of marine mammals and seabirds, across numerous species, which live and breed on them (Shirahai 2007). There are no native amphibians, reptiles or terrestrial mammals, and very few land-based birds (Bergstrom and Chown 1999; Convey 2007). Compared to continental ecosystems, terrestrial ecosystems on SOI are relatively simple, characterised by non-utilized ecological resources and unrepresented functional groups (Convey et al. 2006a; Whinam et al. 2005). Although levels of endemism are high (Chown and Convey 2016), species diversity is generally low, and many taxonomic and functional groups typically found at lower latitudes are absent (Block 1984; Convey and Lebouvier 2009). A lack of functional redundancy is linked to a higher likelihood of establishment by exotic species, given that new arrivals may experience little competitive resistance (Frenot et al. 2005; Convey et al. 2006b). Low temperatures and numerous, but relatively inefficient, invertebrate detritivores mean that organic decay is generally slow (Tréhen et al. 1990; Smith 2008), resulting in 'bottlenecks' in available nutrients (Slabber and Chown 2002). Across the region, vegetation communities are dominated by grasslands, herbfields (including megaherbs) and are characteristically devoid of trees. High altitude areas support feldmark communities populated by cushion plants and bryophytes (Greenslade 2006; Convey 2007; Bergstrom et al. 2006). The absence of native herbivores means that vegetation is generally vulnerable to grazing by non-native herbivorous mammals due to a lack of defences and high palatability (Bowen and van Vuren 1997; Courchamp et al. 1999; Chapuis et al. 2004; Hullé 2012).

Invertebrate assemblages are characterised by few herbivores or predators and a high number of decomposers (Smith and Steenkamp 1990; Vernon et al. 1998). Typically, assemblages feature adversity or stress selection traits (Crafford et al. 1986; Convey 1996a, b, 1997; Chown 2001) such as low reproductive investment, limited competitive and dispersal abilities, investment in stress tolerance (Chown and Convey 2016) and unusually long life cycles (Haupt et al. 2014). The most abundant native invertebrate groups are mites (Acarina) and springtails (Collembola) (Chown and Convey 2016). Flies (Diptera) and beetles (Coleoptera) are the most common insects in the region (Chown and Convey 2016). Other abundant native groups are Araneae (spiders), Lepidoptera (moths), enchytraeids, earthworms, tardigrades, and nematodes (Convey 2007; Chown and Convey 2016). Flightlessness is unusually common (Roff 1990). Given there are very few large, native predators of invertebrates on SOI, the ecology of native invertebrate communities is unlikely to include adaptations to predation pressure (Convey and Lebouvier 2009).

Biogeography

Consistent low levels of immigration from nearby continents have shaped the terrestrial environments of older SOI with continental origins (Chown et al. 1998; Bergstrom and Chown 1999), as per classic island biogeography theory (MacArthur and Wilson 1967). Informative examples are the Falkland Islands and Auckland Island group. For the majority of SOI, which are typically more isolated, younger, volcanic islands, the origin of most biota remains largely unknown (Bergstrom and Chown 1999). Natural colonisation and dispersal in the region occurs broadly via wind, air, water or with assistance from vectors such as animals, birds or marine debris (Gressitt 1970; Barnes et al. 2006; Hughes et al. 2006; Moon et al. 2017). Native insect and vascular plant species richness are linked, but principally explained by island isolation and temperature (Chown et al. 1998; Leihy et al. 2018). Native vascular plant species richness varies widely across SOI, ranging from 180 species on Auckland Island and one species on Bounty Island, but some inter-regional similarities are apparent (Leihy et al. 2018). Native insect assemblages are more similar between island groups close to each other (Greve et al. 2005; Shaw et al. 2010; Leihy et al. 2018), but richness is highly variable across the region—with as few as six species on MacDonald Island to over 230 on Auckland Island (Chown et al. 1998;

Bergstrom and Chown 1999; Chown and Convey 2016). For SOI invertebrates other than insects (e.g. springtails, mites, and spiders), drivers of diversity and distribution are less well known, largely due to imbalanced survey effort and lack of data for many island groups (Chown et al. 1998, 2008). Repeated surveys of some islands reveal incremental increases in diversity over time, likely due to increased search effort in new habitats and documentation of more cryptic species (e.g. Jones et al. 2003c; Green and Mound 1994; Grobler et al. 2011a, b). Non-native species invertebrate richness on SOI is strongly correlated with native species richness, energy availability, island temperature and area, and the frequency of human visitation (Chown et al. 1998, 2005).

Climate and invasive species

Climate change is occurring across the region (Pendlebury and Barnes-Keoghan 2007; Le Roux 2008; Bergstrom et al. 2015). At some locations, warming is occurring rapidly, at more than twice the mean global rate (Le Roux 2008). Warming increases the likelihood of non-native species establishment (Gabriel et al. 2001; Janion et al. 2010; Chown and Convey 2016; Laparie and Renault 2016), while also putting pressure on native species (van der Merwe et al. 1997). Duffy et al. (2017) modelled the future climatic suitability for some of the world's most invasive species to SOI and the Antarctic region. They found all SOI suitable and at invasion risk under future climate scenarios, particularly Macquarie Island and the New Zealand sub-Antarctic islands. Many non-native species are generally more adaptable (Duffy et al. 2017) and have broader climatic tolerance (Chown et al. 2002; Janion et al. 2010), than native species that are cool-climate adapted and vulnerable to increasing thermal conditions (Convey 1996a, b, 1997; van der Merwe et al. 1997). Even if invertebrates that are non-native to SOI originate from a cool region, their competitive advantage in a warming climate is amplified (Lebouvier et al. 2011; Laparie and Renault 2016). Thus, native invertebrate species on SOI are likely to be disadvantaged and outcompeted with rapid climate change (Chown et al. 2004; McGeoch et al. 2006; Duffy et al. 2017).

Concurrently, accidental transport of non-native species has increased as human activity in the region has escalated (Frenot et al. 2005; Convey et al. 2006b; Hughes et al. 2006; Chown et al. 2012; McGeoch et al. 2015; Duffy et al. 2017). Already for some SOI, the rate of natural colonisations has been surpassed by human-facilitated introductions. On Gough Island, the rate of non-native invertebrate establishment is 2–3 orders of magnitude in excess of the natural rate (Gaston et al. 2003), and for Iles Crozet and Kerguelen 3–4 orders of magnitude for plant and invertebrate species respectively (Frenot et al. 2001, 2008; Lebouvier and Frenot 2007).

Literature search

Our primary objective was to determine how invasions on SOI impact native invertebrates. Therefore, we conducted a literature search in Web of Science using the terms "invertebrate*", "insect*", "non-native", "impact" and "invasive" and three groups of invertebrates widespread on SOI "Diptera", "Coleoptera" and "Lepidoptera", searching each term individually but paired with each of one of the 32 named Southern Ocean Islands (between 37°S and 55°S) (e.g. "Campbell Island", "Macquarie Island", "Prince Edward Island" etc), adding "Antarctic" to focus the search where necessary (e.g. where multiple islands of the same name exist). The reference lists of all relevant publications were further examined to identify other relevant publications. The titles and abstracts of these papers were viewed and 45 publications were identified that measure, through experiment or observation, impacts of invasive species on invertebrates on SOI. By island group, the break down was: Marion Island (18—including three also investigating Prince Edward Islands), South Georgia (8), the Kerguelen archipelago (6), Antipodes Island and Bollons Islands (4), Auckland Island (3), Macquarie Island (3), Gough Island (2), and Falkland Islands (1). Impacts were identified for taxa from 11 higher groups of invertebrates. Of the papers examined the most studied taxa were: Coleoptera (21 times), Lepidoptera (19), and Annelidae (10), followed by Araneae (9), Diptera (7), Amphipoda (4), Collembola (4), Hemiptera (3), Orthoptera (1), Mollusca (1) and Chilopoda (1). Many studies did not specifically identify which invertebrate groups were impacted, rather discussing indirect effects through changes to vegetation or soil habitat. In these cases, the impact group was identified as 'Unspecified'. Twenty studies identified impacts on invertebrates from predators (14 of these relating to mice alone, one on mice and rats, two on mice and cats, and four focussing on either, or both, brown and black rats), 17 invasive invertebrate papers, three invasive plant papers, two invasive omnivore papers, and one study which explicitly tested the impacts of herbivores on invertebrate communities. A summary of these papers is presented in Table 1 in Supplementary Material. This table underpins our review of invasive species impacts on native invertebrates on SOI.

Non-native species impacts on native invertebrates

Non-native plants

More than 250 non-native plant species, mostly grasses and small herbs, have established across the SOI (Shaw 2013). Despite the relatively high number and diversity of non-native plants across the region, making up a substantial component of vascular plant species and altering habitat (Frenot et al. 2001; Jones et al. 2003b; Le Roux et al. 2013), their impacts are generally considered to be relatively minor (e.g. Frenot et al. 2005). This assumption may well be a product of limited investigation (Le Roux et al. 2013) as very few studies have investigated SOI invertebrate and non-native plant interactions (Table 1 in Supplementary Material).

There is compelling evidence that habitat quality and composition strongly influence invertebrate assemblages and species richness on SOI (Crafford and Scholtz 1987; Davies and Melbourne 1999; Barendse et al. 2002; Terauds et al. 2011; Errington et al. 2018). Often, specific plants or communities provide habitat and food for native SOI invertebrates (e.g. Hugo et al. 2004, 2006; Nyakatya and McGeoch 2008; Phiri et al. 2009; Greenslade et al. 2011). Some endemic plants are particularly important—for example *Azorella selago* cushions act as climatically benign, resource-rich refuges and support diverse invertebrate communities (Barendse and Chown 2001; Hugo et al. 2004). Habitat specificity by invertebrate fauna on SOI is identified by some studies (e.g. earthworms and flies—Tréhen et al. 1985; weevils and spiders—Davies 1973; Davies et al. 2011). Others show that many arthropod taxa demonstrate broad habitat tolerances (Burger 1985; Gressitt 1971; Convey et al. 1999; Hänel and Chown 1998; Greenslade 2006).

The effect of non-native plants on insect assemblages varies among taxa (Gremmen et al. 1998 and references therein), but they can greatly reduce local invertebrate diversity (Gremmen et al. 1998, 2001). Gremmen et al. (1998) described impacts on both overall insect species composition and individual species population densities of micro-invertebrates and soil macroinvertebrates due to the increasingly dominant non-native grass *Agrostis stolonifera* on Marion Island. They showed that up to 30% of native invertebrate species were absent from drainage areas dominated by *A. stolonifera*, and that enchytraeid worm biomass declined in these areas. Only one other study (Chown and Block 1997) tested and demonstrated detrimental effects of non-native plant species on invertebrates on SOI. This study demonstrated that the poorer nutrition absorption potential of the invasive *Poa annua* compared to native grasses affected the foraging dynamics of the native herbivorous beetle *Hydromedion sparsutum* on South Georgia, with implications for its body size and fitness. *P. annua* is the most widespread weed in the region (McGeoch et al. 2015). Despite the paucity of published data on the effect of *P. annua* on invertebrates from other SOI, detrimental effects on invertebrate taxa or communities are expected, especially where disturbance and grazing pressure by mammalian herbivores has encouraged spread of the grass (eg Macquarie Island, Scott and Kirkpatrick 2008, 2013).

The extent of impacts due to non-native plants on SOI may take some time to be realised due to complicated interactions with native and non-native plants and invertebrates, and associated lag times. For example, mutually beneficial relationships can form between non-native plants and non-native invertebrates, including mutually-assisted dispersal (Barnes et al. 2006). Very few native plants on SOI are insect-pollinated—a consequence of the lack of native pollinating insect fauna (Convey et al. 2006a) and reflected in plant floral structures (Shrestha et al. 2016). Thus, the establishment of pollinating insects such as the hoverfly *Eristalis croceimaculata* and the blowfly *Calliphora vicina* on South Georgia, represent a novel ecological guild, aiding the seed set and dispersal of currently-localised non-native plants such as dandelions (*Taraxacum officinale*) that require pollination (Convey et al. 2010). Moreover, the dandelions themselves are likely to have facilitated the spread of these pollinating flies (Convey et al. 2010). Several other non-native plants on South Georgia have, until recently, also lacked suitable pollinators (Barnes et al. 2006). In time, native plants on SOI may be outcompeted by non-native insect-pollinated plants (Frenot et al. 2005, 2008) as new species of insect pollinators become established (Convey et al. 2010). Invertebrate communities on SOI reliant on native vegetation could be impacted, but this is yet to be tested.

Non-native invertebrates

Non-native invertebrates on the SOI include flatworms, earthworms, moths, terrestrial crustaceans, predatory carabid beetles, parasitic wasps, slugs, isopods, spiders, booklouse, flies, aphids, springtails, mites and more (Frenot et al. 2005). The non-native insects total more than 180 species across the region (McGeoch et al. 2015). Most species are from families that include well-documented pest species worldwide—e.g. Thripidae, Aphididae, Noctuidae and Calliphoridae (Annecke and Moran 1982; Roques et al. 2009). However, the composition of non-native species can vary between islands—for example, non-native springtails comprise 38% of the introduced fauna on Marion, compared to 10% on South Georgia (Frenot et al. 2005). On some islands, non-native invertebrates represent the majority of terrestrial species—60% on the Kerguelen archipelago (Frenot et al. 2005), and 70% on Gough Island (Jones et al. 2003b).

A small number of introduced invertebrates are considered invasive on SOI, with the majority regarded as 'persistent' (i.e. not expanding their range) and/or synanthropic (i.e. occurring in and/around research stations alongside humans) (Frenot et al. 2005; Greenslade 2006; Convey 2011). Some have naturalised with little apparent impact (Frenot et al. 2005), although this may change over time due to potential changes in temperature, nutrient availability and water availability (Crooks et al. 1999; Nielsen and Wall 2013). Non-native invertebrates can change status from transient, persistent or synanthropic to invasive if environmental circumstances change in their favour (Chown and Avenant 1992; Chown and Language 1994; Bergstrom and Chown 1999; Frenot et al. 2005; Lebouvier et al. 2011). For example on Marion Island, the establishment of the diamond-back moth, *Plutella xylostella*, a globally significant crucifer crop pest (Crafford and Chown 1990), is thought due to recent warming in the region (Chown and Avenant 1992). Similarly, the blowfly *Calliphora vicina*, repeatedly arrived but did not establish at Kerguelen Island until a temperature threshold was reached in the early 1970s, facilitating the completion of its life cycle, followed by a rapid increase in range (Lebouvier et al. 2011). *C. vicina* and the hoverfly *Eristalis croceimaculata* larvae are macrodetrivores. Their activity intensifies nutrient cycling naturally performed by microarthropod soil fauna and native insects, thereby altering soil nutrient availability and decomposition dynamics (Convey et al. 2010). Native flies on South Georgia such as *Paractora trichosterna* are likely outcompeted (Convey et al. 2010), as has occurred to native flies on Kerguelen due to *C. vicina* invasion (Laparie et al. 2010).

Some invertebrate species introduced to SOI may impact terrestrial ecosystem structure and function (Chown et al. 2008; Convey and Lebouvier 2009; Convey et al. 2010; Lebouvier et al. 2011). Not only do non-native invertebrates often outcompete native species (Bergstrom et al. 2006; Janion et al. 2010), but by exploiting previously unutilised ecological resources or dominating unsaturated niches, new arrivals can experience little to no competition (Ernsting et al. 1999; Convey 2007; Smith 2007). Their establishment can significantly alter trophic complexity, nutrient turnover, native prey, resource availability and may assist the spread of other non-native species (Lee et al. 2007; Greenslade et al. 2007, 2008; Convey and Lebouvier 2009; Convey et al. 2010). Examples include a new guild of pollinating flies (*E. croceimaculata* and *C. vicina*), which have established on South Georgia Island and two species of invasive, terrestrial crustaceans on Macquarie Island, which as macro-detritivores occupy an unsaturated trophic level. While the long-term effects of the crustaceans are largely unknown, it is likely that they will alter rates of soil nutrient turnover (Greenslade et al. 2008). There are relatively few naturally occuring invertebrate herbivores on SOI (Vernon et al. 1998). Thus, non-native aphids found at the Kerguelen archipelago that are sap-feeders, a guild nearly vacant on these islands, capitalise on plant resources previously unutilized (Hullé et al. 2010). At least one species, *Myzus ascalonicus*, occurs in colones 2-7 larger on native plants than on non-native host plants (Hullé 2012). The parasitic wasp *Aphidius matricariae* (an aphid parasite), is the only kind of species of this guild in the Marion Island ecosystem, and has rapidly expanded its range since its introduction in 2001 (likely by a single gravid female—Lee et al. 2007). Its colonisation and spread is facilitated by an established non-native aphid (Lee and Chown 2016). Non-native, predatory carabid ground beetles on South Georgia Island and Kerguelen Island (*Trechisibus antarcticus, Oopterus soledadinus* and *Merizodus soledadinus)*, occupy a novel guild as arthropod predators (Ernsting et al. 1995, 1999; Chevrier et al. 1997; Laparie et al. 2010; Lebouvier et al. 2011). Through predation, *T. antarcticus* and *O. soledadinus* have reduced the abundance and increased the adult body size of the endemic herbivorous beetle *Hydromedion sparsutum* on South Georgia Island (Ernsting et al. 1995). Larger adult body sizes in *H. sparsutum* increase as predation of juveniles by the invasive carabids increase, a direct response of both selection by the predator in favour of larvae with rapid growth rate and reduced competition for high-quality food for the survivors (Ernsting et al. 1995). Across the Kerguelen archipelago, *M. soledadinus* has steadily increased its dominance in arthropod communities. It lacks competitors as it is the only predatory insect species (Laparie et al. 2010; Frenot et al. 2005). Since the 1990s, it has expanded its range from the introduction site to remote locations (including other islands in the archipelago) at an accelerating rate of colonisation (Chevrier et al. 1997), and dramatically increased in abundance (Laparie et al. 2010). *M. soledadinus* invasion has led to the near disappearance of its preferred prey, the native wingless flies *Anatalanta aptera* (Diptera: Sphaeroceridae) and *Calycopteryz moseleyi* (Diptera: Micropezidae) in some areas (Laparie et al. 2010; Lebouvier et al. 2011). In contrast, *M. soledadinus* on South Georgia only colonises a limited area (Ernsting 1993), is found in lower abundance, and has a much reduced rate of expansion (Brandjes et al. 1999), probably due to cooler annual temperatures than the Kerguelen Archipelago (Lebouvier et al. 2011).

Non-native soil invertebrates compete directly with native species and alter nutrient turnover in soils (Hänel and Chown 1998; Smith 2007; Smith and Steenkamp 1990, 1992a, b; Greenslade et al. 2008). Through competition and/or predation, invasive species can eventually lead to a decline in abundance or local extinction of native species that may play major roles in organic material decomposition (Greenslade et al. 2007; Convey et al. 2011). For example, on Gough Island, the only indigenous terrestrial isopod, *Styloniscus australis*, is abundant only in upland sites where the non-native terrestrial isopod *Porcellio scaber* is rare, and is rare where *P. scaber* is abundant in the lowlands (Jones et al. 2003b). Some of the non-native fauna on Gough Island, including worms (Ogliochaeta), *P. scaber* and a millipede, are the most abundant on the island (Jones et al. 2003b). The long-term effect of such a large biomass of macro-detritivores on Gough Island, in a system naturally lacking such species, is likely to considerably speed up organic nutrient cycling, affecting peat formation, and substantially changing floral and faunal assemblages (Jones et al. 2002, 2003b; Reynolds et al. 2002; Smith 2007, 2008). On Tristan da Cunha, introduced millipedes and earthworms may similarly be impacting soil types, as native litter-decomposing invertebrates are relatively few (Holdgate 1966). Detritivores on Marion Island, including the European slug *Deroceras panormitanum* (also herbivorous), the chironomid midge *Limnophyes minimus* and *P. scaber*, also process considerable quantities of litter in competition with native species, and substantially alter nutrient turnover (Smith and Steenkamp 1992b; Hänel and Chown 1998; Slabber and Chown 2002; Smith 2008). *L. minimus* is estimated to ingest litter at a rate that is an order of magnitude more than that consumed by the endemic flightless moth larvae *Pringleophaga marioni*, the primary native detritivore on the island (Hänel and Chown 1998). The relatively slow rate of litter processing by this native species is thought to represent a nutrient-cycling bottleneck that once released by non-native macro-detritivores will have implications for primary productivity and peat formation in the island's ecosystem (Smith and Steenkamp 1990; Hänel and Chown 1998; Jones et al. 2003c). The non-native slugs greatly exacerbate rates of nutrient mineralisation from litter and ratios of C:N and N:P released are different than for the native caterpillars on Marion Island (Smith and Steenkamp 1992a, b). This also ultimately affects peat nutrient quality, decomposition rates and primary production, which are important drivers of ecological succession (Smith 2007, 2008). If the nutrient-cycling caterpillars become replaced by non-native slugs (which, unlike the indigenous caterpillar, are not palatable to mice), consequences for ecosystem structure and function are inevitable (Smith 2007, 2008). Though it may be difficult to predict cascading impacts of the non-native detritivores, altered vegetation and soil properties will undoubtedly have implications for native invertebrate life.

Non-native vertebrate impacts

Herbivores and Omnivores

Rabbits, cattle, sheep, corsican mouflon, pigs, goats and reindeer were introduced to SOI in the nineteenth century to either provide food for camps of seal-hunters or for farming (Headland 2012). Typically, herbivore introductions on SOI have led to major declines in vegetation cover, particularly of endemic megaherbs and large tussock grasses that are important habitat for invertebrates (Micol and Jouventin 1995; Chapuis et al. 2004; Scott and Kirkpatrick 2008). With the reduction of some plant species through grazing, short grasses and herbs can thrive, associated with the expansion of grazing-tolerant non-native plants (Frenot et al. 2005), such as *P. annua* (Chown and Block 1997; Williams et al. 2013). The largely detritus-based food webs of SOI, which are composed of weakly efficient detritivores (Tréhen et al. 1990; Smith 2008), are further affected by the conversion of plant matter to herbivore dung rather than accumulated litter (Burger 1985; Tréhen et al. 1990).

Rabbits established on many SOI; however, most have been eradicated in recent times or died out (Headland 2012). Rabbits can reach plague proportions on these islands (e.g. Macquarie Island—Terauds et al. 2014) leading to drastic changes in vegetation (Convey and Lebouvier 2009; Scott and Kirkpatrick 2013; Whinam et al. 2014). The flow-on effects of vegetation loss can lead to soil exposure and erosion (Scott 1988; Chapuis et al. 1994; Scott and Kirkpatrick 2008, 2013), degradation of waterways and associated freshwater invertebrate life (Marchant et al. 2011), as well as reduction of seabird nesting habitat (Chapuis et al. 1994; Copson and Whinam 1998). Reduction in seabird nesting habitat ultimately leads to fewer nesting seabirds. In this way, grazing-mediated declines in seabird densities alter the dynamics of terrestrial communities by reducing marine nutrient inputs that underpin vegetation growth, affecting nutrient turnover and soil integrity, with consequences for food webs and invertebrates (Anderson and Polis 1999; Maron et al. 2006; Smith 2008; Pisanu et al. 2011). Such drastic ecosystem changes occurred on Macquarie Island before rabbits were eradicated, where they caused considerable loss of biomass of vegetation such as tall tussock grasslands (dominated by *Poa foliosa*) and herbfields (dominated by *Stilbocarpa polaris* and *Pleurophyllum hookeri*). This led to degradation of seabird habitat, extreme habitat and edaphic modification, landscape denudation, and increased land-slipping and erosion (Copson and Whinam 1998, 2001; Scott and Kirkpatrick 2008; Stevens et al. 2010), and resulted in substantial changes to invertebrate populations (Copson and Whinam 2001). This is especially the case as invertebrate richness is highest in vegetation communities that were impacted by rabbits (Davies and Melbourne 1999; Terauds et al. 2011; Whinam et al. 2014; Errington et al. 2018). Rabbits have had similar impacts on the Kerguelen archipelago, causing erosion and rapid declines in some native plant species, which are often replaced by monospecific communities of the less palatable, and increasingly dominant, *Acaena magellanica* (Holdgate 1966; Burger 1985; Chapuis et al. 1994). Some studies have suggested that the reduced range and abundance of unique SOI invertebrate fauna is related to herbivore-induced disappearance of natural vegetation communities dominated by *Pringlea antiscorbutica* and *Azorella selago* (Holdgate and Wace 1961; Holdgate 1966; Chapuis et al. 1994), but there are no empirical data to support these claims.

Livestock on SOI have caused severe damage to native vegetation (Holdgate 1966; Taylor 1971; Chapuis et al. 1994; Seddon and Maloney 2003), leading to erosion, compaction, elimination of deep organic soils, the spread of non-native plants and presumably, commensurate reductions in associated invertebrates dependant on intact habitat (Holdgate 1966; van Vuren 1992; Chapuis et al. 1994). Many herbivores prefer particular endemic plant species, causing large-scale alteration of plant community composition across a range of islands (e.g. Holdgate 1966; Taylor 1971; Campbell and Rudge 1984; Convey and Lebouvier 2009). Feral cattle, recently eradicated from Iles Amsterdam (Váňa et al. 2014), had major environmental impacts (Micol and Jouventin 1995; Convey and Lebouvier 2009). Monitoring following initial control fencing and cattle removal from half of the island showed some vegetation regeneration (Micol and Jouventin 1995), but there are no published data available that quantify either the initial impacts of livestock on invertebrates, or the benefits of recent livestock control on invertebrates. Pigs remain on Auckland Island where their effects have been described as 'severe' (Headland 2012). They eat large amounts of native vegetative matter, particularly megaherbs, and prey directly on annelids (annelids—26% dry weight of stomach content), insect larvae, and amphipods (Challies 1975; Chimera et al. 1995). Eight of the ten species of annelids found on Auckland Island are endemic (Lee 1959). Whether any of these species are threatened with extinction as a result of pigs is unknown (Chimera et al. 1995).

Reindeer are extant on Iles Kerguelen and South Georgia (Courchamp et al. 2003), although they are near eradicated from South Georgia Island at the time of this publication. While feeding on Iles Kerguelen they turn over *A. selago* cushions (Chapuis et al. 1994), key invertebrate habitat (Phiri et al. 2009; Barendse and Chown 2001). Reindeer grazing and trampling impacts on South Georgia alter soil integrity and destroy large tracts of the dominant vegetation, the grass *P. flabellata* and herb *A. magellanica*, which are succeeded by the grazing resistant native grass *Festuca contracta*, and the grazing tolerant non-native grass *P. annua* (Vogel et al. 1984; Leader-Williams et al. 1987; Chown and Block 1997). Although the impacts of reindeer-mediated vegetation change have not been quantified at an invertebrate community level, some species-specific impacts have been documented (Vogel et al. 1984; Chown and Block 1997). One example is the increased frequency of sciarid flies in grazed areas (which are possibly non-native), likely due to the ability of their larvae to establish larger populations in deep soil and hardened substrates (a result of trampling—Vogel et al. 1984). Another is reduced abundance of the primary decomposer perimylopid beetle (*Hydromedion sparsutum*), and increased frequency of their egg parasite *Notomymar aptenosoma* (Hymenoptera, Mymaridae) (Vogel et al. 1984). Furthermore, trampling may have facilitated a shift in the proportions of Collembola (major prey invertebrates) and spiders (predators) found in pitfall traps—in ungrazed areas the ratio of invertebrates to spiders was 1: 1.3, compared to 1: 0.82 in grazed areas (Vogel et al. 1984).

In general, suppression or extinction of vegetation that invertebrates rely on for food or shelter, strongly influences native invertebrate extinctions (Dunn et al. 2009). Although rodents are omnivorous, in our review we treat them as predators, given their severe direct impacts on invertebrates as prey. However, rodents on SOI can also affect seedling recruitment and vegetation communities through consumption of seeds and plant material (Shaw et al. 2005; Copson 1986), nesting (Barendse and Chown 2001; Phiri et al. 2009), burrowing, sediment removal and erosion (Gremmen and Smith 1981; Eriksson and Eldridge 2014). These activities have consequences for invertebrates dependant on preferred plants or plant communities (Hugo et al. 2004; Phiri et al. 2009; St Clair 2011).

Predators

Native terrestrial mammalian predators are absent from SOI, therefore the introduction of non-native predators has led to severe impacts on a suite of native taxa, predominantly seabirds, that have evolved few defences (Courchamp et al. 2003; Frenot et al. 2005; Convey 2011). These effects have provided the impetus for several eradication programs, both completed and planned (e.g. Angel and Cooper 2006; Russell 2012; Robinson and Copson 2014; Springer 2016). For invertebrates, the impacts of predatory mammals on SOI (such as rodents and cats) are both indirect and direct (Copson 1986; Courchamp et al. 2003; Angel et al. 2009; St Clair 2011; McGeoch et al. 2015). Rats and mice have caused extensive damage to SOI ecosystems, including impacts on invertebrate richness and diversity, exemplified by comparative studies of invaded and uninvaded islands, such as those in the Falkland Islands (St Clair et al. 2011), Marion Island and neighbouring Prince Edward Islands (Crafford and Scholtz 1987; Chown and Smith 1993; Treasure and Chown 2014; McClelland et al. 2018) and uninvaded Bollons and Archway islands, which are offshore from Antipodes Island (Marris 2000; McIntosh 2001; Russell 2012). Globally, there are well-documented impacts by rats on terrestrial communities, ecosystem properties, and other native taxa, particularly seabirds (Fukami et al. 2006; Towns et al. 2006; Jones et al. 2008; Drake and Hunt 2009; Mulder et al. 2009; Wardle et al. 2009; Pisanu et al. 2011). However, rat impacts on invertebrates are less frequently quantified (St Clair et al. 2011). Towns et al. (2006) cite only nine examples of direct rat-invertebrate interactions in their global review of rat impacts, and only a few published studies directly measure these interactions for SOI (e.g. St. Clair et al. 2011; Pisanu et al. 2011). In general, rats on SOI are found to augment their largely plant-based diet, with large-bodied invertebrates such as caterpillars, annelids, beetles and weevils (Pye and Bonner 1980; Copson 1986; Pisanu et al. 2011; St Clair et al. 2011). St Clair et al. (2011) investigated the effects of rats on large-bodied invertebrates in the Falkland Islands (particularly the endemic Falkland camel cricket) across 37 invaded, uninvaded and recently cleared islands. They found uninvaded islands had up to an order of magnitude more camel crickets than invaded or recently rat-free islands, but also that camel cricket populations recover quickly following rat eradication. Alongside their plant diet preferences, the preferences of rats to predate on the most abundant and large bodied terrestrial invertebrates on SOI implicate them in species suppression and ecosystem transformation.

By contrast, the predation effects of mice on SOI invertebrates are better documented. Eleven SOI have been invaded by mice and their predatory impacts are considerable (Angel et al. 2009), especially for invertebrate populations on Gough Island (Jones et al. 2003a, b, c), Guillou Island (in the Kerguelen archipelago) (Le Roux et al. 2002), Antipodes Island (Marris 2000), Macquarie Island (Copson 1986) and Marion Island (Gleeson and van Rensburg 1982; Crafford and Scholtz 1987; Smith et al. 2002; McClelland et al. 2018). Where mice are the sole predator, their effects on invertebrates are typically greater, such as on Antipodes, Marion, and Gough islands (Angel et al. 2009; Russell 2012; McClelland et al. 2018). Furthermore, climate warming in the region underpins increases in mice biomass and further exploitation of invertebrate prey (McClelland et al. 2018). A good example is the 197.6-fold decrease in invertebrate biomass on Marion Island between 1976 and 2006 due to mice, or around 90% loss of biomass each year, linked to climate-driven mice population increases (McClelland et al. 2018). Mice predation is implicated in the extinction of island endemic invertebrate species on Antipodes Island (Marris 2000) and increases the extinction threat for several species on Gough Island (Jones et al. 2003a) and Marion Island (Crafford and Scholtz 1987; Rowe-Rowe et al. 1989; Angel et al. 2009; McClelland et al. 2018). Where mice are abundant they are responsible for localised extinction of invertebrates in lowland and coastal areas on SOI, restricting once abundant species to upland areas (e.g. Gough Island—Jones et al. 2003b; Antipodes Island—Marris 2000). Large-bodied invertebrates are more at risk to suppression or local extinction through rodent predation than smaller-bodied taxa (Chown and Smith 1993; Pisanu et al. 2011; St Clair 2011). Pronounced impacts of size-selective feeding are evident in changes to the size distribution of weevils on Marion (Treasure et al. 2014), and is potentially responsible for the hybridization of two weevil species that may previously have been differentiated by size (Chown 1990; Grobler et al. 2006). Depending on the season and availability of preferred prey, mice can switch preferred food items (Copson 1986; Smith et al. 2002; James C Russell et al. (in review)). For example, on Antipodes Island, mice seem to exhaust their preferred invertebrate prey to the point of severe suppression or local extinction, before moving on to the next preference, thus systematically eating their way through the ecosystem (James C Russell et al. (in review)). Such extirpation of preferred invertebrate prey, particularly during winter on islands with elevated populations of mice as the sole predator, may be a driver behind mice switching diets to seabirds (James C Russell et al. (in review)), such as on Gough Island (Wanless et al. 2012; Dilley et al. 2015) and Marion Island (Jones and Ryan 2010). Through their dynamic dietary preferences, the above studies have shown that mice can drastically modify the structure of ecosystems on SOI.

Mice predation on invertebrates also alters overall ecosystem processes. Suppression of invertebrates influencing nutrient cycling and mineralisation, has profound implications for SOI ecosystems that are already nutrient poor (McClelland et al. 2018). Alteration of ecosystem processes by mice on Marion Island occurs through predation of a keystone nutrient-cycling species, the caterpillar of a flightless moth, *P. marioni* (Smith and Steenkamp 1992a; Klok and Chown 1998), as well as depletion of other invertebrate prey such as spiders, weevil larvae and weevil adults (Crafford and Scholtz 1987; Rowe-Rowe et al. 1989; Chown et al. 2002). The substantial reduction in the flightless moth caterpillars, which are vital to nutrient supply for primary producers, threatens to slow plant growth, reduce litter quality, potentially affect the formation of peat on the island, and alter vegetation success (Smith and Steenkamp 1990; Smith 2008; Haupt et al. 2014).

Caterpillar declines are also linked to a declining population of lesser-sheathbills (*Chionis minor*), whose overwintering diet is dependent on them (Huyser et al. 2000). This is a clear example of the cascading ecosystem effects of invertebrate impacts. Potentially similar effects have been documented on Gough Island, where two endemic brachtyperous moths (*Dimorphinoctua goughensis* and *Peridroma goughi)*, which are key nutrient cycling species, are preferentially eaten by mice (Jones et al. 2002, 2003a). On Macquarie Island, before a successful rodent eradication, amongst a wide variety of invertebrate prey detected in 108 mouse stomachs, spiders were recorded in 67% of them (Copson 1986). Given that all three spider species on Macquarie Island are major predators of small invertebrates (Greenslade 2006), depletion of spiders by rodents likely had flow on-effects in the ecosystem and the invertebrate community as small invertebrates prey were released from spider predation.

Indirect effects on invertebrates can occur through reduction of seabird populations due to rodent predation. Mice can prey-switch to seabirds as invert biomass falls in winter (Jones and Ryan 2010; Dilley et al. 2015), over time reducing seabird-driven marine inputs to the ecosystem and leading to soil impoverishment. Guano deposition by seabirds leads to increased cover, vitality and growth in plant communities (Smith 1976, 1978; Erskine et al. 1998), which in turn support a disproportionately high biomass of invertebrate detritivores and herbivores compared with areas free of seabirds (Burger 1978; Crafford and Scholtz 1987). In this respect, seabirds act as 'ecosystem engineers', influencing the base of food webs (Sanchez-Pinero and Polis 2000; Jones 2010; Russell 2012; Buxton et al. 2014). Thus, predation of seabirds on islands can reduce soil fertility (Fukami et al. 2006; Wardle et al. 2009), affect vegetation recruitment and growth, litter composition and decomposition (Wardle et al. 2007, 2009), and exert considerable multi-trophic, cascading effects in the terrestrial ecosystem (Croll et al. 2005; Fukami et al. 2006; Maron et al. 2006; Wardle et al. 2009; Mulder et al. 2009; Towns 2009). Rodent predation on seabirds can indirectly lead to reduced abundance of major orders of soil and above-ground invertebrates (Fukami et al. 2006; Towns 2009). Furthermore, invertebrate food webs are smaller and less complex on islands not dominated by seabirds, leading to lower trophic-level redundancy and therefore lower ecosystem resistance (Thoresen et al. 2017). These cumulative predator impacts have contributed to severe, sometimes permanent ecosystem alteration (Fukami et al. 2006; Mulder et al. 2009; Towns 2009; Wardle et al. 2009; Jones 2010). In light of these trends, cat eradication success on Macquarie and Marion Islands is predicted to have implications for their ecosystems beyond seabird population increase, including for invertebrates (van Aarde et al. 1996; Raymond et al. 2011). Unexpected consequences of ecosystem change following predator eradication has also been observed, such as the expansion of a non-native springtail on Marion Island, as its preferred habitat, a native grass, responds favourably to recovery of seabirds and associated nutrients since cat removal (Treasure and Chown 2013).

Discussion

Southern Ocean Islands have been visited by scientists for over 100 years. Despite this, some islands and some taxa have received more attention than others (Chown et al. 2008). The significance of such extensive studies in the region is valuable for invertebrate ecology. However, Table 1 in Supplementary Material highlights that research gaps remain for some ecological processes, some taxa and some islands. For example, non-native species on SOI have wide-ranging, sometimes severe, impacts on native invertebrates, either through direct mechanisms (e.g. predation and competition) or indirectly, through habitat modification, changes in soil integrity and reduced nutrient subsides by seabirds. Yet there is still limited understanding of these impacts for invertebrates and empirical data remain scarce. Similarly, non-native plant species are common on most SOI, and in some instances widespread, yet to date, only three studies have investigated the response of invertebrates to non-native plant expansion. This is despite the fact that we know native invertebrates rely on native plant species for food, habitat and cover (e.g. Hänel 1999; Hugo et al. 2004, 2006) and flow on effects are likely for native invertebrates when non-native plants flourish. Furthermore, whilst numerous studies have referred to the likelihood of considerably altered invertebrate populations associated with extensive damage to soils and native vegetation by grazing mammals (e.g. Chapuis et al. 1994, 2004; Copson and Whinam 2001; Courchamp et al. 2003), few have supported their claims with empirical data. Island-wide modification of habitat and soil through grazing and trampling have had wide-ranging ecosystem impacts (e.g. Courchamp et al. 2003; Chapuis et al. 2004; Frenot et al. 2005; Scott and Kirkpatrick 2008). The impacts on lower trophic levels, such as among invertebrates, are often implied (e.g. Chapuis et al. 1994; Micol and Jouventin 2002) but rarely quantified. Only two publications explicitly test the indirect effects of herbivore-induced plant community changes and activity on local associated invertebrates—Vogel et al. (1984) through reindeer trampling effects, and Chown and Block (1997), via the effects of grazing-mediated, non-native *P. annua* grass on native invertebrate fitness (Table 1 in Supplementary Material). More than 50 years have passed since Holdgate and Wace (1961) noted that elimination of native vegetation by rabbits on Kerguelen is accompanied by 'the loss of the remarkable invertebrate fauna associated with it', but there has been few, if any, comprehensive studies measuring invertebrate responses to non-native mammal grazing and vegetation damage on SOI. Even at a global scale, a lack of meaningful reporting on vegetation responses to herbivore eradication persists, which underpins a gap in our understanding for whole-ecosystem conservation benefits (Schweizer et al. 2016), including the fate of invertebrates. As a result, although eradications of mammalian herbivores have occurred on SOI for conservation benefits, to date we can only assume there are associated benefits to invertebrate communities.

While the 17 studies on invasive invertebrates in Table 1 in Supplementary Material include a broad suite of 26 invasive invertebrate species impacting on native fauna and ecosystems, the 20 studies researching the impact of mammalian predators on native invertebrates on SOI is overwhelmingly skewed towards studies of mouse-invertebrate interactions (17 of the 20 predator-related studies). Not only do mice studies dominate predator research for invertebrates, but the native invertebrate taxa studied is skewed heavily towards Coleoptera (beetles—21 times), and Lepidoptera (moths—19 times). Within the Coleoptera studies, the weevils *Ectemnorrhinus* spp. dominated (7 studies) and within the Lepidoptera studies flightless moths, *Pringleophaga* spp., were the primary focus (14 studies). Some of this research bias is due to the profusion of work on certain islands where these species exist. Marion Island, for example, is the site of 18 of our 45 studies incorporating invertebrate and non-native species interactions, with the second most-studied island, South Georgia, producing only 8 studies. The Kerguelen archipelago, which has a suite of non-native mammal, plant and invertebrate species across numerous islands, is the subject of only six studies that investigate their impacts on native invertebrates. This summary highlights gaps in our knowledge for unknown or under-surveyed invertebrate species on SOI that are impacted by invasive species, and also emphasises the lack of survey effort that persists for some SOI.

While it has been widely shown that non-native mammals drastically alter SOI, our review also highlights the considerable impacts of non-native invertebrates on native invertebrates and island ecosystems more broadly. To date these impacts have been underestimated, and their long-term extent is still largely unknown (McGeoch et al. 2015). Moreover, variation remains in the level of survey effort and knowledge among taxonomic groups (Convey et al. 2006b). Despite these impacts and improved biosecurity, non-native invertebrates continue to arrive and establish on SOI (Hughes et al. 2011; Houghton et al. 2016; Phillips et al. 2017). Invasions are expected to increase as the climate warms (Chown et al. 2008; Chown and Convey 2016). Eradications of invertebrates are rare, although recently demonstrated to be possible—for example, a butterfly in the South Island of New Zealand (Department of Conservation 2018); and ants on Tiritiri Matangi, New Zealand (Green (2019), and Lord Howe Island (Boland et al. 2011; Hoffmann et al. 2017). Nevertheless, the most cost-effective management strategy to reduce the impacts of invasive invertebrates on SOI is through improved biosecurity. For this reason, extending our knowledge of native and non-native invertebrate interactions in SOI ecosystems is critical, particularly in identifying high-risk taxa and developing targeted biosecurity procedures. Such knowledge increases the likelihood that island managers can reduce or even avoid completely, incursions of taxa likely to establish, invade and have impact. Similarly, improving our understanding of how established invasive invertebrates interact with flora and other invertebrate in SOI ecosystems, and their influence on food webs and nutrient cycling, is critical to our future management of present non-native species and developing responses to future incursions.

We have a good understanding of rodent impacts on SOI invertebrates from a suite of studies (Table 1 in Supplementary Material). However, the indirect consequences of seabird predation by rodents on above- and below-ground invertebrate communities and food webs can only be assumed from comprehensive studies of the seabird impacts on New Zealand islands (e.g. Fukami et al. 2006; Towns 2009; Thoresen et al. 2017). To date, no published study has measured the consequences of predator-mediated seabird declines for native SOI invertebrates, although the topic is often discussed (e.g. by Crafford and Scholtz 1987 in relation to cat impacts on Marion Island and by Huyser et al. 2000 for cats, mice, seabird invertebrate interactions). Furthermore, although some comparative island studies document rodent impacts on invertebrates on SOI (e.g. Crafford and Scholtz 1987; Marris 2000; McClelland et al. 2018), we still know little about how invertebrate communities respond once the target invasive species is eradicated. Furthermore, we have very little understanding of how these invertebrate responses to such management may influence recovery (or otherwise) of the whole island ecosystem. The study by St Clair et al. (2011) on the Falkland Islands showing camel cricket recovery following rat removal is an exception. How interactions between plants and native invertebrates may change in response to mammal eradications are also not well described (Angel and Cooper 2006).

There are several underlying reasons behind the limited monitoring of SOI invertebrate response to eradications to date. A key contributing factor is that conservation efforts have traditionally focused on large, charismatic megafauna (Samways 2007; Angel et al. 2009; Collen et al. 2012). Invertebrate surveys are time-consuming, and often considered too difficult, yielding enormous abundance and diversity of species for which few specialists are available to process and even less to identify (Ward and Larivière 2004). Finally, the dramatic speed of invertebrate responses (e.g. St Clair et al. 2011; Watts et al. 2011) mean that unless surveys are planned and undertaken before and soon after eradications, nuanced changes can be difficult to identify. The consistent lack of invertebrate baseline data on SOI prior to non-native species introductions means that it is rarely clear which (or if any) species have experienced population declines or been lost altogether. In order to quantify change with confidence, invertebrate monitoring must begin with meaningful pre-treatment baseline surveys, accompanied by comprehensive and timely post-treatment monitoring.

The results of our review support and build on the assessments and findings of McGeogh et al. (2015), and Jones et al. (2016) who suggest that the responses of invertebrate fauna on islands are under-reported and poorly understood. Although critical to ecosystem functioning and high in diversity, invertebrates rarely generate interest in conservation funding (Angel et al. 2009). Furthermore, being inconspicuous, with cryptic habits, invertebrates are often overlooked in restoration programmes to date, even though they comprise the base of trophic pyramids and changes in their abundance and distribution can affect the whole ecosystem (Courchamp et al. 2003; Angel et al. 2009; Shaw et al. 2011). More recently, the importance of invertebrates has been recognised in SOI mammal eradication feasibility studies and planning processes, For example, invertebrate recovery was one of the objectives of the Macquarie Island Pest Eradication program (rodents and rabbits; Parks and Wildlife Service 2008), the Antipodes Island mice eradication (Elliot et al. 2015) and the proposed mice eradication on Gough Island (Parkes 2008). However, given the recent completion or near implementation of these programs (post-eradication monitoring is currently underway on Antipodes and Macquarie Islands, pre-eradication monitoring is underway on Gough), meaningful data and reporting on species interactions and the responses of invertebrates to mammalian predator and herbivore removal remain elusive. While these studies are yet to be completed (or published), they represent an important and necessary shift in thinking by scientists, funders and land managers. As we have highlighted here, the impacts of non-native species on invertebrates are far too wide-ranging to be ignored any longer.

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Compliance with ethical standards

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