# The impacts of invasive plants on springtail diversity on sub-Antarctic Marion island

by

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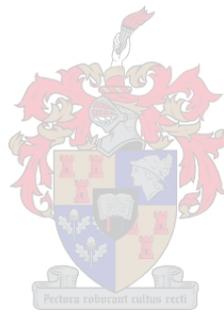
Thesis presented in partial fulfilment of the requirements for the degree of Master of Science in the Faculty of Science at Stellenbosch University

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Declaration

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Stellenbosch March 2019

Abstract

Invasive species have been intentionally and accidentally introduced globally to both mainland and isolated island ecosystems, with the effects more harmful on islands given their isolation and high endemism of species. Several sub-Antarctic islands have been invaded by plants, animals and insects, mostly of European origin. Marion Island forms part of the Prince Edward Islands and has been invaded by species over time. Vascular plants, mainly from the families Poaceae, Caryophyllaceae and Juncaceae from Europe, have successfully established on the island due to their broad environmental tolerance and have managed to dominate most of the six habitat community complexes on Marion Island. Springtails found on Marion Island occupy all of the six habitat complexes, where they are amongst the most abundant invertebrates. In this study, I investigated the influence of vegetation on the distribution and abundance of springtail species on Marion Island specifically. I found that springtails on Marion Island are associated with both invasive and native vegetation, with invasive springtails preferring habitats in lower lying coastal sites where native *Poa cookii* and *Cotula plumosa*, and invasive *Poa annua*, *Agrostis stolonifera* and *Sagina procumbens* dominate. However, this coastal vegetation was dominated by the presence and abundance of invasive springtail species such as *Isotomurus maculatus* and *Ceratophysella denticulata*. *Ceratophysella denticulata* occurs in very high abundance when present, thus this species may have displaced native springtails, such as observed for *Hypogastrura viatica*, which is invasive on other sub-Antarctic islands. Furthermore, *C. denticulata* may potentially reduce native species richness on these islands. While most invasive springtails prefer warmer coastal habitats, *Pogonognathellus flavescens* and *Megalothorax minimus* were found in higher altitudinal habitat. The presence of *P. flavescens* at this higher altitude is surprising, as this species was previously only found at a few coastal sites. From the results, it is clear that both native and invasive springtails respond strongly to altitude. The increase in altitude results in decreased springtail abundance and richness irrespective of whether the species is native or invasive. Principal coordinates analysis showed that six out of the nine native springtail species on the island are found in cooler, mid-altitude habitats with the exception of *Folsomotoma marionensis*, *Mucrosomia caeca* and *Cryptopygus dubius* which prefer lower lying habitats. Other native species such as *Cryptopygus antarcticus travei* and *Tullbergia*

bisetosa were found to be most abundant in moist complexes, for example near rivers and mires that are found in mid-altitude areas. The rare native springtail species could face the risk of becoming extinct due to their current low numbers, which may further decrease as habitats are transformed by invasive vegetation and climate change. With increased climatic warming, it is possible that this change could favour particular invasive species as they can tolerate dry and warmer conditions better than native species. In addition, the increase in altitudinal distribution of invasive vegetation, such as *C. fontanum*, *S. procumbens* and coastal *A. stolonifera*, is of great concern as these species may cause a decline in native vegetation which is essentially habitat to native springtails. Large stands of invasive plants are already present along the altitudinal gradient with their effects on native springtails further exacerbated by the presence of invasive springtail species on the island. The impact of invasive springtails on native species is poorly understood, and should be experimentally tested.

Opsomming

Indringerspesies is doelbewus asook onbewustelik wêreldwyd – in beide vasteland-asook geïsoleerde eilandekosisteme – versprei, met die mees skadelike effekte wat op eilande as gevolg van hul isolasie en hoë endemisme van spesies plaasvind. Verskeie sub-Antarktiese eilande is deur plante, diere en insekte, meestal van Europese oorsprong, ingedring. Marion-eiland vorm deel van die Prins Edward-eilande en is oor tyd deur verskeie spesies ingedring. Vaatplante, hoofsaaklik in die Poaceae, Caryophyllaceae en Juncaceae families uit Europa, het suksesvol op die eiland weens hul breë omgewingsverdraagsaamheid gevestig en het daarin geslaag om die meerderheid van die ses habitat-gemeenskapskomplekse op Marion-eiland te oorheers. Springsterte wat op Marion-eiland aangetref word, bewoon al ses habitatkomplekse, waar hulle een van die vollopste ongewerweldes is. In hierdie studie het ek die invloed van plantegroei op die verspreiding en vollopheid van springstertspesies op Marion-eiland spesifiek ondersoek. Ek het bevind dat springsterte op Marion-eiland met beide indringer- en inheemse plantegroei geassosieer word, met indringerspringsterte wat habitatte in laerliggende kusareas verkies waar inheemse *Poa cookii* en *Cotula plumosa*, asook die indringers *Poa annua*, *Agrostis stolonifera* en *Sagina procumbens* oorheers.

Hierdie kusplantegroei word egter deur die teenwoordigheid en vollopheid van indringerspringsterte soos *Isotomurus maculatus* en *Ceratophysella denticulate* oorheers. *Ceratophysella denticulata* kom in baie hoë vollopheid voor waar dit teenwoordig is en dus kon hierdie spesie moontlik inheemse springsterte verplaas het – soos waargeneem in *Hypogastrura viatica* wat 'n indringer op ander sub-Antarktiese eilande is.   Verder kan *C. denticulata* potensieel inheemse spesierykheid op hierdie eilande verminder. Terwyl die meeste indringerspringsterte warmer kushabitatte verkies, is *Pogonognathellus flavescens* en *Megalothorax minimus* in hoërliggende habitatte gevind. Die teenwoordigheid van *P. flavescens* op hierdie hoogtes is verrassend, aangesien hierdie spesie voorheen slegs in 'n paar kusareas gevind is. Uit die resultate is dit duidelik dat beide inheemse en indringerspringsterte sterk op hoogte bo seespieël reageer. Die toename in hoogte lei tot verlaagde springstert vollopheid en spesierykheid, ongeag of die spesie inheems of 'n indringer is. 'n Hoofkoördinaat-analise het getoon dat ses uit die nege inheemse springstertspesies op die eiland in koeler, middelhoogte habitatte gevind word, met die uitsondering van *Folsomotoma marionensis*, *Mucrosomia caeca* en *Cryptopygus dubius* wat laerliggende habitatte verkies. Ander inheemse spesies soos *Cryptopygus antarcticus travei* en *Tullbergia bisetosa* het die meeste in klam komplekse, byvoorbeeld naby riviere en moerasse wat op middelhoogtes geleë is, voorgekom. Die seldsame inheemse springstertspesies kan die risiko loop om uit te sterf, weens hul huidige lae getalle wat verder kan afneem namate habitatte deur indringerplantegroei en klimaatsverandering gewysig word. Met toenemende klimaatsopwarming is dit moontlik dat hierdie veranderinge spesifieke indringerspesies kan bevorder, aangesien hulle droë en warmer toestande beter as inheemse spesies kan verduur. Daarbenewens is die toename in die verspreiding van indringerplantegroei soos *C. fontanum*, *S. procumbens* en kuslangse *A. stolonifera* na hoërliggende areas van groot kommer, aangesien hierdie spesies 'n afname in inheemse plantegroei kan veroorsaak wat in wese die habitat van inheemse springsterte is. Groot areas van indringerplante is reeds oor die hoogtegradiënt teenwoordig, met die effek daarvan op inheemse springsterte wat deur die aanwesigheid van indringerplante op die eiland vererger word. Die impak van indringerspringsterte op inheemse spesies word nog nie volkome verstaan nie en moet eksperimenteel getoets word.

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Chapter 1

General introduction

Biological invasions

Biological invasions is a global phenomenon, of taxa moved around by humans, and has occurred over centuries, resulting in the exchange of fauna and flora across continents, islands and between oceans (Drake, 1989, Bax *et al.*, 2003, Ricciardi, 2007). Invasions by alien species are a growing threat to biodiversity and ecosystem services. Risks of invasion are shifting on a global scale because of expanding transportation networks, landscape transformation, and climate change (Early, *et al.*, 2016). Introductions of alien species are closely linked to human activity and many plant and animal species have been introduced intentionally and unintentionally. Many intentional introductions have largely been for the purpose of cultivation and agriculture, which has resulted in the spread of alien invasive species across the globe (Reaser & Howard, 2003). This is further exacerbated by increases in global transport (Sakia *et al.*, 2001, Chandrasena, 2009, Vitousek *et al.*, 1997, Devaux, 2013). This mode of dispersal is termed long distance jump dispersal, indicating dispersal over a wide spatial scale during a relatively short period (Drake, 1989, Ricciardi, 2007, Green *et al.*, 2013).

Prior to becoming invasive, introduced organisms must overcome physical barriers, such as mountains, deserts or oceans and biotic factors, such as the existence or absence of enemies and mutualisms with other species (Sakai *et al.*, 2001). Additionally, physiological barriers must also be overcome in the recipient environment and these include abiotic factors such as temperature, altitude and humidity (Drake, 1989, Richardson *et al.*, 2000, D'Hondta *et al.*, 2012). Once alien species are able to reproduce and sustain populations over many life cycles without direct intervention by humans, they are then considered naturalised (Richardson *et al.*, 2000). If the naturalised organisms are able to produce a sufficient number of offspring or propagules that can expand their range over a considerable area, the organism is said to be invasive (Richardson *et al.*, 2000, Steyn *et al.*, 2017).

Successful invasive species have a few broadly-defined characteristics or traits that are thought to give them an advantage over indigenous species (Richardson *et al.*, 2000). Some examples include rapid growth rate, strong dispersal capabilities, large reproductive output, and broad tolerance to a wide range of environmental conditions (Sakia *et al.*, 2001, D'Hondta *et al.*, 2012, Alerding & Hunter, 2013, Steyn *et al.*, 2017).

Consequently, these species can typically reach extremely high abundances in suitable habitats where they can alter the entire community through the displacement of native biota (Pimentel *et al.*, 2001, Ricciardi, 2007, Vilà *et al.*, 2011). For example, Shoko *et al.* (2005) reported that the introduction of Nile perch (*Lates niloticus*) into Lake Victoria (eastern central Africa) lead to the extinction of over 200 species of native fish as a result of cascading effects, which resulted in insect outbreaks due to the loss of fish predators.

Island invasions

Biological invasions have been shown to impact both mainland and island ecosystems (Liebhold *et al.*, 2016), but these effects are more harmful on islands given their isolation (MacDonald & Cooper, 1995, Kühn & Klotz, 2007). In general, islands are more susceptible to biological invasion (D'Antonio & Dudley, 1995) as an island community usually has low species richness and high endemism (MacDonald & Cooper, 1995). This potentially results in a shortened food web structure under saturated communities, lower competitive ability in island species (since island species evolve with few strong competitors and predators compared to continental species), and also vacant niche space (D'Antonio & Dudley, 1995, MacDonald & Cooper, 1995, Moser *et al.*, 2018). Although oceanic islands of South Africa contain considerably fewer alien species than the adjacent mainland, alien species make up a higher percentage of the total island flora since indigenous flora is very species poor (Cooper & Brooke 1986).

Island biogeography theory states that species richness is maintained by equilibrium between opposing rates of colonization, speciation and extinction (Wilson & MacArthur, 1967, Moser *et al.*, 2018). Two major factors determine the equilibrium between extinction and immigration rate: distance from the mainland and island size. Larger islands can support more species and have lower extinction rates than smaller ones because they offer larger areas with a greater diversity of habitats and resources (Simberloff, 1974). Less isolated islands tend to support more species than remote ones, because they have higher rates of immigration (Simberloff, 1974, Russell *et al.*, 2004). However, with the help of humans, invasive organisms have arrived on many isolated islands (Moser *et al.*, 2018), causing numerous extinctions and drastically altering the physical environment (Paulay, 1994, Chown *et al.,* 2005). Examples of

these are the crazy yellow ants (*Anoplolepis gracilipes*) on Christmas Island in the Indian Ocean; the brown tree snake (*Boiga irregularis*) on Hawaii; the small Indian mongoose (*Herpestes javanicus*) introduced to islands in the Caribbean, Fiji, Japan, and elsewhere and invasive house mice (*Mus musculus*) and domestic cats (*Felis catus*) on sub-Antarctic Marion Island and elsewhere (Hunter, 1991, Lowe *et al.*, 2000, Bester *et al.*, 2002, Rodda & Savidge, 2007). Thus alien invasive species on islands alter assemblage structure of native species, often excluding them from their natal environment (Liebhold *et al.*, 2016).

Grasses as invasive plants and climate change

Grasses are the most widely distributed group of flowering plants, occurring from well above the Arctic Circle through the temperate and tropical regions to Antarctica (González-Rodríguez *et al.*, 2010). Moreover, grasses have acclimatised or are genetically modified to thrive in new environments, as seen with crop species worldwide (Pimentel *et al.*, 2001). The availability of forage grasses that withstand grazing and drought conditions, for instance, has led to the conversion of millions of hectares of Sonoran desert woodland to near monocultures (Pimentel *et al.*, 2001). A growing concern to most islands is the increase of several continental invasive grass species from Europe (Chapuis *et al.*, 2004, González-Rodríguez *et al.*, 2010, Crossman *et al.*, 2011, Rojas-Sandoval *et al.*, 2017). These invasive species have broad tolerances and have established in cold to cool temperature ports, and humans have accidentally introduced many to the sub-Antarctic islands (Frenot *et al.*, 2005, Chown *et al.*, 2005, Chown *et al.*, 2012a). With the rise in CO_2 globally due to anthropogenic climate change, alien invasive grasses are expected to thrive since they predominantly utilize photosynthetic processes via the C3 pathway. The invasive grasses are thought more suited to a CO_2 rich environment than other native grass species (Chandrasena, 2009), thus many invasive grasses are predicted to benefit and dominate environments (Jaggard *et al.*, 2010).

Antarctic region ecosystems and biological invasion

The Antarctic region includes three biogeographical zones that are recognized and referred to as the continental, maritime and sub-Antarctic zones (Frenot *et al.*, 2005). The Antarctic region, especially the sub-Antarctic islands with their ice free areas, are important as they support a large proportion of the world's seabird species, seal

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populations and have a high proportion of endemic taxa of flowering plants and invertebrate species (Hänel & Chown, 1999, Frenot *et al.*, 2005, Chown *et al.*, 2007, Chown & Froneman, 2008). Despite its isolation, the Antarctic region has to date been invaded by plants (Chown *et al.*, 2012a), animals and insects, either accidently or deliberately on the main continent and the surrounding islands (Chown *et al.*, 1998, Greve *et al.*, 2017). Human influence has had a major effect on the introduction of alien species over the years, with excessive commercial exploitation taking place in the sub-Antarctic during the late 18th and 19th centuries through sealing and whaling (Watkins & Cooper, 1986, Frenot *et al.*, 2005). The import of livestock by these industries also occurred, before scientific research started in the early 20th Century (Chown *et al.*, 1998, Hänel & Chown, 1999, Frenot *et al.*, 2005, Chown *et al.*, 2007). In addition, a growing tourist industry to the Antarctic and the presence of research stations has led to an increase in propagule pressure and subsequently a rise in the number of alien invasive species on these islands (Watkins & Cooper, 1986, Chown *et al.*, 2005, Frenot *et al.*, 2005, Chown *et al.*, 2012a, Greve *et al.* 2017). Chown and his colleagues (2012a) showed that support staff accompanying tourists and field scientists were the major carriers of seeds to the island.

Marion Island serves as an excellent model system to investigate the impacts of invasive species on ecosystems as it is experiencing rapid climate change (le Roux & McGeoch, 2008), with an increase of more than 1 °C over the last 50 years in mean annual temperature and a decline in annual precipitation of 600 mm (Smith & Steenkamp, 1990; Smith, 2002). Moreover, the presence and distribution of native and introduced species are well documented. For example, the domestic house mouse (*Mus musculus*) is a well-established species on the island (Hunter, 1991), most likely originating from northern Europe (Jansen Van Vuuren & Chown, 2007), and introduced during the sealing period in the early 1800s (Hänel and Chown 1999). Mice negatively affect both native fauna and flora by preying on birds (McClelland *et al.*, 2018) and invertebrates (Crafford & Scholtz, 1987, Bergstrom & Chown 1999), as well as destroying native vegetation through burrowing and seed predation (Smith & Steenkamp, 1990, Gremmen & Smith, 2004). The rapid climate change on the island appears to benefit the mice and consequently these aliens are having increased impacts on the island's biota (Smith & Steenkamp, 1990, McClelland *et al.*, 2018),

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resulting in a major conservation problem on Marion Island and other sub-Antarctic islands such as Gough Island (Cuthbert & Hilton, 2004).

Although the impacts of some invasive animals are well studied, the impact of alien plants in sub-Antarctic ecosystems is not well known (Gremmen *et al.*, 1998, Greve *et al.*, 2017). One study investigated the impacts of the invasive grass, *Agrostis stolonifera*, on Marion Island and Gremmen *et al.* (1998) concluded that the grass does not pose direct threats of extinction to native plants and insects, but does negatively affect the abundance of many native species, ultimately restructuring communities (Gremmen *et al.*, 1998). Another study done on the Antarctic continent and neighbouring regions considered the impacts of the invasive grass, *Poa annua*, on vascular native plants. Similarly, *P. annua* significantly affected the biomass of the vascular plants but also significantly reduced the photosynthetic performance of the native species (Molina-Montenegro *et al.*, 2012).

Winter grasses, mainly from the families Poaceae, Caryophyllaceae and Juncaceae from Europe, have successfully established on Marion island due to their broad environmental tolerance (Frenot *et al.*, 2005) and have managed to dominate most of the six habitat community complexes on Marion Island (le Roux *et al.*, 2013). The first of these habitat complexes, namely the biotic complex, is found mainly near coastal areas, influenced by manure deposits, and trampling of the soils by seabirds and seals. This complex is dominated by native species *Cotula plumosa* and *Poa cookii*, but other species are also found in this complex such as *Callitriche antarctica*, *Montia fontana* as well as invasive *P. annua*, *A. stolonifera*, and *Sagina procumbens*. Second, the salt-spray complex is restricted to the shore-zone on the island and is strongly affected by wind-blown sea spray. This complex is characterised by the presence of *Crassula moschata* and *C. plumosa*. Third, the mire complex where native graminoids *Agrostis magellanica* dominates wet peat. This complex covers extensive parts of the lowlands of the island, and mosses, liverworts, grasses and sedges usually dominate the vegetation. Fourth, the slope complex is overwhelmingly dominated by the fern, *Blechnum penna-marina* and often co-occurs with *Brachythecium* mosses and the dwarf shrub *Acaena magellanica*. The slope complex is mainly found on lowland slopes up to 300 metres above sea level (Fig 1). In the slope complex, *A. stolonifera* is the main invasive species (Huntley, 1971, Gremmen, 1981, Smith & Steenkamp,

2001). Fifth, the fellfield complex, found in rocky habitats above 300 m altitude, is exposed to strong winds. This complex consists generally of bare rock or scoria and is dominated by the cushion plant, *Azorella selago*. Lastly, the polar desert, an important complex, covers about 120 km^2 of the 290 km^2 total area of Marion Island (Fig 1). Although, vascular plants are mostly absent from this habitat community complex, *Azorella selago* may occur in low cover at altitudes below 650 m (Gremmen & Smith, 2008). See Huntley (1971), Gremmen (1981), Smith & Steenkamp (2001), Smith *et al.* (2001), Smith & Mucina (2006) and le Roux *et al.*, (2013) for the detailed classifications of these complexes and their respective habitats (Fig 1).

Alien plants that have invaded Marion Island and other sub-Antarctic islands, such as *Stellaria media*, *Cerastium fontanum* and *Poa pratensis*, have had relatively minor impacts on native vegetation communities (Frenot *et al.*, 2005, le Roux *et al.*, 2013). In contrast, invasive alien plants such as *S. procumbens*, *A. stolonifera* and *P. annua* have established and spread over Marion Island and now occupy most of the eastern side of the island (Gremmen & Smith 2004, Smith, 2008, le Roux, 2013). In most habitat complexes invaded by the grass *A. stolonifera*, the numbers of native plant species are reduced by 50% compared with non-invaded sites (Gremmen *et al.*, 1998). It is thought this species may completely displace unique sub-Antarctic drainage line communities across Marion Island within the next few decades (le Roux *et al.*, 2013).
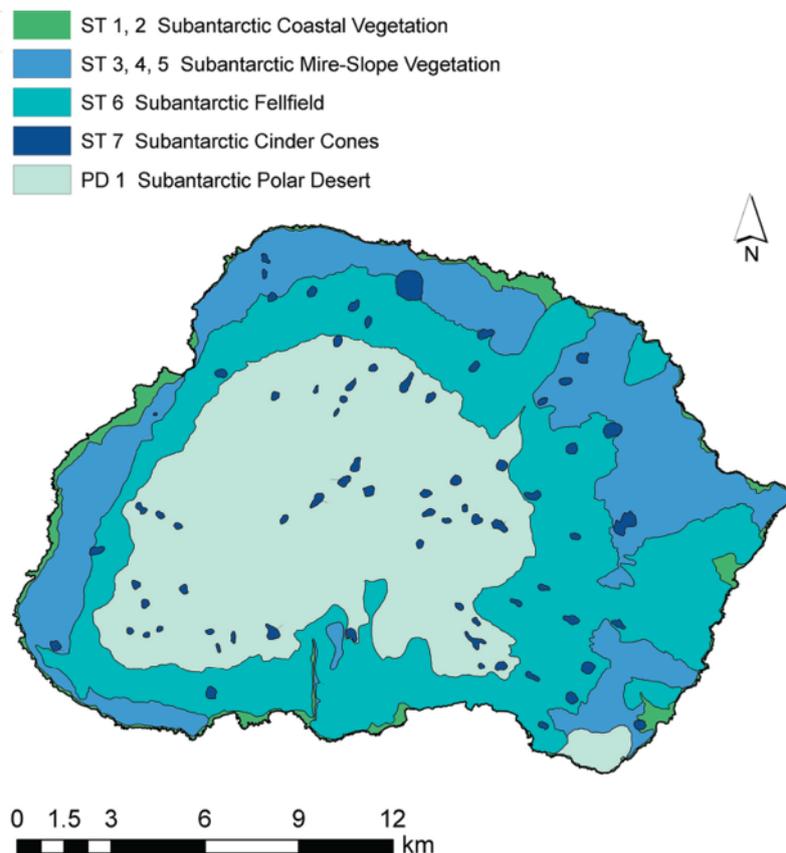
Fig 1: Sub-Antarctic habitat complexes on Marion Island (figure from Treasure & Chown, 2013).

The spread of invasive vegetation, especially *A. stolonifera*, is likely to be facilitated by climate change since the rapid spread of *A. stolonifera* occurred between the 1980s and 1990s during a warm phase on the island (Bergstrom & Chown, 1999). The spread of some invasive plant species on Marion Island should expand upslope as well as into other habitats over the next 45 years, at the same rate as indigenous species have over the last 40 years, owing to climate change. Thus, alien vegetation could potentially occupy 51-86% of the island by 2060 (le Roux *et al.*, 2013). Habitat complexes such as mires have got drier (Chown & Smith, 1993), thus enabling invasive alien plants to invade (Chown *et al.*, 2012b). The predicted decrease in precipitation will be sufficient to halve the moisture content of the mire peats, which would cause up to an 11-fold increase in decomposition rate, resulting in an increase in the rate of nutrient release (Smith & Steenkamp, 1990). As the island's CO_2 concentration has also increased since 1976 (Smith & Steenkamp, 1990), and with most plants on the island being C3, this could lead to increased primary production

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and subsequent changes in microclimate which could affect sensitive soil invertebrates such as springtails (Hopkin, 1997, Wolkovich *et al.*, 2009).

Collembola (springtails)

Globally over 8200 species of springtails (Class Collembola) are described from a range of habitats, from the Arctic to the Antarctic region (Bellinger *et al.*, 2018). They are a monophyletic group characterised by the presence of a spring-like organ known as a furca (hence the common name "springtail"), although this organ has been secondarily lost in some species (Hopkin, 1997). Species identification is also achieved using the presence of a ventral tube or a collophore which is a tube-like structure on the ventral side of the first abdominal segment of the body of springtails, used in maintaining water balance (Hopkin, 1997). The success of springtails is attributed to their small size, as most of them are typically 0.2 mm to 10 mm long (typically between 2 and 4 mm), which enables then to colonise gaps between soil particles, dead vegetation and other confined spaces (Hopkin, 1997). Soil invertebrates are important in driving biogeochemical and ecosystem processes, as they play a major role stabilising soils, aerating soils and affecting plant community succession aboveground (Wall, 2005).

Springtails are classified according to the different vertical soil habitats they occupy. Euedaphic, or soil dwelling, species are usually small, without pigment and live in the soil at a depth of 2.5-5 cm. Epiedaphic, or surface dwelling, species are bigger, pigmented and occupy the upper surface layer of the earth. Hemiedaphic springtails occur near and above the soil surface in a depth of 0-2.5 cm (Gisin, 1943, van Straalen 1994, Hopkin 1997, Detsis 2000). Springtails interact with other organisms, within each of the soil layers they inhabit, and occupy different trophic niches, thus springtails play an important role in food webs (Halaj *et al.*, 2000). They are hosts to many parasitic protozoa, nematodes, trematodes and pathogenic bacteria (Rusek, 1998). Moreover, they are food sources for various predators such as ants (Reznikova & Panteleeva, 2001), mites (Baatrup *et al.*, 2006), other springtails (Hopkin, 1997), frogs, reptiles (Rusek, 1998) and spiders (Agustí *et al.*, 2003, Ellers *et al.*, 2011). Springtails positively influence the ecosystem through the recycling of nutrients from the dead organic matter they feed off (Petersen & Luxton, 1982, Hopkin, 1997, Bardgett & van der Putten, 2014).

Springtail diversity is well investigated on Marion Island and has been shown to decline with elevation, as well as species richness and abundance to vary across vegetation complexes (Table 1 and Deharveng, 1981, Gabriel *et al.*, 2001 Janion-Scheepers *et al.*, 2015), with similar trends shown for springtails found on other islands in the sub-Antarctic region (Hänel, 1999, Terauds *et al.*, 2011). The decreased diversity with altitude differs among the indigenous and invasive species, with indigenous species affected more by disturbances than invasive species (Gabriel *et al.*, 2001). A recent desktop study showed that the more invaded an area is by alien invasive plants; the lower the springtail, and other insect, abundance and species richness are (van Hengstum *et al.*, 2014). These results, together with the expansion of invasive plant species on Marion Island, in combination with the important role of springtails in decomposition and nutrient cycling in polar ecosystems, is of great concern where the diversity of soil fauna is restricted to a few species (Hopkin, 1997, Gabriel *et al.*, 2001).

Table 1: The Collembola fauna that occur on Marion Island and their distribution across the different habitat complexes (Information compiled from Deharveng, 1981; Gabriel *et al.*, 2001; Janion-Scheepers *et al.*, 2015 and Greve *et al.*, 2017). Abbreviations used: E = endemic to Marion Island, S = sub-Antarctic distribution, I = introduced, D = dubious.

Species name	Status	Habitat complex
Hypogastruridae		
Ceratophysella denticulata (Bagnall, 1941)	I	Low coastal and mid-altitude mire complex
Hypogastrura viatica (Tullberg, 1872)	D	Low and mid-altitude mire complex
Neanuridae		
Friesea tilbrooki Wise 1970	S	Low coastal and mid-altitude mire complex
Tullbergiidae		
Tullbergia bisetosa Börner, 1902	S	All habitat complexes
Isotomidae		
Cryptopygus antarcticus travei Deharveng, 1981	E	High altitude mire complex
Cryptopygus dubius Deharveng, 1981	S	All lower lying to mid-altitude mire and fellfield complexes
Cryptopygus tricuspis Enderlein, 1909	S	Fellfield complex
Folsomotoma marionensis (Deharveng, 1981)	E	All habitat complexes
Isotomurus maculatus Müller, 1876	I	Coastal lower and mid-altitude mire complex
Mucrosomia caeca (Wahlgren, 1906)	S	*Azorela selago* cushions in mid-altitude fellfield complex
Parisotoma notabilis (Schäffer, 1896)	I	Coastal lower and mid-altitude mire complex *Ac. magellanica* drainage line and *P. cookii* tussock grassland

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Species name	Status	Habitat complex
Tomoceridae		
Pogonognathellus flavescens (Tullberg, 1871)	I	Low coastal complex with *P. cookii* tussock grassland
Neelidae		
Megalothorax minimus Willem, 1900	I	All low lying, mid-altitude mire and fellfield complexes
Katiannidae		
Sminthurinus granulosus Enderlein, 1909	S	All lowland communities, mid-altitude mire and fellfield complexes
Sminthurinus tuberculatus Delamare Deboutteville and Massoud, 1963	S	All lower to mid-altitude mire and fellfield complexes
Katianna sp.	E	Fellfield complexes in *Blechnum penna-marina*

On Marion Island, springtails occupy all of the six habitat complexes (Gremmen 1981, Gabriel *et al*., 2001, Gremmen & Smith, 2008), where they are amongst the most abundant invertebrates on the island (Gabriel *et al*., 2001, Barendse & Chown, 2001, Chown *et al.,* 2007). With sixteen known species identified on the island, six are invasive and have extended their range across most areas or are cosmopolitan in most habitats (Table 1) (Gabriel *et al*., 2001; Janion-Scheepers *et al*., 2015). Invasive springtails are rapidly spreading across the warmer areas of the South Ocean islands and they seem to adapt better to changes in the microclimate on account of the influence of invasive vegetation (Gabriel *et al*., 2001, Barendse & Chown, 2001). Invasive springtails, especially species belonging to the family Hypogastruridae, dominate areas where they are present, and this could lead to the potential exclusion of native species, as seems to be the case on Macquarie Island (Terauds *et al*., 2011). Species from this family, especially *H. viatica* and *C. denticulata*, are cosmopolitan in low altitude habitat complexes, specifically coastal areas, on several sub-Antarctic islands, such as Marion Island, Macquarie Island and South Georgia (Greenslade & Wise, 1994, Convey *et al*., 1999, Frenot *et al*., 2005, Terauds *et al*., 2011). Invasive springtails prefer warm and moist sites with high levels of organic material and avoid the cold, fellfield complex (Gabriel *et al*., 2001). The success of invasive springtail species, compared to native species, is probably linked to their adaptability to gradual environmental changes, such as rise in temperature, decrease in precipitation and change in microclimate (Gabriel *et al*., 2001, Chown *et al*., 2007, Janion *et al.,* 2010, Treasure & Chown 2014). Furthermore, Chown *et al*., (2007) confirmed that climate change is likely to favour some invasive over native springtails on Marion Island.

Objectives

Invasive species presently pose the most important conservation problem in the sub-Antarctic (Smith, 1987, Greve *et al*., 2017). Due to long-term research undertaken by the South African National Antarctic Programme (SANAP) (Deharveng 1981, Gremmen 1981, Crafford *et at.*, 1986), both the invasive vegetation and invertebrate taxa on Marion Island have been particularly well studied. However, little is known about the changes in sub-Antarctic ecosystems caused by invasive vegetation (Gremmen *et al*., 1998) and their impact on the microfauna. The main aim of the study is therefore to investigate the influence of vegetation on the distribution and abundance of springtail species on Marion Island. In particular, the objectives are:

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i)   To determine the effect of invasive and native vegetation on springtail abundance, species richness and diversity as well as assemblage structure.

ii)   To examine altitude as a variable that drives invasive and native vegetation distribution, which potentially influences springtail abundance, richness and diversity.

iii)   To examine how vegetation and altitude influence individual springtail species abundance on Marion Island.

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Chapter 2

The effect of invasive and native vegetation on springtail abundance and richness on sub-Antarctic Marion Island.

Abstract

Invasive organisms have been introduced on many islands primarily by humans, causing numerous extinctions and drastically altering the physical environment. Islands around the sub-Antarctic region are no exception, where many invasive plants and animals have successfully established. In this study, I examined whether invasive plant species influenced the distribution and abundance of springtail species on Marion Island. The results show that springtails on Marion Island are associated with both invasive and native vegetation, with invasive springtails preferring habitats in lower lying coastal sites where native *Poa cookii* and *Cotula plumosa*, and invasive *Poa annua*, *Agrostis stolonifera* and *Sagina procumbens* vegetation dominate. This vegetation is under high biotic influence where seal and penguin colonies are found. Springtail abundance, diversity and richness of both invasive and native springtail species decreased with an increase in altitude away from these low-lying habitats. Yet native springtails did seem to prefer cooler and wet mid-altitude habitats while invasive springtails preferred habitats that were warmer and moister. The cosmopolitan invasive species *Ceratophysella denticulata* (Hypogastruridae) was found in lower lying areas where they have high abundance on native vegetation and most likely have displaced indigenous springtails. Rapid climate change observed on the island is predicted to cause the spread of invasive vegetation, which could lead to the spread of invasive springtail species and result in further decline of native springtails species.

Introduction

Invasive species constitute a significant environmental risk owing to their profound negative effects on native species, ecosystems, and their economic costs to humankind (Ricciardi, 2007). In consequence, the conditions that promote invasion success raise significant questions in conservation biology (Pyšek *et al.*, 2013). An increasing concern is that current accelerated environmental changes will aggravate the extent and impacts of biological invasions to the cost of indigenous biodiversity (Paulay, 1994, Pimentel *et al.*, 2001, Ricciardi, 2007, Pyšek *et al.*, 2008). Invasive plants are well known for their disruptive biotic impacts on ecosystems (Lowe *et al.*, 2000, Bester *et al.*, 2002, Rodda & Savidge, 2007) and as invaders increase in abundance there is a concomitant decline in the density and diversity of native plants (Sakia *et al.*, 2001). Invasive plants can physically restructure plant biomass, transforming niches, and the chemistry and structure of the soil (Wang *et al.*, 2015).

These changes in microhabitat due to invasive plants dominating and displacing native flora (Dogra *et al.*, 2010) have negative effects on above and below ground soil micro-fauna, especially springtails (Meehan *et al.*, 2010, Krab *et al.*, 2013). Yet, the impacts of invasive plants on local invertebrate populations are rarely studied, and usually focus on herbivorous insects (Morrison & Hay, 2011, Bezemer *et al.*, 2014).

Isolated oceanic islands, such as Marion Island, have been colonised by invasive plants of European origin (Gremmen & Smith, 2008). Humans intentionally or accidentally introduced these plants (Gremmen, 1981, McGeoch *et al.*, 2015, Greve *et al.*, 2017) from as early as the 18th century, and many are now invasive (Watkins & Cooper, 1986, Frenot *et al.*, 2005). Since their introduction, invasive plants have spread through trampling or creation of paths, which have been the main cause of invasive plant propagules spreading to undisturbed areas on the islands (Gremmen *et al.*, 1998, Frenot *et al.*, 2005, le Roux *et al.*, 2013). Invasive vegetation is found in a wide range of habitat complexes, from the lower coastal biotic influenced and salt spray complexes dominated by native vegetation *Poa cookii* and *Cotula plumosa*, to the mid-altitudinal mire and slopes where *Blechnum penna-marina*, *Agrostis magellanica* and *Acaena magellanica* dominate (Gremmen *et al.*, 1998, Gremmen & Smith, 2008). Recent findings have documented range expansion by invasive vegetation to higher altitude fellfield and polar desert complexes which are found in the interior of the island (Chown *et al.*, 2013, le Roux *et al.*, 2013).

Collembola (springtails) are micro-arthropods which constitute an important component of soil meso-fauna in almost all terrestrial ecosystems (Hopkin,1997), and their densities may reach up to several million individuals per m^2 and species richness can range from 1 ± 3 in the desert to 50 ± 60 species in a temperate forest (Petersen & Luxton, 1982, Rusek, 1998). Springtails have a wide global distribution and are found in high abundance on all continents, including Antarctica (Hopkin, 1997). Springtails play an important role in decomposition and nutrient cycling (Gabriel *et al.*, 2001), especially in Antarctic regions where they are the dominant terrestrial fauna. Currently there are 16 species on Marion Island, of which five are invasive (Janion-Scheepers *et al.*, 2015). The invasive springtail species are largely of European origin (Gabriel *et al.,* 2001), most likely having been introduced with invasive plants and

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appear to be associated with particular habitat complexes on the island (Barendse & Chown, 2001, Gabriel *et al.*, 2001, Hugo *et al.*, 2004, Treasure & Chown, 2013).

Small oceanic islands such as Marion Island offer a unique opportunity to study animal and plant communities, and their interrelationship and dependence on the physical environment (see Chown & Froneman, 2008). The number of animal and plant species on the island is low compared to the mainland, making it possible for detailed studies on species assemblages and niche occupancy. Influences of abiotic factors such as temperature, soil characteristics and altitude, that may affect species distributions, as well as the influence of vegetation on these assemblages can also be investigated (Gremmen *et al.*, 1998, Smith & Steenkamp, 1990, Janion *et al.*, 2010, Treasure & Chown, 2014). Furthermore, due to the effect of global climate change, sub-Antarctic islands and Antarctic ecosystems are changing rapidly, influencing the spread of both invasive vegetation and invasive springtails (Smith & Steenkamp, 1990, Chown & Smith, 1993, Gabriel *et al.,* 2001, Janion *et al.*, 2010, le Roux *et al.*, 2013, Liebhold *et al.*, 2016, McClelland *et al.*, 2018). Thus the species of plant and their distributions are likely to influence springtail distribution patterns.

Invasive plants can have a negative effect on native plants and soil fauna; especially springtail communities that are common in terrestrial ecosystems and important in soil ecosystem functioning (Hopkin, 1997, Wardle *et al.*, 2004). Van Hengstum *et al.* (2014) demonstrated, via a meta-analysis, that invasive plants influence arthropod diversity directly through the loss of native plant species richness. In this study, the influence of vegetation (native and invasive) on the distribution, abundance, diversity and richness of springtail species was investigated. Additionally, the springtail assemblage structure and the relationship of springtail abundance, diversity and richness with altitude were investigated on Marion Island, further assessing native and invasive springtail species' responses to altitude.

Material and methods

Study site

Marion Island and Prince Edward Island form the Prince Edward Island (PEI) group. Marion Island (46°54'S, 37°45'E) (Fig. 1, Chapter 1) is separated from the smaller Prince Edward Island (46°37'S, 37°55'E) by 19 km and they are thought to be

geologically young (Crafford, 1990, see Hänel, 1999). The islands are mountainous, with Marion Island and Prince Edward Island reaching 1230 m and 672 m, respectively (Gremmen & Smith, 2004). Marion Island consists of a central highland area sloping down to a coastal plain which on the northern and eastern sides forms a 4 to 5 km wide area rising gently from sea level to the foot of the mountainous interior at about 300 m altitude (see Fig. 1, Chapter 1) (Gremmen & Smith, 2008). The western and southern coastal areas consist of a narrow discontinuous plain of less than 100 m altitude, having been eroded by wave action caused by the strong westerly winds. Much of the low-altitude area supports closed vegetation (see Hänel & Chown, 1999, Gremmen & Smith, 2008). Marion Island is home to 23 indigenous and 12 introduced vascular plant species, while native mosses and liverworts also exist in the six habitat complexes found on the island (Gremmen & Smith, 2008).

Sampling

The sampling was done from the north to south-east of the island. Invasive vegetation and invertebrates are more abundant on the east than on the west side of the island (Gabriel *et al.*, 2001, Hugo *et al.*, 2004, Treasure, 2012), mainly due to the position of the research station (le Roux *et al.*, 2013). Sampling occurred in habitat complexes where invasive vegetation dominated forming large stands, to allow for successive sampling over the 12-month period from April 2012 to May 2013 (Chown *et al.*, 2013). Each major invasive vegetation type sampled included corresponding native vegetation in a matched sampling design (Table 1).

The paired sampling of the 12 vegetation types occurred as follows: 1) The invasive *A. stolonifera* was sampled in coastal manured areas and along river banks, while the native *B. penna-marina* and *Ac. magellanica* mixed vegetation was found more on the slopes and selected as the matched native vegetation; 2) Similarly, the invasive *S. procumbens* was sampled along river banks, coastal areas and lakes where it reaches high density, while *B. penna-marina* and *Ac. magellanica* was the matched native vegetation; 3) Due to the abundance of *A. stolonifera* on the island it was also sampled in coastal areas where it reaches high abundance, with *P. cookii* and *C. plumosa* as the native mixed vegetation matched sample; 4) *P. pratensis* also found along the river banks, lakes and slopes of the south-eastern sectors of the island occur alongside native *Ac. magellanica* inhabiting the dry mire which was sampled as the

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corresponding native vegetation; 5) *C. fontanum* was sampled in areas where dense patches occur on slopes, rocky substrates and along river bank areas, while *B. penna-marina* was the matched native vegetation sample; and 6) *P. annua* established on biotic lawns along the coastal areas from the east to western side of the island was sampled together with the native vegetation dominated by *C. plumosa*. No sampling was done in the polar desert or the fellfield due to low abundance of invasive vegetation (see Barendse & Chown, 2001, Smith & Mucina, 2006). Sites were established away from human influences (such as the station, huts, and walking tracks) (Terauds *et al.*, 2011).

Table 1. Invasive and native vegetation sampled per month from May 2012 to April 2013. The number of sites (each site consisted of four quadrants) for each matched vegetation sample is given.

Invasive vegetation	Native vegetation	Number of sites/matched
Agrostis stolonifera coastal	*Poa cookii / Cotula plumosa*	23
Agrostis stolonifera river	*Blechnum penna-marina* & *Acaena magellanica* on slope	31
Sagina procumbens	*Blechnum penna-marina* & *Acaena magellanica*	37
Poa pratensis	*Agrostis magellanica* dry mire	45
Poa annua	*Cotula. plumosa*	43
Cerastium fontanum	*Blechnum penna-marina*	18

Quadrant sampling was used to record vascular plant species. Two quadrants (1 x 1 m^2 and subdivided by 100 x 1 cm^2 grids) were each laid out in a patch of native and invasive vegetation (matched sample) at 100 m apart, resulting in a total of four quadrants, referred to as a site (Fig. 1). A matched sampling design was used which involved taking samples from invasive vegetation quadrants and corresponding samples from paired native vegetation quadrants. Vegetation was sampled every second month during the sampling period from May 2012 to April 2013 on Marion Island. Not all sites were sampled equally, as no sampling was done during or following heavy rainfall or snow. One hundred metres was kept between each invasive and matched native vegetation quadrant, and a distance of 500 m per site was maintained.

A GPS (Garmin Etrex) coordinate was taken on the NW corner of each quadrant, and altitude was recorded. An inclinometer was used to measure the angle of slope and a compass was used to record the aspect of each site.
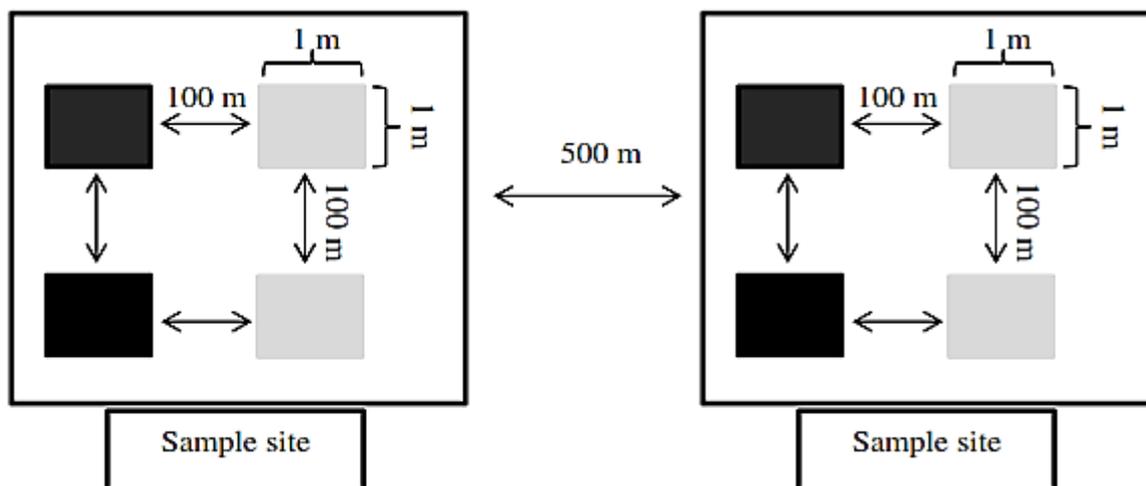
Fig. 1. The diagram illustrates sampling sites. Black squares represent invasive vegetation quadrants and the grey squares represent native vegetation quadrants. Quadrants were placed 100 m apart.

Springtails were sampled from both invasive and native vegetation quadrants using an O' Connor split-corer (inside diameter of corer =70 mm and a height equal to 70 mm; surface area $\approx$ 0.0039 m^2) (Southwood, 1978), an established sampling method for microfauna on Marion Island (e.g. Hänel & Chown, 1999, Barendse & Chown, 2001, Gabriel *et al.*, 2001, Treasure & Chown, 2013). A core sample of about 7 cm depth was used to sample a quadrant. To avoid contamination during sampling between two different quadrants, the corer was washed with water or wiped with a clean cloth before coring again. Five core samples were taken per quadrant, resulting in a total of 20 cores per site per sampling month. Each core was labelled and placed in a plastic bag in its unique plastic collar (to avoid crushing) and transported to the laboratory within seven hours to prevent predation by spiders and mites in the core (Baatrup *et al.*, 2006, Ellers *et al.*, 2011).

A custom-built high gradient extractor (HGE) (Engineering Department, Stellenbosch University) was used to extract the invertebrates from the cores (Macfadyen, 1953,

Block, 1966). This extraction method is the most practical and widely used method for assessing the diversity and abundance of small, less mobile and sedentary arthropods in the soil and litter (Macfadyen, 1953, Block, 1966, Marshall *et al.*, 1994). The HGE uses 60 W clear light bulbs above the samples to produce heat while circulating cool water below using running water, creating a temperature gradient. The animals are then collected in a vial containing 60% ethanol. The temperature regime for extraction was kept at 25°C for the first two days and then put at 30°C for the last two days (Gabriel *et al.*, 2001). After extraction, the extracted animals were drained from the 60% alcohol through a 60μm sieve and preserved in 99% alcohol. Springtails were sorted under a dissecting microscope (Leica MZ 7.5) and identified to species level using an identification key from Gabriel (1999). The springtails were counted and stored in 99% ethanol at Stellenbosch University.

Statistical analyses

To determine sampling adequacy, springtail sampling effort was estimated for each of the 12 sampled vegetation types (see Table 1) using EstimateS V9.1.0 (Colwell, 2013, http://viceroy.eeb.uconn.edu/estimates, Colwell & Elsensohn, 2014). Sample-based rarefaction curves were generated for the six invasive vegetation and the matched native samples to evaluate the degree of sampling effort. The effectiveness of sampling is thought to be adequate when the sample-based rarefaction curves and richness estimators approach a plateau beyond a particular number of samples (Longino *et al.*, 2002). The sample order of each plot was randomised 100 times without replacement as all the samples in the data set were included to compute the estimators of asymptotic species richness. The Chao1 (Chao, 1984) and Bootstrap richness estimators for abundance data were used to assess sampling adequacy, as the Chao and Bootstrap estimators frequently perform better than the other estimators in estimating the number of undetected species from the number of rare species in an assemblage. The Chao estimators were found to be most accurate and least biased, followed by the Bootstrap estimate (Walter & Martin, 2001). Furthermore, diversity measure was calculated using the Shannon-Weiner index (H') which accounts for both abundance and evenness of the springtail species among the sampled vegetation. $H = - P_i (lnP_i)$, where P_i is the proportion of each species in the sample belonging to, the ith species (Magurran, 2004). A scale of 0-1 represents low diversity, while 1-2 indicates high springtail diversity.

A global model was generated that used springtail abundance, species richness, and diversity as the response variable, while the predictor variables included vegetation (12 vegetation types), altitude, aspect, and slope. The best fit model was selected by calculating the Akaike's Information Criterion (AIC) values using the dredge function which generates models using combinations of the terms in the global model. The best-fit model, based on Akaike Information Criterion retained vegetation and altitude as significant predictors.

Generalised Linear Mixed Models (GLMM) are logistic models, catering for both continuous and categorical variables (Manning, 2007), and were run in R using the *lme* package to determine the relationship between springtail abundance (transformed to log 10), species richness and diversity with altitude and vegetation (12 vegetation types) as predictor variables. The Dunn's-test for multiple comparisons of independent samples was used to determine the posthoc pairwise differences in springtail abundance, species richness and diversity across the vegetation types using the PMCMR package R version 3.1.3 (Pohlert, 2014). Dunn's test (1964) calculates the corresponding level of significance for the estimated statistics z, as adjusted to account for Type I error inflation (Pohlert, 2014). The abundance (transformed to log 10) of springtails found in native vegetation was also compared to the abundance of springtails found in invasive vegetation using a GLMM and Dunn's test.

Springtail community structure was analysed using a non-parametric multivariate approach, implemented in PRIMER V6.0 (Plymouth Routine in Multivariate Ecological Research, see Clark & Gorley, 2006). Springtail abundance data were double square-root transformed to weight the common and rare species equally (Clark & Gorley, 2006). The Bray-Curtis similarity coefficient measure was used to construct a similarity matrix among the sampled vegetation, and analysis of similarity (ANOSIM, Clark & Gorley, 2006) was used to test for significant difference between the assemblages from the 12 sampled vegetation types on the island. This is a non-parametric permutation procedure applied to rank similarity matrices underlying sample ordinations that calculate a global R-statistic. The closer a significant global R is to 1.0, the more distinct the difference between those communities (Clark & Gorley, 2006, Clarke & Warwick, 1994). Principal coordinate analysis (PCoA) was performed

using PERMANOVA (Clarke & Gorley, 2006, Anderson *et al.*, 2008) to visualise differences in the springtail community on the basis of vegetation. The vegetation data were graphically represented with vector overlay of springtail species based on Pearson correlation (Anderson *et al.*, 2008).

Results

Springtails were sampled on Marion Island at 26 locations on the eastern side of the island, within 12 vegetation types (six were invasive and the other six were in native vegetation). A total of 151,605 individuals were collected over the sampling period, of which 48,366 individuals (~32%) were found associated with invaded vegetation and 103,239 individuals (~68%) were associated with native vegetation (Table 2). Fourteen springtail species from six families were collected, from a possible 15 known species to occur on the island (Janion-Scheepers *et al.*, 2015) (Fig 2). Of these 14 species, five were invasive and comprised about 36% of the sampled springtails, while nine were native species (~64%, Table 2). These included all the Marion Island endemic species even the rare species such as *Cryptopygus tricuspis* and *Katianna sp.* (Gabriel *et al.*, 2001), which have rarely been found in previous studies (Hugo *et al.*, 2006). Rarefaction curves of sampling effort for springtails across the 12 vegetation types indicated that sampling had reached an asymptote (Figs S1, S2). Sampling was thus considered adequate for the modeling undertaken here.
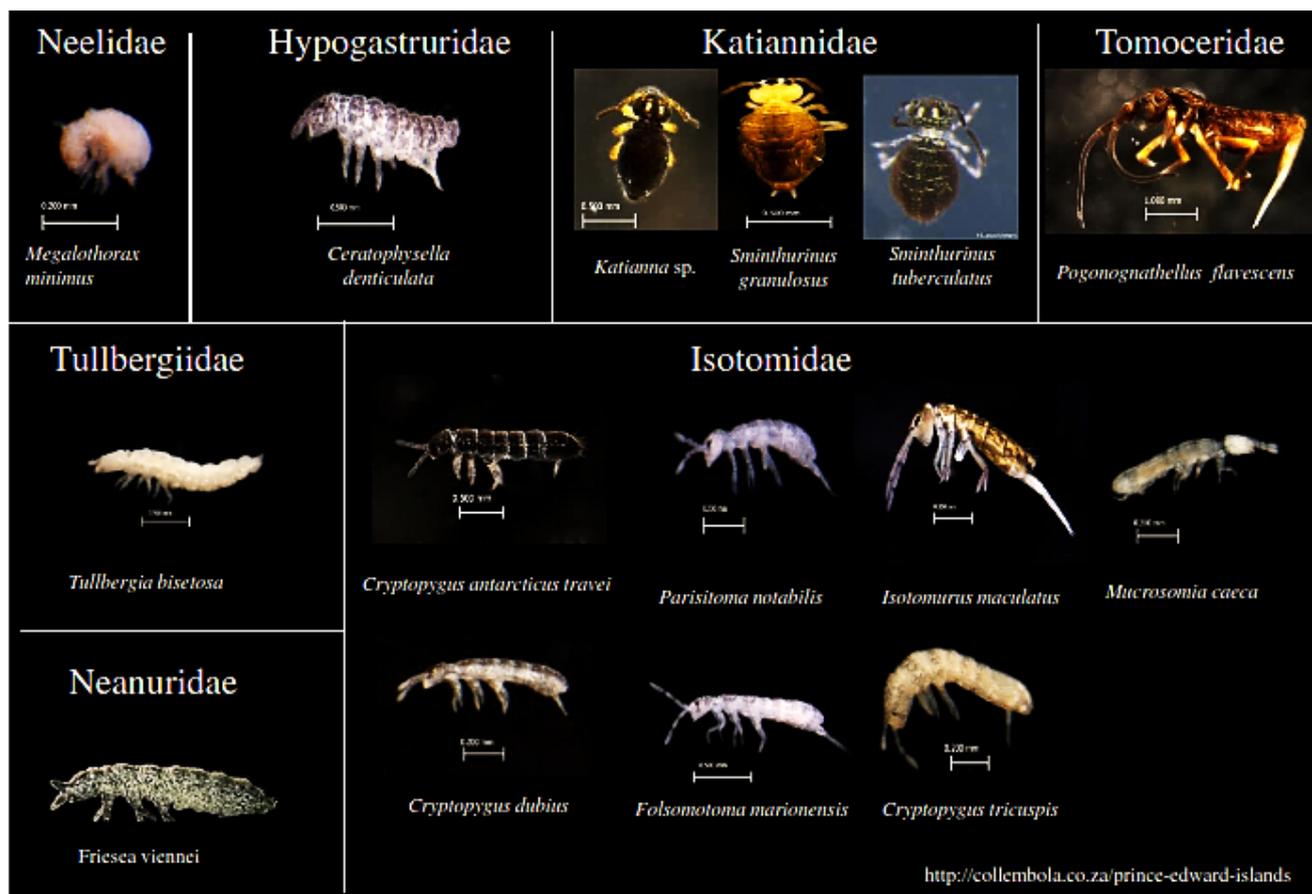
Fig 2. Springtail species found on Marion Island during 2012 to 2013, except for *F. viennei* which was not collected during the trip. All photographs taken by C. Janion-Scheepers.

Springtail abundance was affected by native and invasive vegetation ($F_{(1, 772)} = 4.086$, $p < 0.05$) (Fig. S3) with abundance higher in native vegetation (Table S1). *Ceratophysella denticulata* was the most abundant species in both native and invasive vegetation, while *C. tricuspis*, *M. caeca*, *P. flavescens* and *S. granulosus* were the least abundant. Descriptive statistics revealed that native springtails were most abundant in native vegetation except for *T. bisetosa* that occurred predominantly in invasive vegetation and *F. marionensis* seemed to be abundant in both native and invasive vegetation. While some invasive springtail species such as *C. denticulata* and *I. maculatus* dominated native vegetation, the remaining species were more abundant in invasive vegetation (Table 2).

Table 2. Total springtail abundance per species sampled in invaded and native vegetation on Marion Island during 2012-2013. Invasive springtail species are indicated with an asterisk (*).

Family	Species	Invasive vegetation	Native vegetation
Hypogastruride	*C. denticulata* *	31,471	84,083
Tullbergiidae	*T. bisetosa*	1,832	1,105
Isotomidae	*F. marionensis*	4,719	4,584
	C. dubius	1,474	1,523
	C. antarcticus travei	660	900
	M. caeca	48	120
	C. tricuspis	28	34
	P. notabilis *	1,887	1,288
	I. maculatus *	4,721	7,355
Tomoceridae	*P. flavescens* *	107	26
Neelidae	*M. minimus* *	449	388
Katiannidae	*S. tuberculatus*	167	310
	S. granulosus	42	112
	Katianna sp.	761	1,411

Springtail abundance was significantly different across the 12 vegetation types ($F_{(11,761)}$ = 20.87, p < 0.0001) (Table S2). The invasive coastal *A. stolonifera* (β = 0.30, t = 7.36, p < 0.0001), *C. fontanum* (β = 0.82, t = 2.25, p < 0.001) *P. annua* (β = 0.21, t = 2.34, p < 0.001) and both native *C. plumosa* (β = 0.83, t = 9.20, p < 0.0001) and *P. cookii*/*C. plumosa* (β= 1.02, t = 8.44, p < 0.0001) in coastal areas had significantly higher springtail numbers than S*. procumbens*. While springtail abundance on *Ac. magellanica* dry mire (β = -0.19, t = -2.08, p < 0.001) was significantly less than on *S. procumbens* (Fig. 3a, Table S3).

Springtail diversity was significantly affected by vegetation ($F_{(11, 761)}$ = 8.630, p < 0.0001, Table S2), with high springtail diversity in native *Ac. magellanica* dry mire (β = 1.27, t = -21.88, p<0.0001) (Table S3). In general, the coastal vegetation represented by *P. cookii / C. plumosa*, *C. plumosa*, *A. stolonifera* and *P. annua,* which previously fostered high abundance, now encompasses low diversity (Fig. 3b, Table S3). This coastal vegetation essentially harboured as diverse a springtail community as that of *S. procumbens* (Figure 3b).
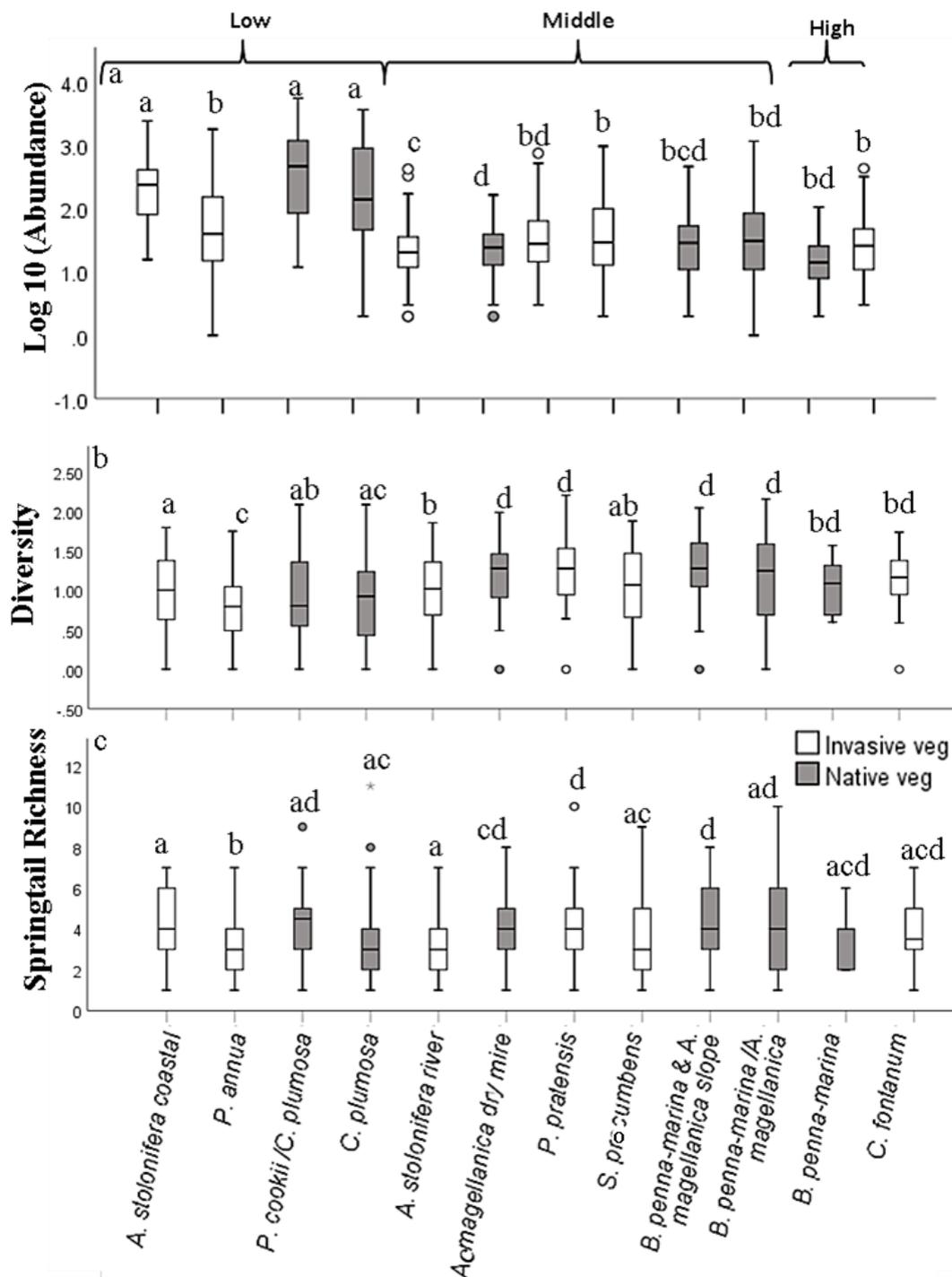
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Fig. 3. Effect of vegetation on springtail abundance (a), species diversity (b) and species richness (c). The lines show the median, the boxes the quartile range and the bars show the interquartile range. Circles depict outliers. Boxes followed by the same letters were not significantly different (p > 0.05) (Dunn's test on ranks following a GLMM). The graphs are divided into three elevation gradients (low = 0-40m, middle = 41-80m and high = 81-110m) shown as categorical groupings for graphical purposes but run as a continuous variable in the models.

Springtail species richness was significantly different across vegetation types ($F_{(11, 761)}$ = 5.79, p < 0.0001) on Marion Island. Springtail species richness was lowest in *P. annua* (β = -1.38, t = -5.15, p < 0.0001) in relation to *S. procumbens*. On average, most sampled vegetation supported between three and four springtail species with the exception of *P. annua* that supported less than three species (Fig. 3c, Table S3).

Altitude had a significant effect on springtail abundance ($F_{(1,761)}$ = 27.37, p < 0.0001), diversity ($F_{(11,761)}$ = 10.17, p < 0.0001) and species richness ($F_{(11,761)}$ = 14.73, p < 0.0001) (Table S2). The output of the model revealed that altitude had negatively affected springtails on Marion Island resulting in a decreased abundance (β = -0.004, t = -5.23, p < 0.0001), species richness (β = -0.002, t = -3.84, p < 0.0001) and diversity (β = -0.002, t = -3.189, p < 0.001) as altitude increased; although, the effect of altitude was not strong (Table S3).

Assemblage composition of springtails across the different vegetation types were distinct (ANOSIM Global R = 0.238, p = 0.001), however their dissimilarity in composition was only 24%. Three distinct assemblages are evident and cluster according to altitude, namely lower, middle and high altitude assemblages (Fig. 4). Springtail diversity was higher at lower and middle attitudes than at high altitude. The majority of invasive springtails are associated with lower altitudes and mostly with the native vegetation *C. plumosa*. Others are strongly associated with *P. pratensis* and *Ac. magellanica* on dry mire. The only invasive springtail species found at high elevation is *P. flavescens* and was associated with invasive vegetation *C. fontanum*.

Fig. 4. Loading of axis 1 and 2 according to PCoA showing the total variance (79.6%) in springtail assemblage on Marion Island (stress = 0.03). Springtail assemblages correlate with trajectory overlay based on Pearson correlations (r > 0.3). Legend ▼ = lower altitude, ▲ = middle altitude and ■ = high altitude. Vegetation abbreviations; ASc* = *A. stolonifera* coastal, PC/CP = *P. cookii / C. plumosa*, ASr* = *A. stolonifera* river, BL & Ac Ms = *B. penna-marina* & *Ac. magellanica* on slope, SP = *S. procumbens*, BL & AcM = *B. penna-marina* & *Ac. magellanica*, PP* = *P. pratensis*, CP = *C. plumosa*, PA* = *P. annua*, AMdm = *A magellanica* on dry mire, CF* = *C. fontanum*, BL = *B. penna- marina*. The asterisks denote invasive species.

Discussion

The springtails collected were associated with both invasive and native vegetation encompassing the eastern to southern parts of the island. This supports previous studies that found both native and invasive springtails occupied these vegetation types on Marion Island (Gabriel *et al.*, 2001, Hugo *et al.*, 2004, Treasure & Chown, 2013). Native vegetation had more springtails in terms of abundance and species richness than invasive vegetation. These finding agree with studies done elsewhere, which showed that native vegetation had higher springtail species richness than invasive vegetation (Maunsell *et al.*, 2013). There was a greater number of springtails found in lower lying coastal areas consisting of native *C. plumosa*, *P. cookii* and invasive *A. stolonifera* coastal vegetation which is most likely due to the influence of increased litter composition and nutrient quality in these biologically influenced sites (Smith & Steenkamp, 1990). Litter composition and nutrient quality are known to influence springtail abundance (Hopkin, 1997, Badejo *et al.*, 1998, Rusek, 1998). However, this coastal vegetation was dominated by cosmopolitan invasive springtail species *I. maculatus* and *C. denticulata*.

The pattern of invasive springtails associating more with native vegetation is largely driven by the high abundance of *C. denticulata*. *C. denticulata* may well have displaced native springtails as observed for *Hypogastrura viatica*, another species from the same family (Hypogastruridae), which is invasive on other sub-Antarctic islands (Bellinger *et al.*, 2018, Convey *et al.*, 1999, Greenslade, 2002, Frenot *et al.*, 2005, Terauds *et al.* 2011). *Hypogastrura viatica* is likely to have caused a reduction of native species richness on those islands (Terauds *et al.*, 2011, van Hengstum *et al.*, 2014). Species from this family are known for being a highly invasive species and commonly dominate areas they invade (see Greenslade, 2002).

In this study I found strong relationships between the composition of plant species and springtails on the island. This may simply result from both groups independently responding to the strong environmental gradient associated with elevation (García-Gómez *et al.*, 2011, Maunsell *et al.*, 2013). At the larger scale, it is clear that both native and invasive springtails respond strongly to altitude. The increase in altitude results in decreased springtail abundance and richness irrespective of whether the species is native or invasive. The PCoA showed that most indigenous springtail

species on the island are found in cooler, mid-altitude habitats with the exception of *F. marionensis*, *M. caeca* and *C. dubius* which prefer lower lying habitats. These three Isotomidae species could have adjusted to the ample food source and microclimate offered by the biotic complex and invasive plants (Usher & Booth, 1984), or they may have physiological adaptations enabling them to survive these conditions (Janion *et al.,* 2010). While most invasive springtails prefer warmer coastal habitats, *P. flavescens* and *M. minimus* were found in higher altitudinal habitat. The presence of *P. flavescens* at this higher altitude is surprising, as this species was previously only found in one coastal site at Kildalkey bay (Treasure & Chown, 2013).

Springtail responses to changes in temperature and humidity seem to differ between invasive and indigenous species. For example, invasive species on Marion Island tend to have a higher egg hatching success and egg development rate than indigenous species (Janion et al. 2010). This implies that changes in soil microclimate due to climate change might lead to new soil invertebrate community assemblages, where both overall abundances and layer-specific species composition could change on the island (Slabber *et al*., 2007, Chown *et al*., 2007, Meehan *et al*., 2010, Krab *et al*., 2013). With increased climatic warming, it is possible that this change could favour particular invasive species as they can tolerate dry and warmer conditions better than native species (Chown *et al*., 2007, Treasure & Chown, 2013).

In conclusion, the present study has demonstrated that invasive and native plant communities influence the distribution of both native and invasive springtails respectively. Springtail species are found in higher abundance in vegetation types in the lower laying parts of the island than in the interior parts of the island. Our study indicates that richness and diversity may respond differently to local-scale environmental factors such as altitude. Invasive springtails such as *P. flavescens*, *M. minimus*, *C. denticulata* and *I. maculatus* together with invasive plants such as *C. fontanum* and *S. procumbens* have increased their distribution along the cooler boundaries of the island due to rising temperatures associated with current global climate change. The increase in altitudinal distribution of invasive vegetation is of great concern as these species may cause a decline in native vegetation, outcompeting native plants with large stands of *C. fontanum*, *S. procumbens* and coastal *A. stolonifera* already present along the altitudinal gradient (le Roux & McGeoch 2008).

The impact of invasive springtails on native species is poorly understood, and should be experimentally tested.

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Supplementary Material

Fig. S1: Sample-based rarefaction curves of springtail assemblages in each invasive vegetation sampled. (A) *A. stolonifera* coastal, (B) *A. stolonifera* river, (C) *C. fontanum*, (D) *P. annua*, (E) *P. pratensis*, (F) *S. procumbens*. The number of expected species from samples collected over a year (S est, shown in blue); Chao 1 richness estimator (Chao1 mean shown in red); Bootstrap (Bootstrap mean shown in green) are presented above.

Fig S2: Sample-based rarefaction curves of springtail assemblages in each native vegetation sampled. Notes; (A) *Ac magellanica* dry mire, (B) *B. penna-marina*, (C) *B. penna-marina* / *Ac. magellanica*, (D) *B. penna-marina* & *Ac magellanica* on slope, (E) *C. plumosa*, (F) *P. cookii* & *C. plumosa*. The number of expected species from samples collected over a year (S est, shown in blue); Chao 1 richness estimator (Chao1 mean shown in red); Bootstrap (Bootstrap Mean shown in green) are presented above.

Fig S3: The influence of native and invasive vegetation on the $\log_{10}$ abundance of different species of springtail. The lines show the median, the boxes the quartile range and the whiskers show the interquartile range. Boxes followed by different letters were significantly different (P < 0.05) (Dunn's test on ranks).

Table S1: The effect of vegetation on springtail abundance. Output from a Generalized Linear Mixed Model that used native vegetation to compare with invasive vegetation.

Springtail	Log 10 Abundance			
Coefficients	β	SE	t	*P*-value
Intercept	1.706	0.036	47.614	***
invasive vegetation	-0.102	0.051	-2.021	0.44

* P< 0.05, ** P<0.001, *** P<0.0001

Table S2: Generalized Linear Mixed Models fixed effect results of springtail log abundance, species richness and diversity.

Mode l	Predictors from model	df1	df2	F-value	*P*-value
Springtail log 10 abundance					
	Intercept	12	761	30.68	***
	Vegetation	11	761	20.87	***
	Altitude	1	761	27.37	***
Springtail species richness					
	Intercept	12	761	5.71	***
	Vegetation	11	761	5.79	***
	Altitude	1	761	14.73	***
Springtail diversity					
	Intercept	12	761	7.98	***
	Vegetation	11	761	8.63	***
	Altitude	1	761	10.17	***

* P< 0.05, ** P<0.001, *** P<0.0001

Table S3: The effects of altitude and vegetation on springtail abundance, richness and diversity. Outputs from Generalized Linear Mixed Models used *S. procumbens* to compare with other vegetation types. * P< 0.05, ** P<0.001, *** P<0.0001. Invasive plant species are indicated with an asterisk (*).

Springtail	Abundance				Richness				Diversity			
Coefficients	β	SE	t	*P*-value	β	SE	t	*P*-value	β	SE	t	*P*-value
Intercept	1.55	0.07	21.33	***	-1.357	0.27	-1.31	0.19	-0.19	0.06	-2.50	*
Altitude	-0.004	0.001	-5.232	***	-0.001	0.002	-3.84	***	-0.002	0.001	-3.18	**
A. stolonifera coastal	0.30	0.11	7.36	***	-0.21	0.31	-0.68	0.49	-0.23	0.08	-2.70	**
*A. stolonifera river**	-0.07	0.09	-0.67	0.50	-0.57	0.28	-2.02	*	-0.13	0.07	-1.71	0.08
B. penna-marina	0.02	0.12	1.16	0.8	0.08	0.37	-0.20	0.84	0.01	0.10	1.11	0.91
B. penna-marina & *Ac. magellanica* on slope	0.06	0.09	0.6	0.53	0.44	0.29	1.55	0.12	0.08	0.08	1.13	0.56
B. penna-marina & *Ac. magellanica*	0.17	0.097	1.87	0.06	0.40	0.27	1.48	0.13	0.04	0.07	0.59	0.55
*C. fontanum**	0.82	0.12	2.25	**	0.24	0.36	0.66	0.51	0.05	0.101	0.57	0.14
C. plumosa	0.83	0.09	9.20	***	-0.50	0.26	-1.90	0.50	-0.173	0.076	-2.356	**
*P. annua**	0.21	0.09	2.34	**	-1.38	0.26	-5.15	***	-0.46	0.08	-6.27	**
P. cookii & *C. plumosa*	1.02	0.10	8.44	***	-0.04	0.32	1.13	0.89	-0.28	0.08	-3.30	***
*P. pratensis**	0.141	0.08	1.49	0.11	0.133	0.26	0.51	0.61	-0.02	0.074	-2.50	0.01
Ac. magellanica dry mire	-0.193	0.093	-2.08	**	4.41	0.213	20.69	***	1.27	0.06	21.88	***

Chapter 3

The impact of invasive and native vegetation and altitude on springtail species on sub-Antarctic Marion: Application of the hurdle model.

Abstract

Invasive plants can disrupt a range of trophic interactions in native communities. Invasive plants can also affect the behaviour of native insects, and as a novel resource have the potential to affect the performance of native springtails either positively or negatively. Studies that compare insects on related native and invasive plants in invaded habitats show that abundances are often lower on invasive plants. In this study, I investigated the influence of both native and invasive vegetation, as well as altitude, on the distribution of springtail species on Marion Island. Hurdle Models, which are two-part statistical models that are effective in dealing with zero-inflated data with over-dispersion (negative binomial) or without (Poisson distribution), were used to investigate the abundance of each springtail species across vegetation and altitude. Invasive springtails such as *Ceratophysella denticulata*, *Iostomurus maculatus* and *Parisotoma notabilis* associated with native vegetation and showed a shift in altitudinal distribution suggesting that invasive springtails will respond more favourably to climate change. The shift of more common springtail species to introduced and/or native vegetation will impact rare native springtail species that are failing to adapt to the change in micro-environments and unable to compete with invasive springtails for resources. Furthermore, with the rise in temperature on Marion Island it is evident that invasive springtail ranges have expanded upwards and are no longer restricted to the island's lowlands.

Introduction

Studies in biological invasions have expanded rapidly over the last 30 years. Belowground invasions have generally received little attention, except for earthworms (Hendrix *et al.*, 2008; Ferlian *et al.*, 2018), which have received attention mainly due to their large body size and their important role as soil ecosystem engineers (Porco *et al.*, 2013). However, smaller-bodied invaders, such as springtails, have not received the same level of attention (Porco *et al.*, 2013). Biological invasions by springtails have been documented worldwide (Hopkin, 1997), yet their impact on habitats are not well documented in spite of their ecological significance (Hopkin, 1997).

To date, invasive springtails have been identified from several sub-Antarctic Islands, such as Macquarie Island (Greenslade & Wise 1984, Gabriel *et al.*, 2001; Greenslade 2002, Greenslade 2008), Marion Island (Myburgh *et al.*, 2007; Janion-Scheepers *et*

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al., 2015), Crozet and Kerguelen (Deharveng 1981) and South Georgia (Convey *et al*., 1999; Greenslade & Convey, 2012). One problem in recognising invasive springtails is the lack of taxonomic expertise (Decaëns *et al*., 2006). This is further exacerbated by the fact that the factors determining diversity, distribution, and abundance of springtails remain unclear.

It is likely that a combination of several abiotic factors; such as vegetative cover, soil type, moisture, temperature, nutrient status and elevation may determine springtail species distributions (Hopkin, 1997). For example, species elevation ranges have shifted over the last several decades due to changes in precipitation and temperature regimes (Kelly & Goulden, 2008, Felde *et al*., 2012). Furthermore, species richness often peaks at low to mid-elevations and decreases rapidly at higher elevations. Invasive springtails in non-native habitats have been shown to competitively exclude certain native species (Convey *et al*., 1999; Terauds *et al.,* 2011), perhaps due to their ability to adapt to warmer and drier conditions (Chown *et al.,* 2007; Slabber *et al*., 2007). Habitat filtering and dispersal limitation may drive rapid species turnover along elevation gradients (Kraft *et al*., 2011, Swenson *et al*., 2011, Bello *et al*., 2013). Thus, understanding which environmental factors influence invasive species distribution patterns would inform projections for shifts in their distributions, given current climate change scenarios.

Altitude is an important parameter to understand the distribution and diversity of invasive organisms (Maunsell *et al*., 2013). Groups such as vascular plants, birds, mammals, and ants show a clear decrease in species diversity and abundance with an increase in altitudinal gradient (Heaney, 2001, O'Donnell & Kumar, 2006). In contrast, edaphic micro-arthropods such as springtails show an increase in diversity with elevation, up to a threshold beyond which there is a significant decrease (Sadaka & Ponge, 2003, Jing *et al*., 2005, Cutz-Pool *et al*., 2010). Globally invasive plants are increasing their distribution in altitude globally (Rintoul *et al*., 2018), which may impact below ground arthropod native assemblages such as springtail. Thus, investigating the distribution of biological invasive species along elevation gradients has important implications for understanding the mechanisms determining community assembly (Pauchard & Alaback, 2004; Pauchard *et al*., 2009; Alexander *et al*., 2011, Pyšek *et al*., 2011).

Habitat filtering is defined broadly, as a process of deletion by which the environment acts as a filter, for example climatic conditions, disturbance regime and biotic interactions, removing species which lack traits for persisting under a particular set of conditions (Keddy, 1992, Diaz *et al.*,2016). Habitat filtering is an important process that shapes ecological communities, and arises from species–habitat niches, or the inability of a species to persist in all environments (Baldeck *et al.*, 2013), and can limit native plant species composition along elevation gradients (Alexander *et al.*, 2011). Habitat filtering has also been identified as a key process in determining compositional changes with elevation for non-native species. Generally, invasive species' populations are highest near lowland anthropogenic sources on Islands, with invasive species richness decreasing with an increase in elevation (Alexander *et al.*, 2011). Steinbauer *et al.* (2016) indicated in their study that extreme climatic conditions typical of high-elevation ecosystems prevent the establishment of non-native species. Hence, it is probable that the majority of invasive species are pre-adapted to mid- or low elevations, while those found at high altitude are specialists and can tolerate a wide range of climatic conditions.

Marion Island has a high representation of globally successful invaders, including one mammal species (*Mus musculus*), several plant species, such as *Agrostis stolonifera* and *Sagina procumbens* (le Roux *et al.*, 2013) and invertebrate species (Frenot *et al.*, 2005). The distribution of invasive springtails on Marion Island has been examined along an altitudinal gradient and the pattern that emerges is a decline in species richness as a function of the interaction between elevation and linear distance from the coast, with highest non-native species richness in the coastal area which is the point of alien introductions (Barendse & Chown, 2001, Gabriel *et al.*, 2001, Hugo *et al.*, 2006, Janion *et al.*, 2010, Treasure and Chown, 2013). Most invasive species on the island are restricted to 50 meters above sea level near huts and the experimental base, both of which are influenced by human and animals (le Roux et al., 2013). The influence of habitat complexes on the distribution of specific springtail species and to what extent environmental variables, such as altitude, affect their distribution on Marion Island has been studied by Gabriel *et al.*, (2001). They found that disturbed areas, especially nutrient rich regions, host more invasive springtail species and abiotic factors such as altitude significantly influence invasion by springtails. They did

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not, however, specifically investigate the relationship between invasive plants and the springtail fauna. This study aims to do so. Specifically, I investigate: 1) the influence of invasive and native vegetation on individual springtail species abundance and, 2) to what extent altitude affects their distribution on Marion Island.

Material and methods

Study site

Marion Island has two major biomes: tundra, which predominates in lowland areas, and polar desert, restricted to high elevations (Smith & Mucina 2006, Gremmen & Smith 2008). Within those biomes the island supports a broad array of habitats ranging from high altitude polar fellfield, devoid of most vegetation, to lush, nitrophilic tussock grasslands surrounding coastal seabird and seal colonies. The climate on Marion Island is cool, wet and windy, with limited seasonal temperature variation and high annual precipitation (Gremmen & Smith, 2008). Thus, low and high temperatures (in the context of local ranges of variability) can occur at any stage of the year, and warm periods in winter and cold periods in summer are common (Deere & Chown 2006). Marion Island receives precipitation as rainfall, snow, hail and mist, with some form of precipitation falling on most days and total annual precipitation averaging 1 975 mm. Rainfall is the dominant form of precipitation at lower altitudes (Schulze, 1971). Rainfall events of ≤ 5 mm and > 5 mm occur on roughly 45% and 35% of days, respectively (le Roux & McGeoch 2008). Relative humidity is high on the island (averaging 80%), although short periods (usually < 5 hours) of low (< 50%, even dropping below 20%) humidity can occur due to Föhn winds (Schulze, 1971). Similarly, the island's narrow mean daily temperature range of only 1.9ºC corresponds with the low amplitude of the daily temperature cycle in the surrounding open ocean (Schulze, 1971). Chapter 1 provides further details on the study site.

Sampling

Springtails were sampled on the island in a wide range of habitat complexes at different altitudes; from the coastal to the fellfield habitat complexes (see Table 1). Altitude was recorded for each sampling site using a GPS (Garmin Etrex). Within habitat complexes, twelve vegetation types were sampled; six having invasive vegetation and the remaining six, native vegetation (see Chapter 1 for sampling details). Springtail and all other arthropods sampled were obtained from the soil using

an O' Connor split-corer (Southwood, 1978, see Chapter 1) and in the laboratory, invertebrates were extracted from the soil cores using a modified MacFadyen high-gradient extractor (Stellenbosch University Engineering Department, Stellenbosch, South Africa) for two days at 25°C followed by two days at 30°C (see MacFadyen, 1953, Gabriel *et al.*, 2001). Springtails were extracted into 96% ethanol and were sorted into morphospecies using a binocular dissecting microscope (Leica M80).

Table 1: Sampled habitat complexes with vegetation type showing highest location of distribution, and altitude classifications (low = 0-40m, middle = 41-80m and high = 80-110m), where springtails were sampled on Marion Island. *Indicates invasive species

Habitat complex	Vegetation	Highest distribution of vegetation	Altitude classifications
Biotic and salt spray	*Poa cookii /Cotula plumosa*	20	Low
	C. plumosa	30	
	Poa annua*	20	
	Agrostis stolonifera coastal*	17	
Mire and slope	*Agrostis magellanica* on dry mire	49	Middle
	Blechnum penna-marina /Acaena magellanica	57	
	A. stolonifera river*	42	
	Sagina procumbens*	51	
	*Poa pratensis******	49	
	B. penna-marina & *Ac. magellanica* on slope	53	
Fellfield	*B. penna-marina*	104	High
	Cerastium fontanum*	105	
Polar desert	N/A	N/A	Very high

Species were identified using available keys (Gabriel, 1999) and in consultation with taxonomic experts. All specimens were counted and the total counts were used as the final units of analysis. Voucher specimens will be deposited at the Iziko South African Museum, Cape Town. The vegetation complexes were assigned to one of three

altitude categories, depending on the altitude at which sampling occurred, and were arbitrarily divided into low (0-40 m), medium (41-80 m) and high (81 -110 m) respectively on Marion Island.

Statistical analyses

The difference in distribution and abundance of each springtail species (n=14) was analysed independently across the 12 vegetation types. The distribution and abundance of each springtail species was also analysed according to plant status (i.e. native or invasive). Zero-inflated negative binomial and Poisson hurdle models were fitted to the data using the pscl and lmtest packages in R version 3.1.3. Hurdle Models are a two-part statistical model and have been found most effective to cope with zero-inflated data with over-dispersion (negative binomial) or without over-dispersion (Poisson distribution) (Zuur *et al.*, 2009, Hu *et al.*, 2011). The first part of the model describes the probability of observing the specific species at all and the second part analyses the nonzero values treating the zeros as censored data (Martin *et al.*, 2005). Descriptive statistics were used to determine springtail species richness based on their occurrence at the study sites. This was done according to the following criteria: R = rare: species occurred in 1-10 sampled sites, I = intermediate: species occurred in 11-50 sampled sites and C = common: species occurred in 51-100 sampled sites (Table 2) (see Brand & Dunn, 1998).

Results

Fourteen springtail species were identified during the sampling period. Six of the 14 species found across the twelve vegetation types were intermediate in occurrence, namely, *Tullbergia bisetosa, Cryptopygus antarcticus travei*, *Parisotoma notabilis*, *Cryptopygus dubius*, *Megalothorax minimus* and *Katianna* sp. The two most common species found were invasive species, *Ceratophysella denticulata* and *Isotomurus maculatus*, while the native *Folsomotoma marionensis* contributed ~6% of all springtails sampled and was found in all sampled vegetation on the island (Table 2). Of the 14 springtail species, five were rare, with *Pogonognathellus flavescens* being the only invasive species found in low numbers (Table 2, Fig 1).

Table 2: Springtail occurrence across all the sampled sites on Marion Island dependent on the number of sites in which they occurred (common, intermediate, rare), and the mean species abundance ±SE for those sites in which the species occurred. *Indicates invasive species.

Springtail species	Common	Intermediate	Rare	Mean abundance	Std. error
C. denticulata*	+			1806	17.279
T. bisetosa		+		47	0.568
F. marionensis	+			148	1.217
C. dubius		+		48	1.119
C. antarcticus travei		+		24	0.316
M. ceacus			+	3	0.069
C. tricuspis			+	1	0.028
P. notabilis*		+		50	0.646
I. maculatus*	+			190	1.431
P. flavescens*			+	2	0.051
M. minimus*		+		30	0.376
S. tuberculates			+	8	0.095
S. granulosis			+	2	0.044
Katianna sp.		+		34	0.271

Invasive species

The presence of invasive springtails *C. denticulata* (β = -0.035±0.002, Z = -13.73, p ≤ 0.0001), *P. notabilis* (β = -0.02±0.002, Z = -5.8, p ≤ 0.0001) and *I. maculatus* (β = -0.014±0.001, Z = -12.17, p ≤ 0.0001) are negatively affected by altitude, meaning that it is less likely to find these species as altitude increases (Table 3). These three invasive species largely occupy lower altitude habitats (Fig. 4 in Chapter 2). The abundance of *C. denticulata* was only high in lowlands, with few springtails found along the altitudinal gradient (β =-0.036±0.003, Z =-9.71, p ≤ 0.0001, Table 3, Fig. 1a). Springtail abundance of *I. maculatus* was highest at low altitude and declined with increased altitude (β = -0.02±0.001, Z = -11.91, p ≤ 0.0001, Table 3, Fig 1b). *Parisotoma notabilis* was occasionally found at high altitude, and when present, their abundance was relatively high (Fig. 1c). Overall, *P. notabilis* abundance was not affected by altitude (β = -0.003±0.002, Z= -1.32, p = 0.185, Table 3, Fig. 1c).

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The different vegetation types influenced the presence of *P. notabilis* across sampling sites, except for *A. stolonifera* river and *B. penna-marina* & *Ac. magellanica* where there was a low likelihood of finding this springtail species, with no record from *B. penna-marina* (Table S1, Fig. 1c). This species is found in both native and invasive vegetation respectively, however, the abundance of *P. notabilis* is positively influenced by native vegetation (β = 2.11±0.16, Z = 12.67, p ≤ 0.0001, Table 3, Fig. 1c). Similarly, the presence of *I. maculatus* was affected by vegetation types, except for *S. procumbens*, where its presence was not significantly influenced by this vegetation type (β = 0.27±0.16, Z = 1.66, p = 0.08). *I. maculatus* had a very low probability of being found in *B. penna-marina* (β = -0.05±0.23, Z = -0.22, p ≤ 0.001), *Ac. magellanica* on dry mire (β = -0.52±0.17, Z = -3.1, p ≤ 0.001) and S. pratensis (β = -0.38±0.16, Z = -2.28, p ≤ 0.05, Table S1, Fig. 1b). *Isotomurus maculatus* was generally more predominant in native vegetation (β = 0.366±0.069, Z = 5.27, p ≤ 0.0001) than in invasive vegetation (Table 3). The abundance of *I. maculatus* is low in *B. penna-marina* and *P. pratensis* compared to that of *Ac. magellanica* on dry mire but marginally so. The greatest number of *I. maculatus* was associated with *A. stolonifera* (coastal), *C. plumosa*, *P. annua* and *P. cookii*/*C. plumosa* (Table S1, see Fig. 1b).

Ceratophysella denticulata was more likely to be associated with low altitude vegetation and found in high numbers in low lying vegetation (Table S1). Its abundance was found to be lowest in *C. penna-marina* (β -2.71±0.83, Z = -3.28, p ≤ 0.001) and *C. fontanum*, another high-altitude plant (Fig 1a, Table S1). Moreover, the species is abundant in both native and invasive vegetation, with numbers decreasing in invasive vegetation (Table 3). These data suggest that most invasive springtails on Marion Island prefer lower lying coastal vegetation and are as likely to associate with native and invasive vegetation at this altitude. Indeed, invasive springtail species that were classified as common and intermediate were more likely to inhabit vegetation found in lower habitat complexes than high altitude complexes, such as coastal *A. stolonifera, C. plumosa* and *P. cookii* /*C. plumosa* and *P. annua* (Table S1, Fig 1), where they reached large populations. Invasive *P. flavescens* and *M. minimus* could not be analysed using hurdle models, due to their low species count (Table 3). However *M. minimus* was most abundant in mid-altitude vegetation complexes, particularly in *B. penna-marina* and *Ac. magellanica* on slope and *B. penna-marina* &

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Ac. magellanica (Fig 1d). The invasive springtail, *P. flavescens*, was described as rare and found in extremely low numbers and in contrast to the common invasive springtails, was most prevalent at high altitude in *C. fontanum* vegetation (Fig 1e).

Native species

Native *F. marionensis* and *C. dubius* are likely to inhabit all vegetation types compared to *B. penna*-marina & *Ac. magellanica* on slope, with high abundance of *F. marionensis* in most costal and high altitudinal vegetation (Table S2, Fig. 2f). *C. dubius* was found abundantly in lowland *C. plumosa* (β = 3.24±0.54, Z = 6.03, p ≤ 0.001) and *P. annua* (β = 2.97±0.63, Z=4.74, p ≤ 0.001), *P. cookii /C. plumosa* (β = 1.52±0.57, Z = 2.66, p ≤ 0.001) and mid-altitude *S. procumbens* (β = 2.67±0.55, Z=4.88, p ≤ 0.0001, Table S2, Fig 2n). *C. antarcticus travei was significantly more abundant in native Ag. magellanica on dry mire (β = 1.44±0.41, Z = 3.49, P ≤ 0.0001) and S. procumbens (β = 2.59±0.54, Z = 4.78, P ≤ 0.0001) than in other vegetation types (Table 4, Fig. 2h). The species is, however, also present in other vegetation types, including both native and invasive vegetation (β = -9.971±56.47, Z = -0.18, P = 0.85, Table 4). This species is present on *B. penna-marina* and *Ac. magellanica* on slope, *Ag. magellanica* on dry mire, *C. fontanum*, *A. stolonifera* river, *C. plumosa*, *P. pratensis,* and *B. penna-marina* (Table S2, Fig. 2h).
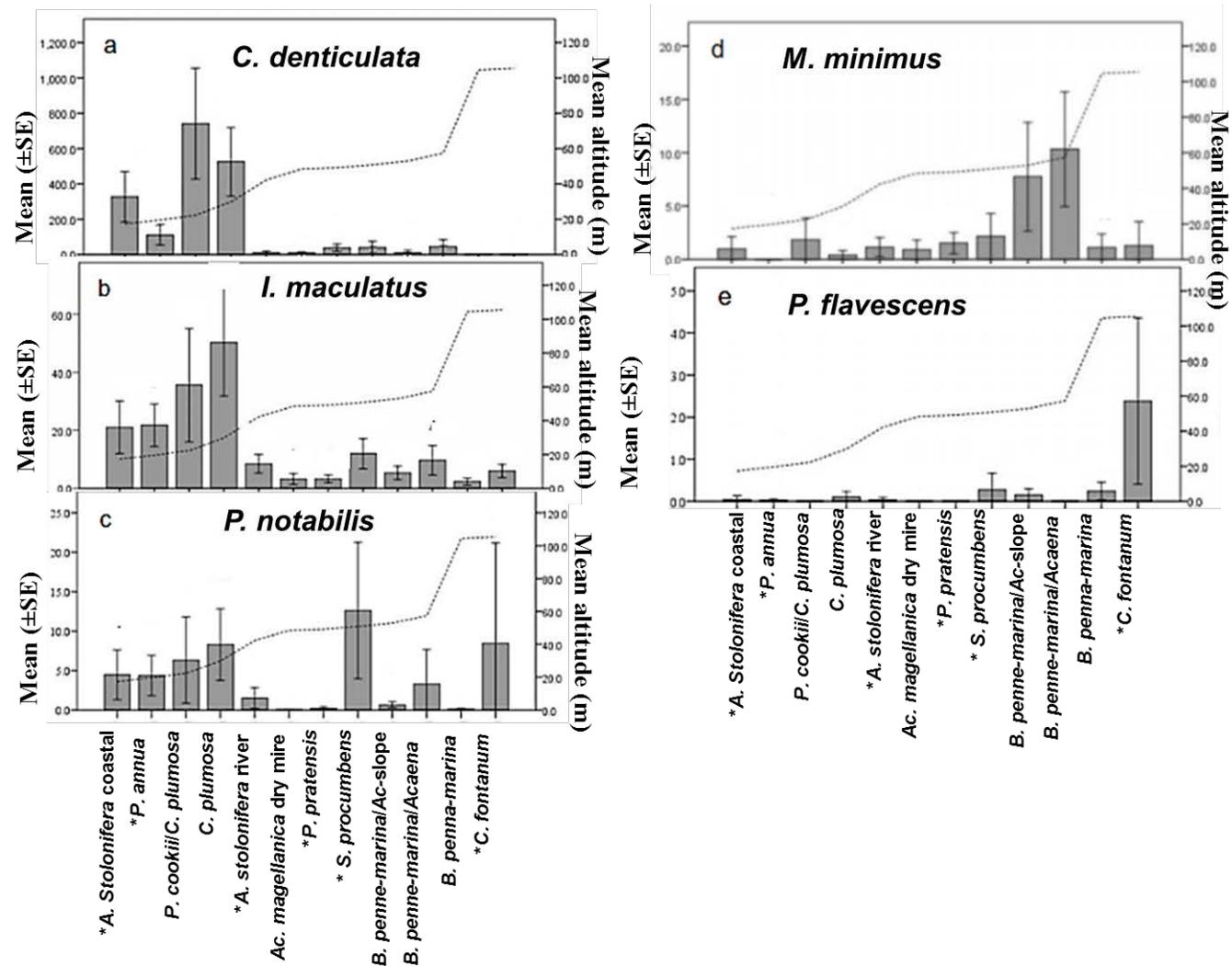
Fig. 1: Mean abundance (±SE) of the invasive springtail species present on Marion Island across the 12 vegetation types and the influence of altitude on these springtails. The stipple line represents mean altitude from the lowest to the highest point. Invasive vegetation types are denoted with an asterisk.

Table 3: Hurdle models of each invasive springtail species abundance with environmental variables per plant status. * indicates P < 0.05, **P < 0.001, ***P < 0.0001.

		C. denticulata			*I. maculatus*			*P. notabilis*		
		Estimate ± SE	Z statistic	*P*	Estimate ± SE	Z statistic	*P*	Estimate ± SE	Z statistic	*P*
Count model coefficients	Intercept (Invasive veg)	-1.103±0.152	-8.123	***	-0.59±0.09	-6.37	***	0.104±0.16	0.61	0.53
	Native vegetation	5.45±0.152	35.7	***	1.571±0.212	7.38	***	2.11±0.16	12.67	***
	Altitude	-0.036±0.003	-9.71	***	-0.02±0.001	-11.91	***	-0.003±0.002	-1.32	0.19
	Log (theta)	-1.869±0.135	-13.77	***	-2.057±0.26	-7.82	***	-0.795±0.19	-4.04	***
Zero hurdle model coefficients	Intercept	-0.2±0.07	-2.62	**	-0.102±0.06	-1.54	0.123	0.306±0.12	2.48	**
	Native vegetation	0.565±0.102	5.535	***	0.366±0.069	5.27	***	-2.038±0.14	-14.72	***
	Altitude	-0.035±0.002	-13.73	***	-0.014±0.001	-12.17	***	-0.02±0.002	-5.8	***
Theta: count		0.154			0.1278			0.4515		
Log likelihood		-7700			7076			-1995		
AIC		15414.11			14166.57			4004.083		

		P. flavescens			*M. minimus*		
		Estimate ± SE	Z statistic	*P*	Estimate ± SE	Z statistic	*P*
Count model coefficients	Intercept (Invasive veg)	1.75±0.48	3.58	***	-0.26±0.17	-1.46	0.14
	Native vegetation	-0.206±0.55	-0.37	0.71	2.40±0.138	17.3	***
	Altitude	-0.004±0.006	-0.71	0.47	0.001±0.002	0.38	0.70
	Log (theta)	0.074±0.72	0.10	0.91	0.055±0.16	0.32	0.74
Zero hurdle model coefficients	Intercept	0.47±0.32	1.46	0.14	-0.94±0.17	-5.33	***
	Native vegetation	-5.20±0.32	-16.22	***	-2.69±0.14	-18.22	***
	Altitude	0.007±0.003	2.10	*	-0.001±0.002	-0.63	0.53
Theta: count		1.0772			1.057		
Log likelihood		-294.1			-1224		
AIC		602.2007			2462.047		

Katianna sp. inhabited both native and invasive vegetation types sampled (Table 4, Fig 2k), but were found in very low numbers. The presence of the native springtail species *M. ceacus* was less widely distributed but also found in low numbers and this species was mostly associated with *C. plumosa* (Fig. 2i), a low altitude coastal plant (Table S2 and see also Fig. 4 in chapter 2). The native species, *S. tuberculatus* was rare and had low probability of being present within native vegetation (β=-1.84±0.093, Z=-19.67, P ≤ 0.001, Table 4). *S. tuberculates* was found in particularly low numbers in *A. stolonifera* river, *C. plumosa, P. pratensis*, *B. penna-marina*, *S. procumbens*, *C. fontanum* and *P. cookii /C. plumosa* (Fig. 2m, Fig. S2).

Invasive vegetation affected the presence of *T. bisetosa* positively, with this species less likely to be found in native vegetation (β = -1.804±0.07, Z = -22.97, p ≤ 0.0001, Table 4, Fig. 2g). *Tullbergia bisetosa* is abundant in invasive vegetation (β = 0.97±0.15, Z = 6.37, p ≤ 0.0001, Table 4) and is positively influenced by invasive *P. pratensis*, *C. fontanum* and *A. stolonifera* river and native *B. penne-marina* (Table S2, Fig 1g). The two rare native species, *C. tricuspis* and *S. granulosus*, were restricted to very low numbers, with *C. tricuspis* present in both native and invasive vegetation (Fig 2j). *S. granulosis* was more evenly distributed across the sampled sites (Fig. 2l). A caveat to these results is that model outputs for those species with very low numbers are less robust than for those species that were found in higher abundance.
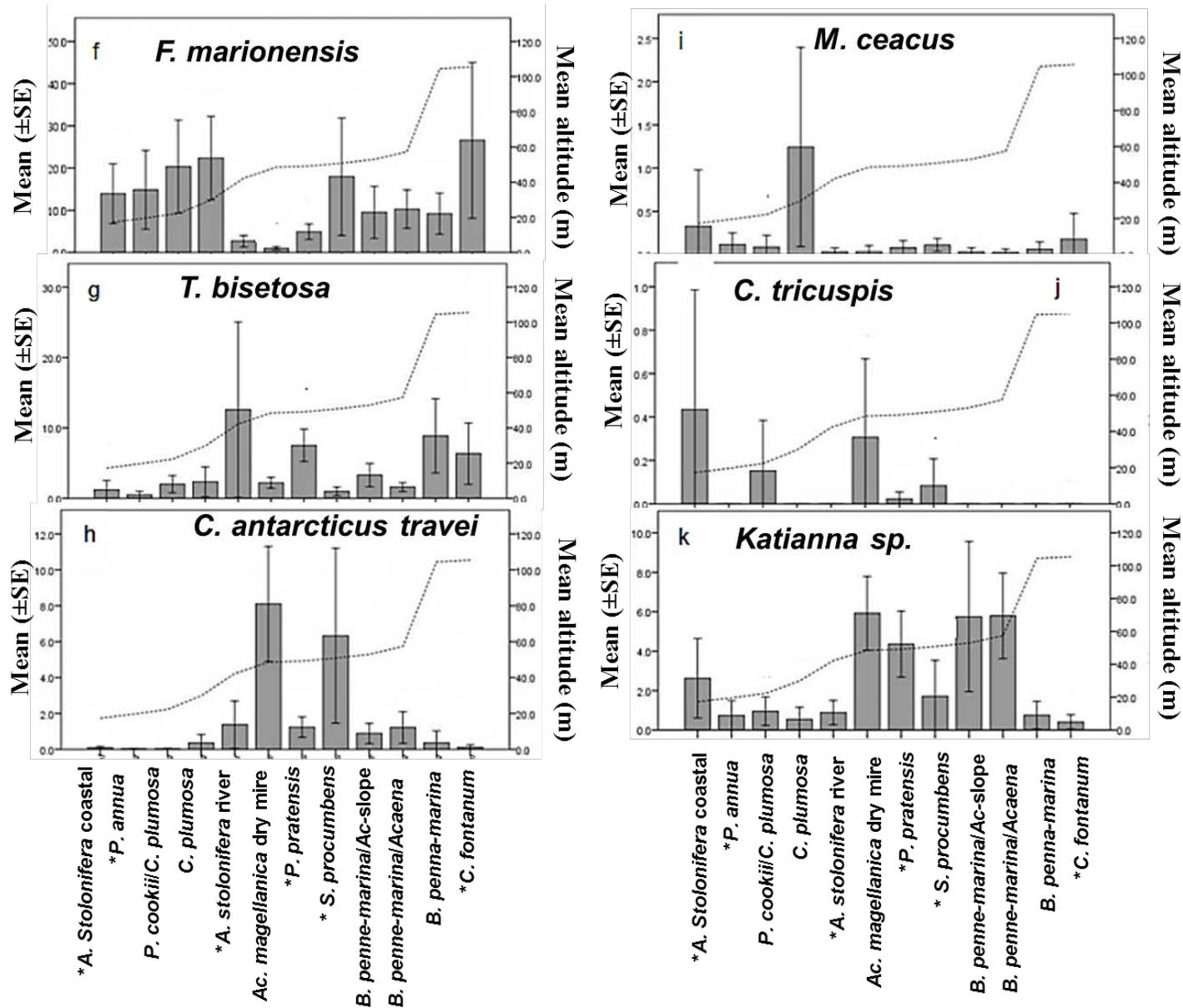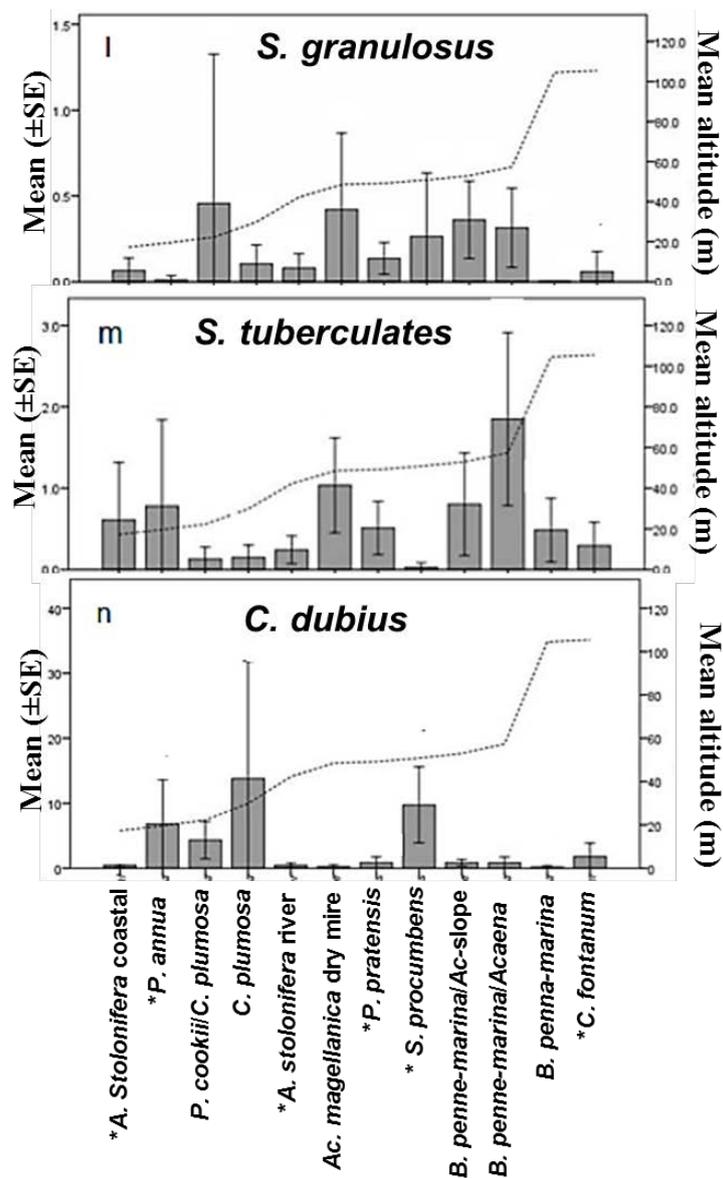
Fig. 2: Mean abundance of the nine native springtail species present on Marion Island across the 12 vegetation type and the influence of altitude on these springtails. The stipple line represents mean altitude from the lowest to the highest point. Invasive vegetation types are denoted with an asterisk.

Table 4. Hurdle models of the native springtail species abundance with environmental variables per plant status. *indicates P< 0.05, **P < 0.001, ***P < 0.0001.

		C. antarcticus travei			*C. dubius*			*F. marionensis*		
		Estimate ± SE	Z statistic	P	Estimate ± SE	Z statistic	P	Estimate ± SE	Z statistic	P
Count model coefficients	Intercept (Invasive veg)	0.15±0.26	0.58	0.55	-0.07±0.29	-0.24	0.81	0.19±0.13	1.39	0.53
	Native vegetation	-9.971±56.47	-0.18	0.85	-6.93±46.32	-0.15	0.81	-4.85±40.76	-0.12	0.90
	Altitude	0.01±0.004	2.25	*	-0.01±0.003	-2.71	***	-0.004±0.001	-3.34	***
	Log (theta)	-11.74±56.47	-0.21	0.83	-11.08±46.33	-0.24	0.81	-8.42±40.78	-0.21	0.83
Zero hurdle model coefficients	Intercept	-0.59±0.12	-4.96	***	-0.11±0.13	-0.85	0.39	-0.16±0.072	-2.22	*
	Native vegetation	-2.49±0.104	-23.82	***	-2.033±0.14	-14.29	***	-1.01±0.07	-14.52	***
	Altitude	0.007±0.001	5.31	***	-0.014±0.002	-5.11	***	0.001±0.001	1.40	0.16
Theta: count		0			0			0.0001		
Log likelihood		-1842			-1686			-5250		
AIC		3697.573			3385.725			10514.16		

		Katianna sp.			M. ceacus			S. tuberculatus		
		Estimate ± SE	Z statistic	P	Estimate ± SE	Z statistic	P	Estimate ± SE	Z statistic	P
Count model coefficients	Intercept (Invasive veg)	-0.54±0.30	-1.78	0.07	-0.97±0.59	-1.64	0.09	-0.102±0.14	-0.73	0.46
	Native vegetation	-0.30±1.67	-0.18	0.86	-5.43±60.78	-0.08	0.92	1.37±0.17	7.96	***
	Altitude	-0.01±0.005	-2.31	*	-0.08±0.02	-3.33	*	-0.004±0.002	-1.93	*
	Log (theta)	-2.35±1.93	-1.21	0.22	-9.59±60.79	-0.15	0.87	-0.65±0.21	-3.06	*
Zero hurdle model coefficients	Intercept	-0.75±0.16	-4.69	***	-0.61±0.26	-2.29	*	-0.61±0.104	-5.84	***
	Native vegetation	-2.72±0.14	-18.66	***	-3.05±0.29	-10.39	***	-1.84±0.093	-19.67	***
	Altitude	0.001±0.002	0.54	>0.58	-0.02±0.007	-3.01	*	0.001±0.001	0.903	0.36
Theta: count		0.0953			0.0001			0.5196		
Log likelihood		-1050			-401.6			-2471		
AIC		2114.154			817.1011			4956.725		

		T. bisetosa			*S. granulosus*			*C. tricuspis*		
		Estimate ± SE	Z statistic	*P*	Estimate ± SE	Z statistic	*P*	Estimate ± SE	Z statistic	*P*
Count model coefficients	Intercept (Invasive veg)	0.97±0.15	6.37	***	-0.194±0.51	-0.37	0.71	-0.43±1.83	-0.23	0.81
	Native vegetation	-10.67±58.99	-0.18	0.86	-8.17±37.50	-0.21	0.83	-5.97±N/A	N/A	N/A
	Altitude	-0.002±0.002	-0.99	0.31	-0.006±0.01	-0.73	0.46	-0.002±0.004	-0.041	0.97
	Log (theta)	-12.44±58.99	-0.21	0.83	-9.33±37.51	-0.25	0.80	-8.46± N/A	N/A	N/A
Zero hurdle model coefficients	Intercept	-0.03±0.081	-0.37	0.71	-0.94±0.25	-3.69	***	0.42±0.57	-0.73	0.46
	Native vegetation	-1.804±0.07	-22.97	***	-3.35±0.25	-13.606	***	-5.51±0.81	-6.82	***
	Altitude	0.007±0.001	7.63	***	-0.002±0.004	-0.59	0.55	-0.006±0.02	-0.29	0.76
Theta: count		0			0.0001			0.0001		
Log likelihood		-3395			-473.9			-212.2		
AIC		6803.117			961.7946			238.4039		

Discussion

In this study a total of 14 out of the 15 springtail species previously found on Marion Island were collected. The species not found in this study was *Friesea tilbrooki*, which is the only neanurid springtail found on the island, and is most likely due to the sampling regime that did not incorporate this species' habitat. On Marion Island, *F. tilbrooki* has previously only been found in intertidal and marine habitats in then only low numbers; however, this species is abundant on the nearby Prince Edward Island and elsewhere.

The hurdle model analyses suggested that the majority of the springtail species on Marion Island have broad habitat preferences, which is in keeping with previous investigations of sub-Antarctic and temperate springtails (Ponge 1993, Hopkin 1997, Convey *et al.*, 1999; Gabriel *et al.*, 2001). However, it's clear that where habitat specificity (or plant community specificity) exists, it is more distinct for native than for the introduced species. *C. denticulata*, together with *I. maculatus* and *P. notabilis*, are the most abundant invasive springtails in coastal vegetation, but the two Isotomidae are also present in most inland vegetation. The success of *Isotomurus maculatus* and *P. notabilis* in invading new vegetation from their introduction point could be due to two reasons; firstly both could be generalist feeders, which does not restrict them to one particular type of food source. Hasegawa and Takeda (1995) found that generalist feeders are able to switch their feeding habits according to the availability of different food items (fungi and detritus). The ability to switch feeding habits likely promotes exploitation of a wider food niche (Hasegawa and Takeda 1995). Secondly these species can tolerate dry and warmer conditions better than native species and with the island getting warmer in the interior, it's predicted that invasive springtail species will perform better than their native counterparts (Chown *et al.*, 2007).

Invasive springtails are present and abundant in both invasive and native vegetation, except for *P. notabilis* and *P. flavescens* which prefer invasive vegetation (see chapter 2). Marion Island is getting dryer and invasive species are increasing their range up the elevation gradient, although most invasive springtails dominate the lower lying areas, except for *M. minimus* which is found abundantly in native vegetation consisting of *Ac. magellanica* on slopes with *B. penna-marina* at high altitude. The difference

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between this invasive species and the others found on the island, is that *M. minimus* is found in the deeper layers of the soil in open vegetation where light penetrates evenly during most times of the year (Gabriel *et al.*, 2001).

Native springtails on Marion Island are present and abundant in a wide variety of habitat complexes and vegetation types across the elevation gradient. For example, the native *F. marionensis* is present in wide range of vegetation types but prefers invasive rather than native vegetation. This may be due to the species preferring new food sources brought in by invasive vegetation. Other native springtail species are most abundant in moist complexes for example near rivers and mires, which are found in mid to high altitude, such as *C. antarcticus travei*. Elnitsky *et al.* (2008) documented that *C. antarcticus travei* prefers suitable vegetation where it can move easily into the deep part of the soil where it's much cooler and water is regularly available. Furthermore, this species is known to select moist micro-habitat sites that don't reduce the rate of water loss (Hayward *et al.*, 2001).

Tullbergia bisetosa seems to be using the same behavioural strategy as *C. antarcticus travei* to reside in a wide variety of habitats and although this strategy is currently successful, there might be fewer suitable habitats in the future as the island gets warmer and dryer. It's predicted that native euphotic (soil dwellers) springtail species will shift up the elevation gradient as the lower lying habitats are expected to become warmer and dryer. Physiological studies have indicated that invasive species will perform better in warmer, drier conditions (Slabber *et al.*, 2007, Chown *et al.*, 2007). Rare native species such as *M. caeca*, *C. tricuspis* and *S. granulosus* face the risk of becoming extinct due to their low numbers, which may further drop due to habitat transformation by invasive vegetation and climate change. The ability of native and invasive springtails to exploit both invasive and native plant sources was evident in this study, especially from intermediate native species.

It is expected that invasive springtails will be the predominant dispersers to new areas, and exploit new resources, and this is the same for Marion Island, as the most common and intermediate springtails are the invasive *P. notabilis, I. maculatus* and *C. denticulata*. Native springtails also seem to exploit new resources provided by invasive plants as observed in this study with a number of native springtails exploiting invasive

plants (*C. antarcticus travei* and *F. marionensis*). This switching to invasive plants might be linked to nutrient value associated with these plants. Bezemer *et al.*, (2014) reported that invasive plants may possess certain unique chemical or morphological traits that are absent in food associated with native plants, while invasive plants can also be important substitutes as food plants for soil insects. Several studies have reported shifts from native host plants to invasive plants by native generalist and specialist herbivores. For instance, larvae of the southern cabbageworm, *Pontia protodice*, which is native to the south-eastern United States, feed on a range of well-established invasive vegetation (Keane & Crawley, 2002).The change in micro-organisms moving from native to invasive plants may result in a nutrient shift, that might increase the possibility of invasive plants changing their distributions on Marion Island.

In conclusion, these results suggest that invasive springtail species have similar patterns of habitat associations with native species and have spread from coastal to interior vegetation zones as predicted by climate change models with an increase in average annual temperature and decrease in average annual rainfall. Native species adapted to cooler and moist conditions, characteristic of higher elevations, might be particularly vulnerable to future directional climate changes. Invasive species are more abundant at lower elevations, especially those more generalist common species such as *P. notabilis, I. maculatus* and *C. denticulata* but with the rise a rise in temperature these species may shift their ranges up the altitudinal gradient. Moreover, species with drought-tolerant traits such as large epiedaphic species, will most likely be more tolerant to climate change than smaller eudaphic species (Makkonen *et al.*, 2011). Although, many native springtail have broad habitat preferences and have shifted from native to invasive vegetation, rare springtail species may face extinction due to the changing abiotic environment (climate change) and from biotic interactions, which are dominated by the effects of invasive vegetation and springtails.

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Supplementary Material

Table S1. Hurdle model outputs for the presence and abundance of three invasive springtail species associating with a particular vegetation type and the influence of altitude. *B. penna-marina* and *Ac. magellanica* on slope is the intercept. *P. flavescens* and *M. minimus* could not be analysed using hurdle models. *Indicates invasive vegetation and * indicates P< 0.05, **P < 0.001, ***P < 0.0001.

		C. denticulata			*I. maculatus*			*P. notabilis*		
		Estimate ± SE	Z statistic	*P*	Estimate ± SE	Z statistic	*P*	Estimate ± SE	Z statistic	*P*
Count model coefficients	Intercept	1.76±0.44	4.04	***	0.76.±0.21	3.56	***	0.0079±0.0039	1.99	*
	B. penna-marina /Acaena	1.63 ± 0.40	4.05	***	0.36 ± 0.22	1.69	0.09	0.0019±0.0046	4.29	***
	Ag. magellanica on dry mire	0.63±0.31	-2.01	*	-0.34±0.23	-1.43	0.15	-0.0015±0.001	-0.01	0.98
	A. stolonifera coastal*	2.32±0.39	5.1	***	0.81±0.23	3.53	***	0.0010±0.0042	2.37	*
	A. stolonifera river*	-0.02±0.37	-0.04	0.96	0.14±0.22	0.62	0.53	0.0089±0.0046	1.92	0.05
	B. penna-marina	-2.71±0.83	-3.28	**	-0.57±0.34	-1.66	0.09	-0.006±0.0013	-0.44	0.65
	C. fontanum *	-0.24±1.19	-0.1	0.84	0.36±0.21	1.22	0.22	0.0029±0.0048	6.09	***
	C. plumosa	3.37±0.36	9.48	***	1.72±0.11	8.75	***	0.0018±0.0039	4.8	***
	P. annua *	1.97±0.38	5.13	***	0.83±0.21	3.99	***	0.0013±0.0040	3.18	**
	P. cookii /C. plumosa	3.34±0.38	8.83	***	1.22±0.22	5.66	***	0.0016±0.0042	3.71	***
	P. pratensis *	0.80±0.30	2.64	**	-0.57±0.23	-2.49	*	0.0033±0.0063	0.05	0.95
	S. procumbens*	1.65±0.42	3.91	***	0.66±0.22	3.02	**	0.0022±0.0039	5.74	***
	Altitude	0.01±0.01	1.21	0.19	-0.01±0.002	-4.98	***	-0.009±0.0030	-2.92	**
	Log (theta)	-1.24±0.09	-14.33	***	-1.28±0.14	-8.96	***	-0.004±0.0015	-1.6	0.10

		C. denticulata			I. maculatus			P. notabilis		
		Estimate ± SE	Z statistic	P	Estimate ± SE	Z statistic	P	Estimate ± SE	Z statistic	P
	Intercept	-0.98±0.24	-4.09	***	-0.37±0.14	-2.59	***	-2.49±0.29	-8.53	***
	B. penna-marina /Acaena	0.49±0.23	2.18	*	0.36.±0.16	2.17	*	-0.19.±0.36	-0.54	0.58
	Ag. magellanica on dry mire	0.73±0.11	3.66	***	-0.52±0.17	-3.1	**	-0.53±0.75	-3.36	***
	A. stolonifera coastal*	2.54±0.26	9.94	****	0.78±0.19	4.19	***	0.80±0.33	2.42	*
Zero hurdle model coefficients	A. stolonifera river*	0.15±0.22	0.69	0.49	0.35±0.17	2.08	*	-0.02±0.36	-0.06	0.95
	B. penna-marina	-0.71±0.49	-1.43	0.15	-0.05±0.23	-0.22	**	-1.16±0.76	-1.153	0.12
	C. fontanum*	-1.83±0.74	-2.48	*	0.83±0.21	3.93	***	0.92±0.38	2.39	*
	C. plumosa	1.11±0.20	5.45	***	1.28±0.16	8.01	***	0.79±0.29	2.69	**
	P. annua*	0.57±0.22	2.54	*	0.83±0.17	5.04	***	0.63±0.31	2.03	*
	P. cookii /C. plumosa	2.00±0.24	9.48	***	1.41±0.19	7.29	***	073±0.33	2.99	*
	P. pratensis*	0.90±0.11	4.54	***	-0.38±0.16	-2.28	*	-1.27±0.46	-2.77	**
	S. procumbens*	0.24±0.24	1.02	0.30	0.27±0.16	1.66	0.08	1.12±0.29	3.76	***
	Altitude	-0.02±0.003	-4.54	***	-0.01±0.001	-6.01	***	-0.01±0.002	-3.02	**

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Table 2: Hurdle model outputs for the presence and abundance of each native springtail species associating with a particular vegetation type and the influence of altitude. *B. penna-marina* and *Ac. magellanica* on slope is the intercept. *C. tricuspis* and *S. granulosus* could not be analysed using hurdle models. *Indicates invasive vegetation and * indicates P< 0.05, **P < 0.001, ***P < 0.0001.

		C. antarcticus travei			**C. dubius**			**F. marionensis**		
		Estimate ± SE	Z statistic	*P*	Estimate ± SE	Z statistic	*P*	Estimate ± SE	Z statistic	*P*
Count model coefficients	Intercept	-14.26±822.58	-0.02	0.98	-0.98±0.81	-1.2	0.22	0.32±0.31	1.04	0.29
	B. penna-marina /Acaena	0.69±0.53	1.31	0.19	1.11±0.68	1.63	0.10	0.18±0.25	0.72	0.47
	Ag. magellanica on dry mire	1.44±0.41	3.49	***	0.79±0.91	0.87	0.38	-1.59±0.34	-4.71	***
	A. stolonifera coastal*	-12.52±220.30	-0.06	0.95	-0.01±0.88	-0.01	0.99	0.95±0.31	3.09	**
	A. stolonifera river*	0.099±0.58	1.69	0.08	-0.02±0.65	-0.04	0.96	-0.84±0.30	-2.76	**
	B. penna-marina	1.09±1.24	0.88	0.37	-0.83±1.23	-0.68	0.49	-0.21±0.30	-0.69	0.48
	C. fontanum*	-1.54±1.45	-1.06	0.28	1.44±1.35	1.07	0.28	1.17±0.29	3.97	***
	C. plumosa	1.55±0.94	1.65	0.09	3.24±0.54	6.03	***	1.32±0.24	5.45	***
	P. annua*	-11.39±176.19	-0.07	0.94	2.97±0.63	4.74	***	1.34±0.28	4.67	***
	P. cookii /*C. plumosa*	-10.27±142.96	-0.07	0.94	1.52±0.57	2.66	**	1.16±0.29	4.04	***
	P. pratensis*	0.13±0.47	0.26	0.79	0.79±0.58	1.37	0.17	-0.31±0.95	-1.24	0.21
	S. procumbens*	2.59±0.54	4.78	***	2.67±0.55	4.88	***	1.19±0.26	4.54	***
	Altitude	0.001±0.004	0.41	0.68	-.0006±0.009	-0.06	0.95	0.001±0.001	0.56	0.57
	Log (theta)	-15.026±822.6	-0.09	0.98	-2.17± 0.64	-3.37	***	2.05±0.31	-6.7	0.51

		C. antarcticus travei			C. dubius			F. marionensis		
		Estimate ± SE	Z statistic	P	Estimate ± SE	Z statistic	P	Estimate ± SE	Z statistic	P
Zero hurdle model coefficients	Intercept	-2.81±0.23	-12.33	***	-1.92±0.27	-7.04	***	-0.49±0.14	-3.63	***
	B. penna-marina /Acaena	-0.31±0.28	-1.1	0.27	-0.79±0.36	-2.19	*	-0.10±0.16	-0.65	0.36
	Ag. magellanica on dry mire	1.59±0.22	7.21	***	-1.96±0.50	-3.91	***	-1.68±0.20	-8.37	0.09
	A. stolonifera coastal*	-1.39±0.55	-2.56	*	-1.32±0.46	-2.91	**	-0.47± -0.19	-2.39	*
	A. stolonifera river*	-0.24±0.29	-0.81	0.41	-0.69±0.36	-1.89	0.05	-1.00±0.19	-5.2	***
	B. penna-marina	-2.36±0.63	-3.73	***	-0.94±0.63	-1.49	0.13	0.19±0.21	0.92	0.36
	*C. fontanum**	-2.45±0.64	-3.8	***	0.35±0.39	0.91	0.36	0.34±0.21	1.65	0.09
	C. plumosa	-1.83±0.46	-3.99	***	0.82±0.27	1.04	0.29	-0.26±0.16	-1.67	0.09
	*P. annua**	-2.66±0.74	-3.59	***	-0.56±0.32	-1.74	0.08	-0.77±0.18	-4.38	***
	P. cookii /C. plumosa	-2.85±1.02	-2.78	**	0.37±0.31	1.23	0.22	-0.17±0.79	-0.89	0.37
	*P. pratensis**	0.15±0.25	0.62	0.53	-0.56±0.32	-1.64	0.08	0.362±0.16	-3.82	***
	S. procumbens*	0.12±0.26	0.43	0.64	0.54±0.28	1.97	*	-0.37±0.17	-2.25	*
	Altitude	0.09±0.002	4.67	***	-0.01±0.03	-3.99	***	-0.002±0.001	-1.48	0.13

		Katianna sp.			*M. ceacus*			*S. tuberculatus*		
		Estimate ± SE	Z statistic	*P*	Estimate ± SE	Z statistic	*P*	Estimate ± SE	Z statistic	*P*
Count model coefficients	Intercept	0.097±0.65	0.15	0.88	-0.0011±0.0064	-0.01	0.98	1.35±0.21	6.22	***
	B. penna-marina /Acaena	0.64±0.42	1.52	0.12	-0.0066±0.0095	-0.001	0.99	0.045±0.21	0.21	0.83
	Ag. magellanica on dry mire	0.61±0.44	1.37	0.17	0.0013±0.0064	0.02	0.98	0.06±0.20	0.31	0.75
	A. stolonifera coastal*	0.25±0.63	0.39	0.69	0.0013±0.0064	0.02	0.98	-0.11±0.31	-0.37	0.71
	A. stolonifera river*	-1.25±0.72	-1.73	0.08	-0.0058±0.001	-0.001	1.00	-0.33±0.39	-0.85	0.39
	B. penna-marina	-0.23±0.78	-0.3	0.76	-0.0031± N/A	N/A	N/A	-0.61±0.53	-1.13	0.25
	C. fontanum	-0.69±0.83	-0.83	0.40	0.0014±0.0064	0.02	0.98	-2.32±0.64	-3.6	***
	C. plumosa	0.913±0.55	1.63	0.10	0.0013±0.0064	0.02	0.98	0.03±0.46	0.08	0.93
	P. annua *	-0.29±0.63	-0.45	0.64	0.0011±0.0064	0.01	0.98	0.003±0.42	0.009	0.99
	P. cookii /C. plumosa	-2.31±1.20	-1.92	0.05	0.001±0.0064	0.01	0.98	-0.72±0.40	-1.76	0.07
	P. pratensis *	0.44±0.51	0.87	0.38	0.0011±0.0064	0.01	0.98	-0.08±0.21	-0.4	0.68
	S. procumbens*	-0.15±1.74	-0.08	0.92	-0.008±0.0081	-0.001	0.99	0.49±0.36	1.35	0.17
	Altitude	-0.012±0.005	-2.15	***	-0.0072±0.0052	-1.39	0.16	-0.003±0.002	-1.11	0.26
	Log (theta)	-1.12±0.73	-1.52	0.12	-0.0018± N/A	N/A	N/A	-0.51±0.19	-2.56	*

		Katianna sp.			M. ceacus			S. tuberculatus		
		Estimate ± SE	Z statistic	P	Estimate ± SE	Z statistic	P	Estimate ± SE	Z statistic	P
Zero hurdle model coefficients	Intercept	-2.31±0.26	-8.75	***	-4.23±0.82	-5.15	***	-1.05±0.17	-6.17	***
	B. penna-marina /Acaena	0.53±0.26	2.01	*	-0.25±1.00	-0.25	0.80	-0.01±0.18	-0.1	0.91
	Ag. magellanica on dry mire	-0.10±0.28	-0.36	0.71	-0.02±0.91	-0.02	0.98	-0.02±0.17	-0.13	0.89
	A. stolonifera coastal*	-0.72± 0.40	-1.81	0.06	-0.22±1.04	-0.22	0.82	-0.99±0.26	-3.82	***
	A. stolonifera river*	-0.76±0.36	-2.11	*	-0.15±1.00	-0.15	0.87	-1.86±0.30	-6.11	***
	B. penna-marina	-0.41±0.45	-0.9	0.36	1.26±1.01	1.24	0.21	-1.52±0.37	-4.01	***
	C. fontanum*	-0.47±0.47	-1.00	0.31	0.44±1.23	0.35	0.71	-1.41±0.36	-3.88	***
	C. plumosa	-1.08±0.35	-3.07	**	1.88±0.75	2.49	*	-2.79±0.36	-7.64	***
	P. annua*	-1.16±0.38	-3.03	**	0.20±0.87	0.22	0.81	-2.33±0.32	-7.09	***
	P. cookii /C. plumosa	-1.24±0.47	-2.62	**	0.25±0.94	0.26	0.78	-1.61±0.31	-5.16	***
	P. pratensis*	-0.65±0.31	-2.07	*	0.47±0.84	0.56	0.57	-0.28±0.18	-1.56	0.11
	S. procumbens*	-3.44±1.02	-3.36	***	1.06±0.80	1.32	0.18	-1.89±0.28	-6.54	***
	Altitude	-0.003±0.002	-1.09	0.27	-0.01±0.008	-1.84	0.06	-0.003±0.001	-1.53	0.12

		T. bisetosa		
		Estimate ± SE	Z statistic	*P*
Count model coefficients	Intercept	-6.86±15.04	-0.45	0.64
	B. penna-marina /Acaena	-0.90±0.34	-2.62	**
	Ag. magellanica on dry mire	-0.46±0.31	-1.49	0.13
	A. stolonifera coastal*	-0.20±0.49	-0.42	0.67
	A. stolonifera river*	1.67±0.32	5.12	***
	B. penna-marina	1.18±0.36	3.23	**
	C. fontanum	1.20±0.40	2.93	**
	C. plumosa	0.47±0.36	1.29	0.19
	P. annua	0.03±0.59	0.04	0.96
	P. cookii /C. plumosa	-0.33±0.41	-0.82	0.41
	P. pratensis	0.93±0.28	3.23	**
	S. procumbens*	-0.36±0.42	-0.86	0.38
	Altitude	-0.007±0.003	-2.55	*
	Log (theta)	-8.80±15.04	-0.58	0.55
Zero hurdle model coefficients	Intercept	-1.21±0.15	-7.96	***
	B. penna-marina /Acaena	-0.41±0.18	-2.16	*
	Ag. magellanica on dry mire	-0.21±0.17	-1.22	0.22
	A. stolonifera coastal*	-1.06±0.26	-4	***
	A. stolonifera river*	0.32±0.18	1.79	0.07
	B. penna-marina	0.61±0.21	2.77	**
	C. fontanum	0.15±0.22	-0.68	0.49
	C. plumosa	-0.87±0.19	-4.41	***
	P. annua	-2.11±0.31	-6.88	***
	P. cookii /C. plumosa	-0.47±0.22	-2.08	*
	P. pratensis	0.39±0.16	2.39	*
	S. procumbens*	-1.23±0.22	-5.41	***
	Altitude	0.001±0.001	1.18	0.23

Chapter 4

Conclusions

In this study it was found that 36% of the sampled springtails were invasive, and they associated more with native vegetation than with invasive vegetation. Nine species were native and these included all the Marion Island endemic species even the rare species such as *Cryptopygus tricuspis* and *Katianna* sp. (Gabriel *et al.*, 2001), which have rarely been found in previous studies (Hugo *et al.*, 2006). However, the abundance of springtails was higher on native vegetation with approximately 68% of all individuals associating with native vegetation.

Springtail diversity has been shown to decline with elevation on Marion Island (Gabriel *et al.*, 2001) and the results from this study support this pattern, with native and invasive springtail species abundance and richness decreasing with an increase in altitude (Chapter 2). The majority of the native springtail species on the island were found in cooler, mid-altitude habitats while most invasive springtails preferred warmer coastal habitats, except for *P. flavescens.* This species seems to have increased its range and now inhabits higher altitude areas whereas previously was only found along the coast from Kildalkey Bay to Trypot Beach (Treasure & Chown, 2013). The higher abundance and richness of invasive springtails at low lying coastal habitats might be explained by invasive species being less affected by disturbance than native species (Gabriel *et a*l., 2001), while physiological studies have also indicated that invasive species prefer warmer, drier conditions (Slabber *et al.*, 2007, Chown *et al.*, 2007). Climate change is thus likely to favour invasive over native springtails on Marion Island (Chown *et al.*, 2007, Janion *et al.*, 2010). In addition, springtails have been shown to increase in abundance with nutrient quality (Hopkin, 1997), thus the coastal vegetation of Marion Island, under biological influence (Smith & Steenkamp, 1990), has increased nutrient quality and consequently a greater abundance of springtails

The cosmopolitan springtail species, *C. denticulata,* belonging to the family Hypogastruridae, dominated areas where it was present and is found on several sub-Antarctic islands, such as Macquarie Island, South Georgia and Marion Island (Convey *et al.*, 1999, Greenslade and Wise, 1984, Frenot *et al.*, 2005, Terauds *et al.*, 2011). Seventy-six percent of all springtails collected during sampling were *C. denticulata,* by far the most common species on the island and found in low altitude habitat complexes, specifically coastal areas that are warm and moist with high levels of organic material (Gabriel *et al.*, 2001). Furthermore, *C. denticulata* together with

other invasive springtails species such as *I. maculatus* are now commonly found and are dominant in lower lying parts of the island. Their range has shifted inwards from the coastal edge and are associated with invasive vegetation such as coastal *A. stolonifera* and *P. annua*, native vegetation *P. cookii /C. plumosa* and *C. plumosa* respectively. In this study I suggest that *C. denticulata* may have displaced native springtails, such as observed for *H. viatica* which is invasive on other sub-Antarctic islands (Bellinger *et al.*, 2018, Convey *et al.*, 1999, Greenslade, 2002, Frenot *et al.*, 2005, Terauds *et al.*, 2011) and potentially reduced native species richness on these islands (Terauds *et al.*, 2011, van Hengstum *et al.*, 2014).

In contrast, native species such as *C. antarcticus travei* and *T. bisetosa* were found to be most abundant in moist complexes, for example near rivers and mires that are found in mid-altitude areas. Furthermore, these two species use a similar strategy of associating with suitable, moist vegetation complexes where they can easily move through the various soil layers. This offers them the opportunity to reside in deeper, cooler habitats but as the island warms and gets increasingly drier over time, this strategy might no longer be effective. Native soil-dwelling springtail species are predicted to move up the elevation gradient as the lower lying habitat complexes are expected to become warmer and drier. The rare native springtail species such as *M. caeca*, *C. tricuspis* and *S. granulosus* already having low numbers, face the risk of being displaced, as habitats are transformed by invasive vegetation and climate change. With increased climatic warming, it is possible that this change could favour particular invasive species as they can tolerate dry and warmer conditions better than native species (Chown *et al.*, 2007, Treasure & Chown, 2013).

In addition, due to increased human activity in the Antarctic Region (Frenot *et al.*, 2005, Greve *et al.*, 2017), the potential for the spread of invasive springtails to other regions in the Antarctic could increase (see Hughes *et al.*, 2017). For example, if pristine Prince Edward Island (Hugo *et al.*, 2006), was to get more annual visitors more frequently, as is the case with Marion Island, I predict that invasive springtail numbers of *C. denticulata* and *M. minimus* may rise (Hugo *et al.*, 2006). Strict quarantine measures should be implemented on both islands to reduce introduction and spread of invasive insects and plants to Prince Edward Islands.

From this study, the following research areas have been identified, which can expand the knowledge regarding both native and invasive springtail species found on the island. First, further research investigating the seasonal effects of springtail abundance and richness on the island over an extended period should be conducted. Second, environmental parameters that may influence springtail distribution, such as soil temperature, soil type, nutrient content, moisture content, pH, the leaf litter layer, as well as characteristics of the fungal community in native and invasive vegetation needs to be investigated. Third, feeding attributes of springtail species, through gut content and stable isotope analysis should be performed which will enable us to determine the diet of springtails on Marion Island.

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