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Invasional meltdown in *Sagina procumbens* facilitates the establishment of some invasive taxa on sub-Antarctic Island

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Walk away quietly in any direction and taste the freedom of the mountaineer. Camp out among the grasses and gentians of glacial meadows, in craggy garden nooks full of nature's darlings. Climb the mountains and get their good tidings, Nature's peace will flow into you as sunshine flows into trees. The winds will blow their own freshness into you and the storms their energy, while cares will drop off like autumn leaves. As age comes on, one source of enjoyment after another is closed, but nature's sources never fail.

John Muir (1838 - 1914)

Declaration

I, ……………………………… declare that the thesis/dissertation, which I hereby submit for the degree………………………at the University of Pretoria, is my own original work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signature: ________________

Date: _____________________

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Abstract

Invasional meltdown occurs when one invasive species facilitates the establishment, spread and increase of other invasive species, and subsequently increases their impacts. Most studies on invasional meltdown have assessed facilitation of a single invasive species by another invader, but few have assessed meltdowns across different taxa. Therefore, the aim of this study was to evaluate whether an invasive plant, *Sagina procumbens* L. (procumbent pearlwort, Caryophyllaceae), causes an invasional meltdown in two different taxa (vascular plants and Collembola) on sub-Antarctic Marion Island. Additionally, some direct impacts of *S. procumbens* on native taxa were assessed. *Sagina procumbens* is an invasive cushion or mat-forming vascular plant that has spread extensively in the sub-Antarctic. While little is known about the species' ecological impacts, it is thought to negatively impact biodiversity on Marion Island. Invasional meltdown was tested by comparing the richness of plants growing epiphytically on *S. procumbens* to those growing on two indigenous plant species (*Azorella selago* and *Clasmatocolea humilis*) that are being locally outcompeted by *S. procumbens*. Additionally, the richness, abundance, and biomass of native and of invasive Collembola extracted from these three focal plant species were compared between *S. procumbens* and the two indigenous plant species. The direct impacts of *S. procumbens* on native species were assessed by comparing the composition of plants growing epiphytically and of Collembola associated with *S. procumbens* to those of the two indigenous plant species. Additionally, native and invasive Collembola richness and abundance in *S. procumbens* were compared. Hardly any invasive plants grew on any of the three focal plant species. The richness of native plants did not differ between *S. procumbens* and the indigenous focal species. Invasive Collembola had a higher abundance, richness and biomass in *S. procumbens* than in both *A. selago* and *C. humilis*. However, native Collembola were also more abundant in *S. procumbens* than in the two native focal plant species. In contrast, the richness of native Collembola was not significantly different between the focal species, and the biomass of native Collembola did not differ significantly between *S. procumbens* and *A. selago*, although it was higher in *S. procumbens* than *C. humilis.* The composition of plants growing on *S. procumbens* did not differ significantly from those of plants growing on the two native focal species, though native Collembola assemblages did differ somewhat between the three focal species. Additionally, there was no significant difference between the richness of native and invasive Collembola assemblages in *S. procumbens*, although the abundance of native Collembola was significantly higher than that of invasive Collembola. Therefore, while I found no evidence for invasional meltdown in plants brought about by *S. procumbens*, some evidence for invasional meltdown in Collembola exists: *S. procumbens* leads to an increase in the species richness and biomass of invasive Collembola, but not native Collembola. Therefore, *S. procumbens* impacts Collembola community structure and composition, and may affect ecosystem processes, like decomposition, which are strongly linked to Collembola.

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Chapter 1: General introduction

Biological invasions have gained increasing recognition as an important component of anthropogenically driven global environmental change (Vitousek, 1986, Vitousek et al., 1996, Elton, 2000, Rosenzweig, 2001). The frequency and geographic extent of biological invasions worldwide is alarming due to the negative ecological and economic consequences that are associated with invasive species (Mack et al., 2000, Prinzing et al., 2002, Frenot et al., 2005b, Blackburn, 2008). Biological invasions can induce extensive changes in native populations, in community structure, and in ecosystem functioning and processes, potentially leading to a loss of native biota and the disruption of ecosystem services (Mack et al., 2000, Frenot et al., 2005b, Reaser et al., 2007, Vilà et al., 2011, Rojas-Sandoval et al., 2016). The impacts of biological invasions may, moreover, be exacerbated by other forms of global environmental change, including, for example, warmer temperatures associated with climate change (Bellard et al., 2012, Bellard et al., 2013, Ihlow et al., 2016).

Over the last 500 years, invasive species have come to dominate over 3% of the Earth's ice-free surface (Mooney and Cleland, 2001). Some of these invasive species can cause complex ecological changes operating at ecosystem, habitat, community, species and even genetic levels in the native environments (Kairo et al., 2003, O'Dowd et al., 2003, Barber et al., 2008, Wundrow et al., 2012, Priyanka and Joshi, 2013, Čuda et al., 2015). However, our knowledge of the ecological impacts of certain invaders remains limited (Pyšek et al., 2008), especially when considering the impacts of an invading species on multiple taxa (Parker et al., 1999). Studies often fail to decouple the direct and indirect ecosystem- or community-level changes induced by invasive species from those of environmental change. Thus, by overlooking the impacts and the roles of invasive species or precluding the invading species in driving ecosystem or community level changes, the ability to effectively predict the ecosystem conditions as a result of changes in the abundance of invading species is lessened (Rejmánek, 2000, Kolar and Lodge, 2001, Strayer et al., 2006).

Changes induced by invasive species to community structure can affect ecosystem functioning, both directly and indirectly (Nentwig, 2007, Jeschke et al., 2014). Direct effects of invasive species include, for example, the reduction in the abundance and biomass of habitat-forming species to the point where those species no longer have a considerable role in ecosystem processes (Waser et al., 2015). Additionally, the reduction in the abundance and diversity of native species as a result of invasive species can lead to changes in community composition (Sax and Gaines, 2003, Olden and Poff, 2003, Vilà et al., 2011, Pyšek et al., 2012). The indirect effects of invasive species include a potential decline in ecosystem resistance (i.e. the maximum perturbation species in a system can handle) and resilience (the amount of perturbation that an ecosystem can handle whilst remaining in the same state) to change (Downing et al., 2012), via their impact on biodiversity, which is suggested to be positively correlated with ecosystem stability (Hooper et al., 2005, Nentwig, 2007). Subsequent to a loss of native species, the lowered diversity of the system makes it more vulnerable for invasive species to dominate, and may cause the eventual collapse of a system (e.g. predation of Nile perch on Lake Victoria's cichlids, which then no longer control the population of their prey; Downing et al., 2012, Oliver et al., 2015). Diverse ecosystems that possess a high functional complementarity amongst native species are more resilient, whereas diverse ecosystems with a high level of functional redundancy are more resistant to invasive species (Downing et al., 2012). The loss of resilience in an ecosystem can give an early warning sign of a possible imminent collapse but a loss in resistance would not.

At larger scales, the effects of invasions can cause changes in native assemblages (Smart et al., 2006, Olden et al., 2011). The effects of invasions can lead to taxonomic and functional simplification, a phenomenon known as homogenization, as originally different phytogeographical communities become similar over space and time as they are invaded by similar species (Rooney et al., 2004, Schwartz et al., 2006, Shaw et al., 2010). Biological homogenization is driven by the invasion of widespread species and/or loss of specialized species or functional groups (Olden et al., 2011). Biological homogenization can lead to a system's decline, making the system more susceptible to further invasions (Olden et al., 2011). Invasive species can also hybridize with native species, resulting in the generation of new genetic variations, which may increase the fitness of the hybrids (Nentwig, 2007). Thus, hybridization involving non-native plant species can lead to the origin of new, and sometimes invasive species (Abbott, 1992).

Already established invasive species may also affect other non-native species in a number of ways. An established invader could negatively impact another non-native species through competition (e.g. for resources; Ross et al., 2004, Rauschert and Shea, 2017). Alternatively, invading species may have no observable impact on each other (Cope and Winterbourn, 2004). However, invasive species can also facilitate the spread and abundance of other invasive species, enhancing their ecological impacts and stimulating establishment (Simberloff and Von Holle, 1999, Grosholz et al., 2000, Ricciardi, 2001, O'Dowd et al., 2003, Green et al., 2011, Von Holle, 2011, Montgomery et al., 2012, Meza-Lopez and Siemann, 2015) through positive interactions.

Positive interactions between invasive species may enhance the susceptibility of the ecosystem to further invasions, and the potential degradation of ecosystem functioning and extinction of some native species (Johnson et al., 2009). Several examples of invasive species driving natives to local extinction exist (especially on islands; Abbott and Green, 2007, Sax and Gaines, 2008, Spatz et al., 2017). These invasions can lead to complex interactions among other invasive species in habitats that are invaded (Richardson et al., 1989, Pyšek and Pyšek, 1995, O'Dowd et al., 2003). For example, invasive species may act as agents of disturbance, causing a shift that alters the environment to such an extent that it becomes more favorable for invasive species and less favorable for native species (Zavaleta, 2000, O'Dowd et al., 2003, Green et al., 2011, Jackson, 2015).

The effects of the interactions of invasive species may be considerably greater on islands where the importance of inhibiting the introduction of invasive species on islands is emphasized by the increasing rates of invasion (Simberloff, 1995, Ricciardi, 2001, O'Dowd et al., 2003, Greve et al., 2017). Islands are more prone to invasions and more inherently sensitive to invader impact than mainlands (Mooney and Cleland, 2001, Reaser et al., 2007, Pearson, 2009, Clavero et al., 2009). The low species richness, trophic complexity, and lack of functional diversity (relative to mainland ecosystems) makes islands highly susceptible and inherently sensitive to the impacts of biological invasions (Diamond, 1989, Vitousek, 1990, Simberloff, 1995, Elton, 2000), as invasive plant species encounter less competition from native species (Vitousek et al., 1996). Consequently, this results in native biota and systems often having less biotic resistance to biological invasions than mainland systems (Vitousek et al., 1996). Subsequently, invading species often establish and proliferate on island systems more successfully than they do on mainlands (Vitousek et al., 1997). Invasive plant species that dominate or outcompete functionally integral native species can modify entire ecosystem dynamics on islands (Vitousek et al., 1987, O'Dowd et al., 2003, Croll et al., 2005, Abbott and Green, 2007, Green et al., 2011). Indeed, meta-analyses by Vilà et al. (2011) and Pyšek et al. (2012) found that invasive plants are most likely to cause significant impacts on resident communities of islands than on mainlands.

Due to the low diversity of island systems and low functional redundancy, some species have unique and vital functional roles (McConkey and Drake, 2015). When these functional integral species are outcompeted by invading species, no functional equivalents can replace them (Pearson, 2009). Hence, on islands, a loss of a native species often equates to a loss of integral ecosystem functions (O'Dowd et al., 2003, Croll et al., 2005, Abbott and Green, 2007, Green et al., 2011). Biological invaders which differ functionally from native species may also have impacts that could be disastrous to island ecosystems (Abbott and Green, 2007, Green et al., 2011). For example, the leguminous *Myrica faya*, a typical invasive plant that occurs in disturbed areas in Hawaii (Vitousek et al., 1987), has altered ecosystem properties by elevating the levels of nitrogen in the soil. This has led to the facilitation of other invasive species and inhibited the establishment and growth of native species (Vitousek, 1986, Vitousek et al., 1987, Walker and Vitousek, 1991).

Study system

The sub-Antarctic islands are the only fragments of land in the vast Southern Ocean (Bergstrom and Chown, 1999, Gabriel et al., 2001, Chown et al., 2005, Shaw, 2013). Their ecosystems are unique – they are the only landmasses at these high southern latitudes – and they contain a number of endemic taxa, which make the islands of considerable conservation value (Dingwall, 1992, Shaw, 2013). Biological invasions constitute a serious risk to the sub-Antarctic islands (Frenot et al., 2005b, Greve et al., 2017). Despite the isolation of the islands, several non-native species have been introduced to most of them (Shaw et al., 2010), with some invaders causing considerable impacts to both the biota and ecosystems (Bergstrom and Smith, 1990, Frenot et al., 2005b, Bergstrom et al., 2009, Jones and Ryan, 2010, Greve et al., 2017). The taxon that has the most established invasive species on the sub-Antarctic islands is vascular plants (le Roux et al., 2013). Some of the most species rich invasive plant taxa in the sub-Antarctic are Poaceae, Asteraceae, and Fabaceae (Shaw, 2013), with invasive species from these taxa originating from the Northern Hemisphere (Frenot et al., 2005b).

Marion Island (46°50'S, 37°50'E) is a sub-Antarctic island situated approximately 2300 km southeast of Cape Town, South Africa, in the sub-Antarctic Region (Smith, 1987) and is one of two islands comprising the Prince Edward Island group (PEIs). The island has a total area of approximately 290 km^2 (Verwoerd et al., 1981). It is situated in a belt of strong westerly atmospheric circulation known as the "Roaring Forties" (Schulze, 1971), meaning the island is exposed to frequent gale-force winds averaging > 36 $km.h^{-1}$. It also experiences high levels of humidity (annual mean humidity: 80%; Smith, 2002, le Roux and McGeoch, 2008a). The skies on Marion Island are mostly overcast (± 6.5 hours of sunlight on average per day; le Roux and McGeoch, 2008a), resulting in low levels of direct radiation to the island. Due to the high incidence of precipitation on the island, soil moisture content is high and many of the more peaty soils are permanently saturated (Schulze, 1971). The total annual precipitation on the island is *c*. 1900 mm, falling on more than 300 days per year (le Roux and McGeoch, 2008a). The annual mean temperatures on Marion Island are consistently low (approximately 6°C), with only a small difference (approximately 4°C) between the mean temperatures of the coldest and the warmest months of the year (le Roux and McGeoch, 2008a). However, in the last half-century sub-Antarctic Marion Island has experienced rapid climatic changes. The ambient temperature has increased by a cumulative 1.2°C and the annual precipitation has decreased by more than 1000 mm (Smith, 2002, le Roux and McGeoch, 2008).

Marion Island is volcanic in origin, with the oldest lava predating 0.45 mya (McDougall et al., 2001). All three types of black lavas (pahoehoe, aa, and block lava) occur on Marion Island (Verwoerd et al., 1981, Boelhouwers et al., 2008). However, block lava dominates the largest part of the island (Smith and Mucina, 2006). In many places, the older Pleistocene grey lavas are covered by younger Holocene black basaltic lava and conical scoria hills formed during previous eruptions (Verwoerd et al., 1981, McDougall et al., 2001).

Marion Island is characterized by two major biomes: barren polar desert at higher altitudes (> 650 m), and tundra, which dominates the lower altitudes (Smith and Mucina, 2006). The latter supports six habitat complexes (mire, slope, fellfield, polar desert, saltspray, and biotic herbfield; Gremmen and Smith, 2008) (Fig. 1). Vascular plants are comprised of low-growing herbs and graminoids, including the long-lived keystone cushion plant *Azorella selago* (Gremmen and Smith, 2008; Fig. 1A). On Marion Island, *A. selago* is widespread, occurring from sea level to approximately 850 m a.s.l (Hugo et al., 2006). Its growth form reduces wind stress and heat moisture loss and allows the plant to survive in adverse climatic conditions, and facilitates the growth of other vascular plants (most notability *Agrostis magellanica*) and microarthropods at high altitudes (le Roux and McGeoch, 2004). The vascular plants growing epiphytically on *A. selago* at high altitudes are not obligatory epiphytes as they grow independently from *A. selago* in less adverse climatic conditions (Hugo et al., 2006). The cushion plant has contributed significantly to the survival of flora and fauna on the island (Smith, 1987, le Roux and McGeoch, 2004).

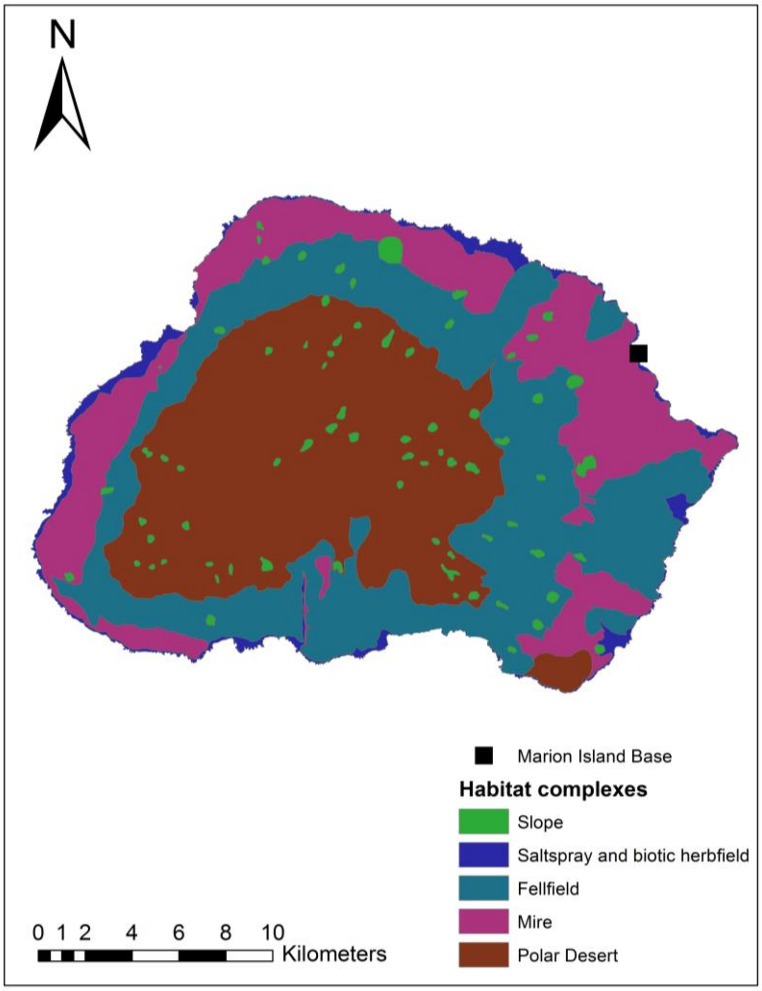

Fig. 1: Map of the habitat complexes of sub-Antarctic Marion Island. The location of the research base, around which samples for this project were collected, is also shown (Smith and Mucina, 2006).

The native species on Marion Island are adapted to the abiotically harsh environment on Marion Island. However, they seem particularly sensitive to the competition of biological invaders (Smith et al., 2001). Studies indicate that biological invasions constitute a serious risk to the sub-Antarctic (Frenot et al., 2005b, Greve et al., 2017). In the sub-Antarctic, Marion Island is an ideal system for examining the impacts of biological invasions due to its isolation, relative pristineness and closed systems, and relatively low species richness (Smith et al., 2001). A substantial number of invasive species have been introduced and have established on Marion Island since the first people set foot on the island approximately two centuries ago (Cooper, 2008, Frenot et al., 2005b, Chown et al., 2002, Jones and Ryan, 2010, Chown et al., 2011, Greve et al., 2017). Invasive vascular plants on Marion Island are predominately grasses and herbs (much like the dominant native plants) and have a natural weedy tendency (Shaw, 2013, Greve et al., 2017; i.e. seeds germinate early, seedlings grow faster, can survive under abiotically harsh conditions, and are prolific and have high reproductive capacity).

Sealers were associated with the first invasions on the PEIs (in the 1800s), during the active hunting period of seals (Greve et al., 2017). Several more invasive species are thought to have been introduced to Marion Island during the initial establishment of scientific research and weather stations in the 1950s (Frenot et al., 2001, Smith and Mucina, 2006) from the building material, in particular sand and other cargo (Bergstrom and Smith, 1990). Consequently, stringent biosecurity protocols have been imposed on these and other pathways of introduction (Greve et al., 2017). Seabirds and seals influence the distribution of invasive plant species on Marion Island (Smith and Mucina, 2006, Greve et al., 2017). Their excrement (faeces and guano) provide nutrient rich areas, which form suitable conditions for the growth of several invasive species (Smith, 1976, Frenot et al., 1999). Prince Edward Island has fewer invasive species (three vascular plant species and one invertebrate species; Frenot et al., 2005b) than Marion Island. The conservation practices and permitting system on Prince Edward Island are stricter and visits to the island are infrequent (one visit every four years, for a maximum of 10 people and for a duration of no more than eight days), all of which reduces the risk of introductions to the island (Greve et al., 2017). However, it is thought that seabirds have acted as vectors of some invasive plant introductions from Marion Island to Prince Edward Island (Bergstrom and Smith, 1990).

Currently, approximately 18 non-native vascular plant species occur on Marion Island, of which six have become invasive (Greve et al., 2017). Other introduced species are persistent, but have a restricted distribution, with little to no observable effects on the island's biota and ecosystem (Bergstrom and Smith, 1990, Gremmen, 1997, Gremmen and Smith, 1999, Frenot et al., 2005b, Greve et al., 2017). So far, the impact of only one plant invader, namely *Agrostis stolonifera*, a fast growing perennial grass, has been assessed on Marion Island (Gremmen et al., 1998). *Agrostis stolonifera* is most abundant on drainage lines (wet slopes and on river banks; Gremmen et al., 1998). It reduces the bryophyte biomass and alters the vegetation structure into dense grasslands in the regions it invades (Gremmen et al., 1998). The impacts of the other plant invaders to the island (e.g. *Cerastium fontanum, Poa annua, Poa pratensis, Stelleria media* and *Sagina procumbens*) have so far received no attention, although a number of studies have demonstrated that with time and increased disturbances, invasive species can expand their distributional ranges and displace native plant species (Gremmen and Smith, 1999, Chown et al., 2012). Likewise, invasive Collembola may displace native Collembola (Greenslade, 2002).

Collembola constitute some of the few herbivore and detritivore species on Marion Island and are described as both indicator and keystone species (Gabriel et al., 2001, Hugo et al., 2004, 2006, Slabber et al., 2007). Over Marion Island's 500,000-year lifespan, ten springtail species have naturally colonized the island. However, with the arrival of humans, a further six species have accidentally been introduced (Chown et al., 2002, Hugo et al., 2004, Chown and Convey, 2016), of which five are currently invasive on the island (Slabber et al., 2007, Greenslade and Convey, 2012, Janion-Scheepers, 2017). Collembola communities are significant contributors to soil ecosystem nutrient cycling and their distribution and abundance is thus of considerable importance and interest on Marion Island (Gressitt, 1970, Gabriel et al., 2001, Chown et al., 2002, Hugo et al., 2004, 2006, Chown and Convey, 2016).

Some Collembola species typically have fast growth rates and strong responses (due to phenotypic plasticity) to increasing temperatures (Gabriel et al., 2001, Chown et al., 2007, Janion et al., 2010). On Marion Island, native Collembola tend to be distributed in cooler habitats, while invasive Collembola prefer moist, warm, low altitudinal habitats (Gabriel et al., 2001, Hugo et al., 2004). Therefore, it is thought that the warming climate of Marion Island (Chown et al., 2007, le Roux and McGeoch, 2008a) has led to an increase in the spread rate of invasive species, including Collembola (Slabber et al., 2007).

Study species

Sagina procumbens was first collected on Marion Island near the old research base in 1965. However, its initial introduction to the island is posited to have occurred in the late 1950s (Cooper et al., 2011, Gremmen et al., 2001). *Sagina procumbens* (Fig. 2B) is a mat-forming stoloniferous ruderal perennial plant (Dumroese et al., 2014), native to the cool and temperate climates of Eurasia and North Africa (Visser et al., 2010, GISD, 2015). In its native range, it can be found in either natural or disturbed habitats (Dumroese et al., 2014). It's thought to be phenotypically plastic and genotypically variable (Grime et al., 1990). Its root system consists of a shallow reaching taproot which divides frequently to form secondary roots (Dumroese et al., 2014). Since its introduction, *S. procumbens* has spread extensively on Marion Island and Prince Edward Island (and on 11 other sub-Antarctic islands), due to its spread rate of 1.84 km^2 and 2.36 km^2 per year on Marion and the less frequented Prince Edward Island respectively, making it the fastest spreading invasive plant species on the Prince Edward Islands (le Roux et al., 2013, Shaw, 2013). On Marion Island *S. procumbens* has invaded six of the seven habitat complexes (Gremmen et al., 2001). Its robust growth in cool and wet climates allows it to dominate over slower growing plant species (pers. obs; Fig. 2C & D). It is particularly abundant and dominant at low altitudes (along the coast) and on disturbed and uncolonized bare soil on Marion Island (pers. obs). However, the impacts of this widespread invasive on Marion Island and on other sub-Antarctic islands are poorly understood (Gremmen et al., 2001, Visser et al., 2010, Cooper et al., 2011).

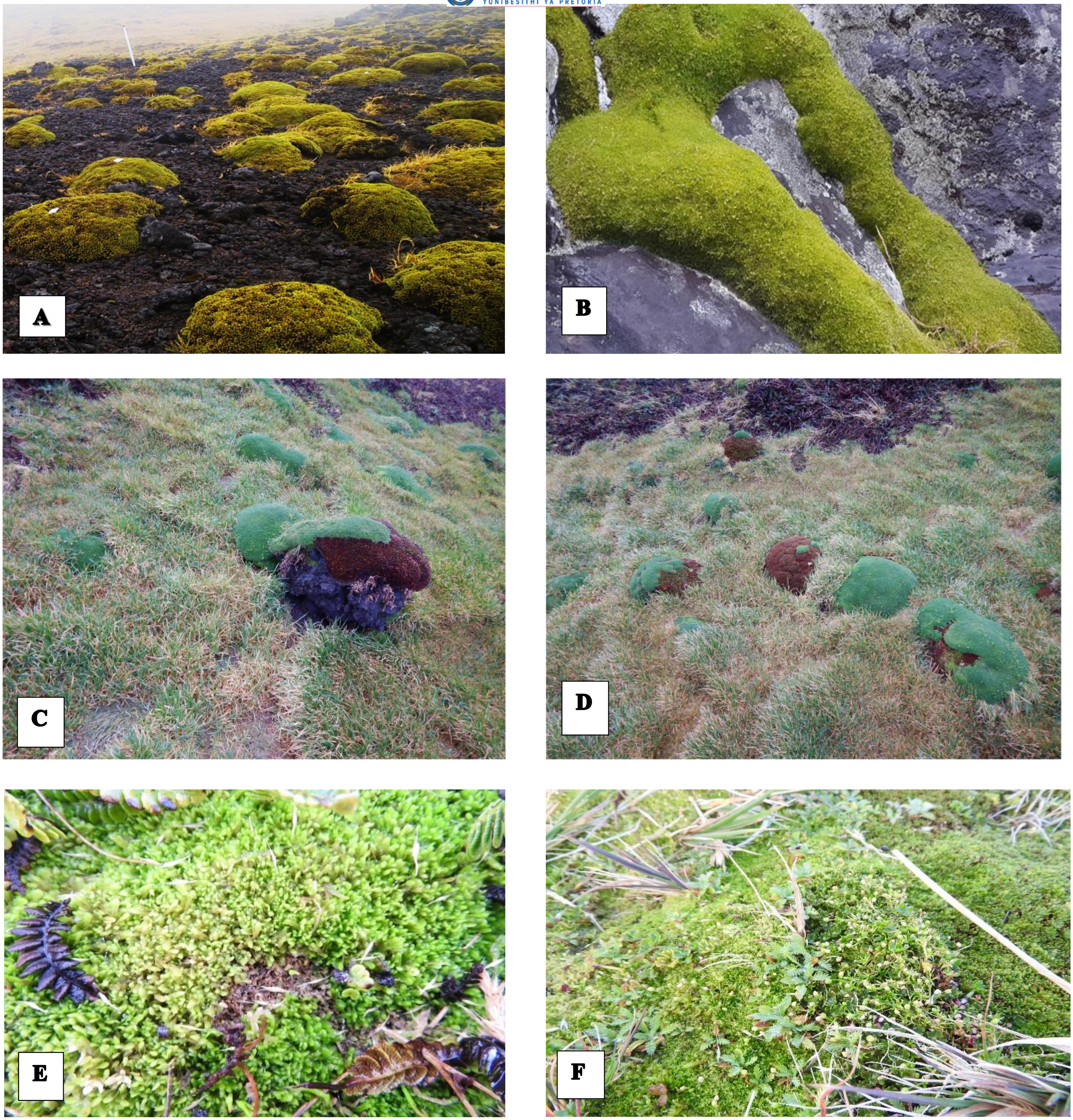

Fig. 2: (A) *Azorella selago* growing extensively in fellfield, (B) *Sagina procumbens* growing aggressively on rock surface, (C-D) *Sagina procumbens* (green) dominating and outcompeting *Azorella selago* cushions (brown) in an area otherwise dominated by the grass *Poa annua*. (E) *Clasmatocolea humilis* growing in mat form. (F) *Sagina procumbens, Azorella selago* and

Clasmatocolea humilis growing in similar conditions on Marion Island. (Photo credits (A) Peter le Roux, (B) Mthokozisi Twala, (C-D) Marike Louw, and (E-F) Michelle Greve)

The objective of this dissertation was to examine the impacts of *S. procumbens* on the biota of Marion Island. I tested whether *S. procumbens* facilitates the establishment of multiple invasive taxa (namely plants and Collembola) and investigated the effects that it has and could have on the ecosystem functioning on Marion Island. Few studies have considered the impacts of one invasive species on multiple taxa across the region. This research will provide insight into the likely impacts of *S. procumbens* and the possible implications that these impacts may have on Marion Island biota and ecosystem functioning.

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Chapter 2: A test of the invasional meltdown hypothesis using the invasive plant, *Sagina procumbens*, on sub-Antarctic Marion Island.

Introduction

Invasive species have significant ecological impacts (Flory and Clay, 2010, Ricciardi et al., 2013, Jeschke et al., 2014). Globally, the impacts of invaders, along with their magnitude, extent and complexity, are increasing (Pyšek and Richardson, 2010). Invasive species that dominate ecosystems can potentially influence the performance and population dynamics of indigenous species in invaded habitats (Richardson et al., 1989, Pyšek and Pyšek, 1995). As a result, the changes induced by invasive species may be dramatic, affecting native biodiversity, and ecosystem structure and function, potentially even resulting in the extinction of native species (Simberloff, 2000).

At the current juncture of increasing rates of biological invasion (Jackson and Grey, 2013), the interaction between multiple invaders has received increasing attention (Barney et al., 2013). The outcome of interspecific interactions can be neutral, negative (e.g. competitive or amensal), or positive (e.g. mutualistic or commensal; Jackson, 2015, Kuebbing and Nuñez, 2015). Due to the potential complexity of the interactions between multiple invasive taxa, relatively little is known about the impacts stemming from these interspecific interactions (Johnson et al., 2009). This makes predicting the overall impact of invasive species more difficult. Classic ecological theory postulates that, through competitive interactions, established invasive species negatively affect other, more recently established alien species, and inhibit them from establishing by occupying any vacant niches (Levine and D'antonio, 1999). However, the recognition of the importance of positive species interactions challenge this ecological paradigm (Bruno et al., 2003, Callaway, 2007). Thus, an opposing hypothesis was proposed by Simberloff and Von Holle (1999), where one or multiple invasive species have a positive effect on other invasive species, causing an accelerating cumulative increase in the success of invaders, coined the ‘invasional meltdown’ hypothesis.

The ‘invasional meltdown’ model suggests that established invasive species facilitate the establishment of other invasive species, as established invaders induce changes in the ecosystem which make the ecosystem more susceptible to further invasions (Gurevitch, 2006, Jackson, 2015). The positive feedback between invaders in an invasional meltdown scenario can lead to an increase in invasive richness, spread and abundance, and a greater impact than the summed impact of individual invasive species (Cushman et al., 2011). Impacts of invasive species are mostly a product of abundance (Vilà et al., 2011); therefore, if the abundance of one invasive species can be significantly increased by facilitative interactions with another invasive species, an invasional meltdown scenario may arise (Simberloff and Von Holle, 1999, Simberloff, 2006). The synergistic impacts of invasive species could very well replace native communities to a point of no return (Simberloff, 2006, Gurevitch, 2006, Green et al., 2011, Jackson, 2015). Facilitation of this nature has been deemed common, but has received limited attention (Richardson et al., 2000, Ricciardi, 2001, Gurevitch, 2006, Green et al., 2011, Jackson, 2015).

Invasional meltdown has, for example, been demonstrated in an aquatic system, through the synergistic interaction of co-occurring freshwater invaders, the omnivorous rusty crayfish (*Orconectes rusticus*) and the herbivorous Chinese mystery snails (*Bellamya chinensis*) (Johnson et al., 2009). The larger and thicker shell size of adult *B. chinensis* protects it from crayfish predation relative to native snail species, which it predates on as well. *Orconectes rusticus* thus reduces the abundance and biomass of native snail populations, consequently reducing competition for resources between the invasive herbivorous *B. chinensis* and native snail community. Therefore, the impacts derived from the synergistic interaction of *O. rusticus* and *B. chinensis* negatively affects the abundance and biomass of native snails (*Physia*, *Helisina*, and *Lymnaea* sp.), leading to the eventual reduction in abundance of native snails. The synergistic effect on the native snail communities is more detrimental than the individual effects of *O. rusticus* and *B. chinensis* (Johnson et al., 2009).

Islands can serve as ideal natural systems for assessing and understanding how ecosystems and community structure react to biological invasions (Gillespie and Clague, 2009) due to their isolation and simplicity. The sub-Antarctic islands, located at approximately 40° – 60° latitude south of the equator (Holdgate, 1970), are some of the most remote and pristine habitats on Earth. However, owing to their isolation from major land masses and unfilled ecological niches (Foxcroft et al., 2013), and their climate (Pendlebury and Barnes-Keoghan, 2007), they are relatively susceptible to invasions (Chown et al., 1998). The escalation in the rate of introduction of invasive species to the sub-Antarctic Islands over the last two centuries coincides with increasing human activities in the region (Chown et al., 1998, 2005). The Prince Edward Islands (Marion Island and Prince Edward Island) are a group of South African islands which have been declared Special Nature Reserves under the South African Environmental Management: Protected Areas Act (De Villiers et al., 2006, Cooper et al., 2009, Foxcroft et al., 2013), as well as a Marine protected area under the Marine Living Resources Act (Foxcroft et al., 2013). Marion Island hosts more invasive species than the neighbouring Prince Edward Island (which is only visited by a select group of researchers every four years), due to an annual turnover of researchers visiting the research base on Marion Island since 1947 (de Villiers and Cooper, 2008, Greve et al., 2017). However, little is known about the ecological impacts of non-vertebrate invaders on these two islands (Greve et al., 2017), as the impacts are seldom reported or quantified (Lee and Chown, 2016). Current knowledge of invasive non-vertebrate alien impacts on Marion Island is largely from *ad hoc* observations and from few structured investigations (Hänel and Chown, 1998, Jones and Ryan, 2010, Lee and Chown, 2016, Greve et al., 2017). Here, I investigate whether an aggressive invasive plant, *Sagina procumbens* (Caryophyllaceae), is causing an invasional meltdown on sub-Antarctic Marion Island.

Sagina procumbens is a cushion and mat-forming vascular plant species that was introduced to Marion Island at least 70 years ago (Gremmen and Smith, 1999), and is native to Eurasia and North Africa (Visser et al., 2010). *Sagina procumbens* has also spread to neighboring Prince Edward Island, where it was dispersed either by birds or wind (Ryan et al., 2003). Its spread rate of 100 to 300 m per year on Marion Island, along with its ability to spread both vegetatively and by seed (Cooper et al., 2011, le Roux et al., 2013), has rendered it practically uncontrollable by known methods. As a result of a wide geographic expansion and ecological tolerance, *S. procumbens* has been listed in the Global Invasive Species Database among the 100 of the "World's Worst" invaders (Lowe et al., 2000). This plant occurs on several sub-Antarctic islands, namely the Falkland Islands, Gough, South Georgia, South Sandwich Islands, Tristan da Cunha, the Prince Edward Islands, the Kerguelen and Crozet Archipelagos, and Amsterdam Island (Lowe et al., 2000).

Little is known about the impacts of *S. procumbens* on the biodiversity and ecosystem functioning in the sub-Antarctic, although observations suggest that it could be negatively impacting biodiversity and ecosystem functioning in the region (Gremmen, 1997, Gremmen and

Smith, 1999, Gremmen et al., 2001, Visser et al., 2010). The aim of this study was thus to test whether *S. procumbens* causes an invasional meltdown in two invasive taxa on sub-Antarctic Marion Island. I investigated whether invasive plant and invasive Collembola communities benefit from the presence of *S. procumbens*. The abundance, species richness and composition of invasive plant and Collembola communities found on *S. procumbens* mats or cushions were compared to those growing in two native plant species, *Azorella selago* (Apiaceae) and the liverwort, *Clasmatocolea humilis* (Geocalycaceae), with similar habits. *Azorella selago* and *C. humilis* are overgrown and killed by *S. procumbens* on Marion Island (pers. obs). Specifically, I tested whether a high invasive plant and Collembola species richness and abundance was associated with *S. procumbens*, but not with *A. selago* and *C. humilis*, and thus whether *S. procumbens* may lead to an invasion meltdown in two very different taxa. In addition, I assessed the impacts of *S. procumbens* on native diversity by comparing numbers, biomass and habitat preference, of native plant and Collembola species found on *S. procumbens* to those found on the two native species (*A. selago* and *C. humilis*).

Under an invasional meltdown scenario, I expected to observe a higher abundance and species richness of invasive taxa, but an unchanged or lower abundance of native species in comparison to *A. selago* and *C. humilis*. A higher abundance and richness of both invasive and native species in both taxa in *S. procumbens* would indicate that *S. procumbens* is a good facilitator for both invasive and native taxa, which would not be in agreement with the invasional meltdown hypothesis. Where evidence of an invasional meltdown is provided, the established invader facilitates the establishment of other invaders, which dominate and lead to the subsequent extinction of native species (Simberloff and Von Holle, 1999, Ricciardi, 2001, O'Dowd et al., 2003, Green et al., 2011, Montgomery et al., 2012). Likewise, I expected *S. procumbens* to enhance the presence of secondary invaders and increase the abundance of invasive species on the invaded communities, leading to the reduction or extirpation of the native species.

Most studies on invasional meltdown have assessed facilitation of one invasive species on only one other invader, or one taxon. Here, I assessed facilitation of one invader on two different taxa; more specifically, I assessed whether *S. procumbens* is facilitating the invasional meltdown of plant and Collembola communities on Marion Island.

Methods

Field sampling

Sampling was conducted on the east coast of Marion Island, during the annual relief expedition in April-May 2017. The coastal areas on Marion Island are characterized by biotic herbfield and fernbrake complexes (Smith and Mucina, 2006, Gremmen and Smith, 2008). Biotic herbfield complex has a higher plant species richness than other vegetation complexes on Marion Island and is dominated by *Poa cookii*, *A. selago*, *Acaena magellanica*, and *C. humilis* (Gremmen and Smith, 2008). Fernbrake vegetation is dominated by the fern *Austroblechnum penna-marina*, although *P. cookii* and *Agrostis magellanica* also occur in this vegetation type (Gremmen and Smith, 2008).

Coastal areas were selected for sampling because *S. procumbens* was observed outcompeting native plant species, including *A. selago* and *C. humilis*, and *S. procumbens* occurred in a higher abundance here than in the other parts of the island (pers. obs.) *Azorella selago* is a cushion-forming plant which is considered to be a keystone species on Marion Island (Hugo et al., 2004). It forms nutrient-rich habitats with a more moderate microclimate than the surrounding substrates (Hugo et al., 2004, le Roux and McGeoch, 2004, Nyakatya and McGeoch, 2007, Cerfonteyn et al., 2011), and several plant and microarthropod species have significantly higher densities on *A. selago* than in other microsites (Hugo et al., 2004, Nyakatya and McGeoch, 2007, Cerfonteyn et al., 2011). *Azorella selago* is the most widespread vascular plant on the island, occurring from sea level to 840 m a.s.l. (le Roux and McGeoch, 2008a). *Clasmatocolea humilis* is a liverwort with a mat growth form. The species is found in the sub-Antarctic and Tristan da Cunha Island, and is more susceptible to desiccation than other species with a cushion growth-form (Gremmen, 1981). On Marion Island it grows mainly in nutrient-enriched low altitude areas (Smith and Mucina, 2006).

Thirty-five study sites were identified in the coastal zone. At each site *S. procumbens* was growing with the two native species: *A. selago* and *C. humilis* (these three species are henceforth referred to as the 'focal plant species'). The focal plant species all support a range of vascular species growing epiphytically on (i.e. rooted within) their cushion or mat form. These two species were selected as comparisons to *S. procumbens* because they are outcompeted by *S. procumbens*, they possess a similar growth form to *S. procumbens*, and, like *S. procumbens*, they support plants growing epiphytically on them. At each study site, the three focal plant species were growing in similar conditions, at a distance of ≤ 2 m from one another. The location of each site was recorded using a hand-held GPS unit (Garmin Montana 610).

To determine whether the cushion volume was a significant contributor to the richness or the abundance of Collembola, the dimensions (length, width, and height) of each cushion plant (*A. selago* and some *S. procumbens*) were measured. Where *S. procumbens* grew as a mat, this was noted and no dimensions were measured. As *C. humilis* was always growing as a mat, its dimensions were not measured. For mat-growing *S. procumbens* and *C. humilis*, an area similar in size to the paired *A. selago* cushion would be delineated for sampling.

The percentage cover of each plant species growing epiphytically on the focal plants was visually estimated to quantify the ability of the focal plant to facilitate other plant species. In addition, a core (with a height of 10 cm and an inner diameter of 7 cm) was extracted from each focal cushion/mat using a stainless steel split corer fitted with PVC pipes (following, e.g., Terauds et al. (2011), Kawaue et al. (2016)) to obtain Collembola samples. After coring, the holes made in the plants by the corer were filled with excess plant and soil material from the core to ensure minimal disturbance to the cored plant. The PVC pipes containing the cores were bagged into labelled airtight plastic bags and stored in cool conditions (similar to field conditions) in the laboratory for a maximum of eight hours until microarthropod extraction started.

Microarthropods were extracted from the plant cores into 96 or 99.9% ethanol using Tullgren-Berlese funnels (Berlese, 1905, Tullgren, 1918, Macfadyen, 1961, Janion-Scheepers, 2013) over a period of three days at room temperature with the blinds drawn and lights switched on (to standardize light conditions). All Collembola extracted from the cores were sorted under a standard stereo microscope, identified to species level and counted using a complete reference key for Marion Island (Janion-Scheepers, 2017).

Temperature was measured inside cushions/mats of the three focal plant species to ascertain whether *S. procumbens* changes the microenvironment experienced by the epiphytic plants and Collembola relative to the two native focal plants. Fifteen sites were selected, each consisting of the three focal plant species growing in similar conditions at a maximum distance of *ca.* 2 m from each other. One plant of each of the three focal species was selected at each site and its dimensions (length, width, and height) recorded if the plant under consideration was growing in a cushion-form (no measurement was taken if plants were growing in mat form).

Thermochron iButton dataloggers (DS1922L#F50 and DS1923#F5, Semiconductor Corporation, Dallas/Maxim, TX, USA) were used to record temperature at 15-minute intervals at a resolution of 0.0625°C. The iButtons were placed in labeled Ziploc bags for waterproofing. A 3 cm deep incision was made in each focal plant, into which the dataloggers were inserted. The iButtons were left in the cushions for 16 consecutive days (15 April – 1 May 2017) before being collected. Of the 45 iButtons that were deployed, three were missing (two from *S. procumbens* and one from *A. selago*) at the end of the sampling period.

Analyses

Sampling effort and effect of cushion volume

Site-based rarefaction curves were used to assess whether sampling effort of epiphytic plant and Collembola communities was adequate (Gotelli and Colwell, 2010) for each of the focal plant species across the 35 sites.

General linear models (McCullagh and Nelder, 1989) with square-root transformed data (for the analyses to meet model assumptions) were used to assess whether the cushion volume of the two cushion-forming focal species (*S. procumbens* and *A. selago*) was a significant contributor to the richness or the abundance of Collembola. Cushion volume (V) was calculated using the geometric volume formula for half a sphere ($V = (2/3)\,\pi\, r^3$), where half the length of the cushion was used as the radius (r) of half the sphere.

Testing the invasional meltdown hypothesis

Only two invasive plant species were found growing epiphytically on the focal species, both of which were recorded infrequently; therefore, no comparison between the richness of invasive plants growing on *S. procumbens* and those growing on the two native focal species could be conducted. Only a generalized linear mixed model (Rabe-Hesketh and Skrondal, 2008; using a Poisson distribution and an identity link function) was run to assess whether the native species richness of plants growing on *S. procumbens* was significantly different to that growing on either of the other two native focal species. Site was included as a random variable. Hence, analyses to assess whether invasive species richness of plants growing on *S. procumbens* was significantly different to those growing on the native focal species could not be conducted. A pairwise comparison for the model was done using the Tukey Honest Significant Difference test.

For Collembola, generalized linear mixed models (Rabe-Hesketh and Skrondal, 2008; using a Poisson distribution and an identity link function) were used to test whether the richness and abundance of Collembola in *S. procumbens* was significantly different to that in *A. selago* and *C. humilis* for both invasive and native species: models for invasive species and native species were run separately. Site was included in all models as a random variable.

As a result of the different Collembola species possessing different body sizes, the invasional meltdown hypothesis was also tested using biomass to evaluate whether invasive Collembola were benefitting more from *S. procumbens* than from the native focal plant species. The biomass (an indicator of the size of each Collembola species and thus a proxy of how much they consume) of each of the Collembola species was estimated by using the length of the individual Collembola species obtained from Janion-Scheepers (2017) in association with the regression equation of Ganihar (1997: Biomass = $(0.153 \times \text{length})^{2.3}$). Subsequently, the biomass of each Collembola species was multiplied by its total abundance per focal plant core, and the values for all invasive and for all native species summed, to obtain the total biomass of both invasive and native Collembola. General linear mixed effects models (Rabe-Hesketh and Skrondal, 2008) with log-transformed data were used to assess whether the biomass of Collembola differed between the three focal plant species for both invasive and native species: again, separate models were run for invasive and native species. Pairwise comparisons for all models were done using the Tukey Honest Significant Difference test.

Testing whether S. procumbens has a negative impact on native taxa

Generalized linear models (McCullagh and Nelder, 1989; with a Poisson distribution and an identity link function) were used to compare native with invasive Collembola richness and abundance extracted from *S. procumbens*, to assess whether *S. procumbens* has an overall negative effect on native Collembola diversity.

PERMANOVA (with site included in all models as a random variable) was used to test for significant differences in the composition (Anderson, 2014) of plant and Collembola communities from the three focal plant species. The difference in composition of plant and Collembola communities was visualized using non-metric multidimensional scaling (NMDS) using R3.3.3 (R Core Team, 2016). Separate models were run for plant, invasive and native Collembola species.

Furthermore, to assess whether the preferred habitat (i.e. euedaphic (living within the soil) or hemiedaphic (litter dwelling)) of Collembola on *S. procumbens* is different to that of *A. selago* and *C. humilis*, a hierarchical clustering analysis was used (Maechler et al., 2013). The hierarchical clustering analysis groups pairs of samples that are similar (i.e. samples that have the lowest dissimilarity) and represents them in a compact visualization of a dendrogram.

Microclimatic parameters of focal plants

To test whether *S. procumbens* changes the microclimatic conditions experienced by the epiphytic plants and Collembola, the minimum, mean, maximum and range of temperatures of *S. procumbens* were compared to those of the two native focal species using generalized linear mixed models (McCulloch and Neuhaus, 2014; using a Gaussian distribution with an identity link function). Temperature statistics were calculated from iButton data collected on 15 April 2017; with the collection of temperature data in all three focal plants commencing at 19:59 EAT (East African Time), and terminated at 08:59 EAT on 1 May 2017. Site was added to the models as a random effect. Pairwise comparisons for all models were done using the Tukey Honest Significant Difference test.

All models were run in R 3.3.3 (R Core Team, 2016) using the basic packages ‘car’ (for fitted regression models; Fox and Weisberg, 2011), ‘lme4’ (for analyzing linear mixed models and generalized linear mixed models; Bates et al., 2015), ‘lmerTest’ (provides anova and summary tables for linear mixed models and generalized linear mixed models; Kuznetsova et al., 2017), ‘vegan’ (used for multivariate analyses; Oksanen et al., 2016) and Multcomp (for pairwise comparisons; Hothorn et al., 2008).

Results

Sampling effort and effect of cushion volume

A total of 19 plant species were found growing epiphytically on *S. procumbens*, *A. selago* and *C. humilis*, of which two were invasive. Fifteen Collembola species, with a cumulative abundance of 10,689 individuals, were collected from cores taken from the three focal species.

Site-based species rarefaction curves of plant species growing epiphytically on, and of Collembola collected from, the three focal plant species indicated that sampling was approaching, or had reached, an asymptote (Fig 3).

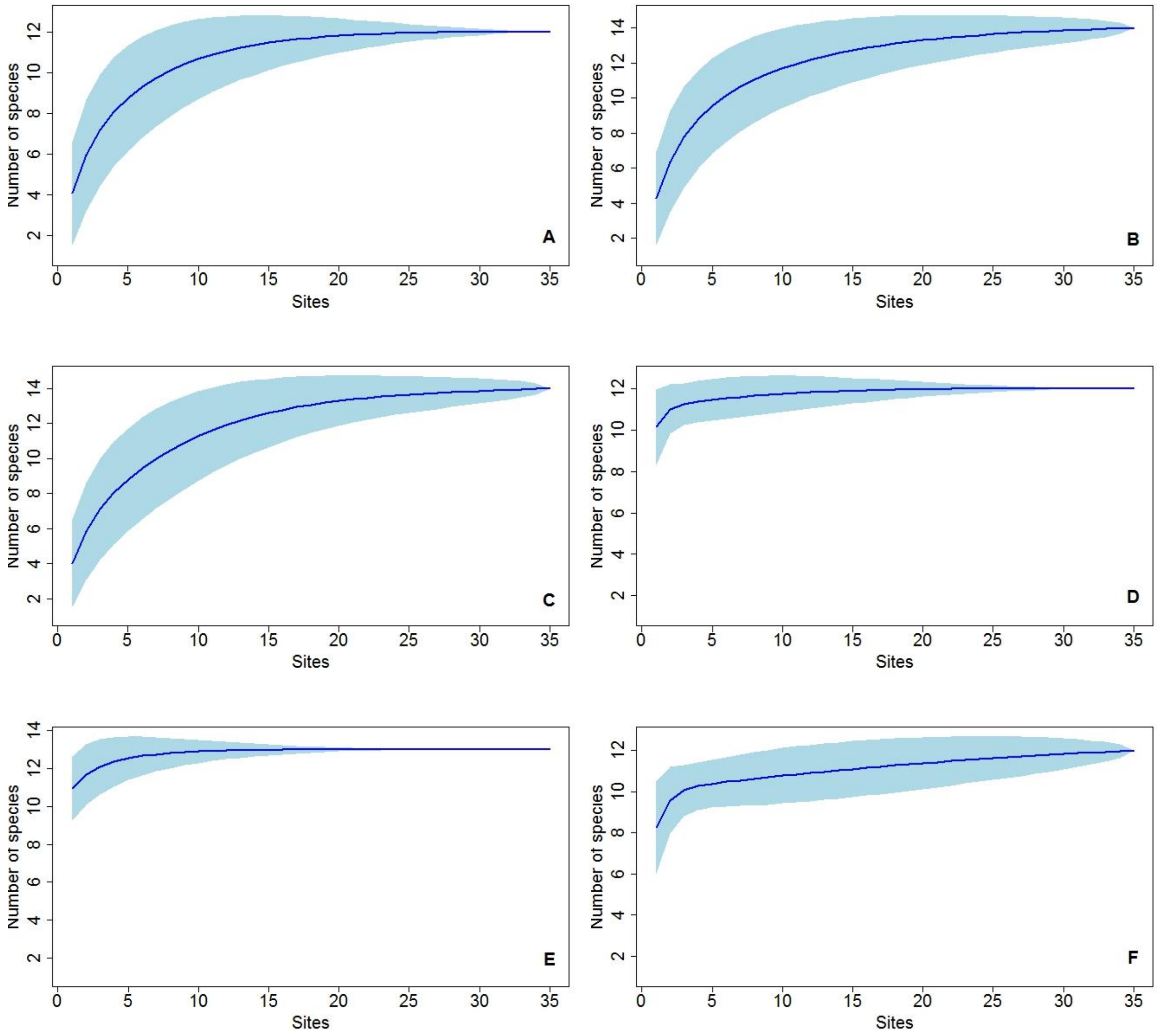

Fig. 3: Site-based rarefaction curves for plant species growing epiphytically on (A) *Sagina procumbens*, (B) *Azorella selago*, and (C) *Clasmatocolea humilis*, and of Collembola collected from (D) *Sagina procumbens*, (E) *Azorella selago*, and (F) *Clasmatocolea humilis.*

The cushion volume of both *A. selago* and *S. procumbens* plants did not significantly affect the richness and the abundance of Collembola species on either focal plant species (p > 0.1; Table 1). This indicates that cushion size did not significantly affect the outcome of this study, and cushion size was thus not considered in any further analyses.

Table 1: Results from general linear models evaluating whether cushion volume affects the richness and abundance of Collembola species found in *Sagina procumbens* and *Azorella selago*.

Species	**Measure**	**Estimate**	**F-value**	**Degrees of freedom**	**p-value**	**Model R^2 (%)**
Sagina procumbens	Richness	0.615	0.023	1, 12	0.216	8.312
Azorella selago	Richness	0.169	0.017	1, 33	0.581	2.977
Sagina procumbens	Abundance	2616.850	0.853	1, 12	0.538	1.145
Azorella selago	Abundance	-6.951	0.009	1, 33	0.595	3.002

Testing the invasional meltdown hypothesis on epiphytic plant communities

As the number of invasive vascular plants growing epiphytically on *S. procumbens* and the two native focal plant species was less than two plants on average, invasive plants were excluded from analyses. Native plant richness did not differ significantly between the focal plant species (p > 0.859; F = 0.15; df = 2, Fig. 4, Table S1).

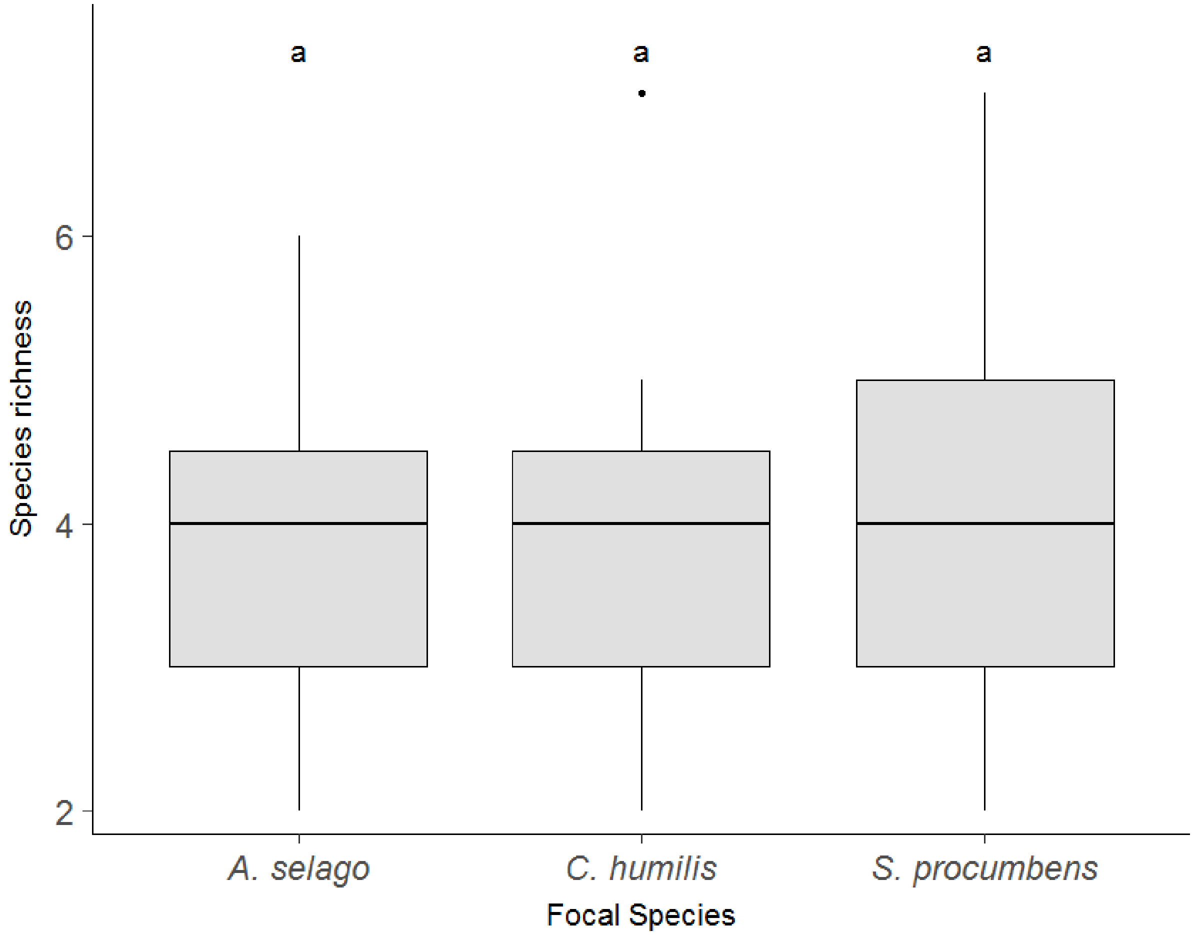

Fig. 4: Richness of native plant species growing on the three focal plant species. Richness of native plant species did not differ significantly between any of the focal plant species (p > 0.859). The extremes of the box indicate the interquartile range, while the horizontal bar in the center of the box represents the median. The whiskers show the first and third quartile. Dots represent outliers. Different letters indicate significant statistical differences between focal plant species.

Testing the invasional meltdown hypothesis on Collembola communities

Invasive Collembola species richness was significantly higher in *S. procumbens* ($p < 0.001$; F = 13.76; df = 2), than in the two native focal plant species (Fig. 5A, Table S1); in contrast, the richness of native Collembola species in *S. procumbens* was not significantly different ($p > 0.1$; F = 2.09; df = 2) to that in the native plant species (Fig. 5B, Table S1).

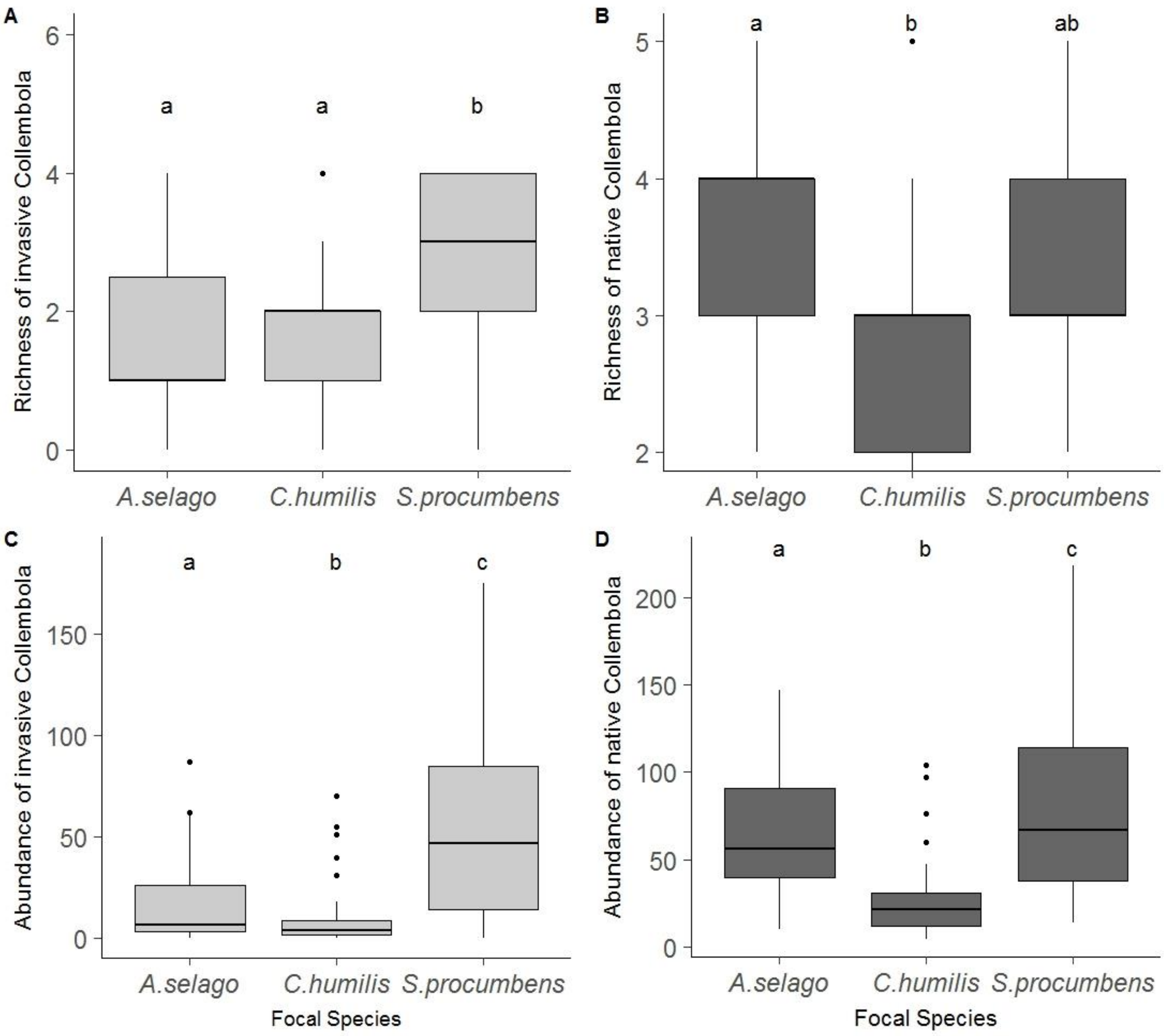

Fig. 5: Species richness of (A) invasive and (B) native Collembola species, and abundance of (C) invasive and (D) native Collembola species from the invasive plant *Sagina procumbens* and the native focal plants *Azorella selago* and *Clasmatocolea humilis*. The extremes of the box indicate the interquartile range, while the horizontal bar in the center of the box represents the median. The whiskers show the first and third quartile. Dots represent outliers. Different letters indicate significant statistical differences between focal plant species.

A higher abundance of both invasive (Fig. 5C, Table S1) and native Collembola (Fig. 5D, Table S1) was found in *S. procumbens* than in the two focal native plant species. The higher abundance of Collembola in *S. procumbens* was mainly due to three dominant species, namely the invasive

Ceratophysella denticulata (which constituted 19.9% of all individuals sampled and 53.7% of all individuals from invasive species sampled in *S. procumbens*), and the two native Collembola species; *Cryptopygus dubius* and *Folsomotoma marionensis*, which constituted 27.5% and 23.8% of all Collembola species sampled in *S. procumbens* respectively (Table S4). The latter two native species were also the two most abundant species in the two native focal plant species. *Megalothorax minimus*, an invasive species, was fairly abundant in *A. selago*. No Collembola species were particularly abundant in *C. humilis*. (Table SII).

The biomass of invasive Collembola species was significantly higher in *S. procumbens* than in the other two native focal species ($p < 0.001$; $F = 28.08$; $df = 2$, Fig. 6A), and the biomass of native Collembola did not differ significantly between *S. procumbens* and *A. selago* (Fig. 6B, Table S1); however, the biomass of native Collembola was higher in *S. procumbens* than *C. humilis*.

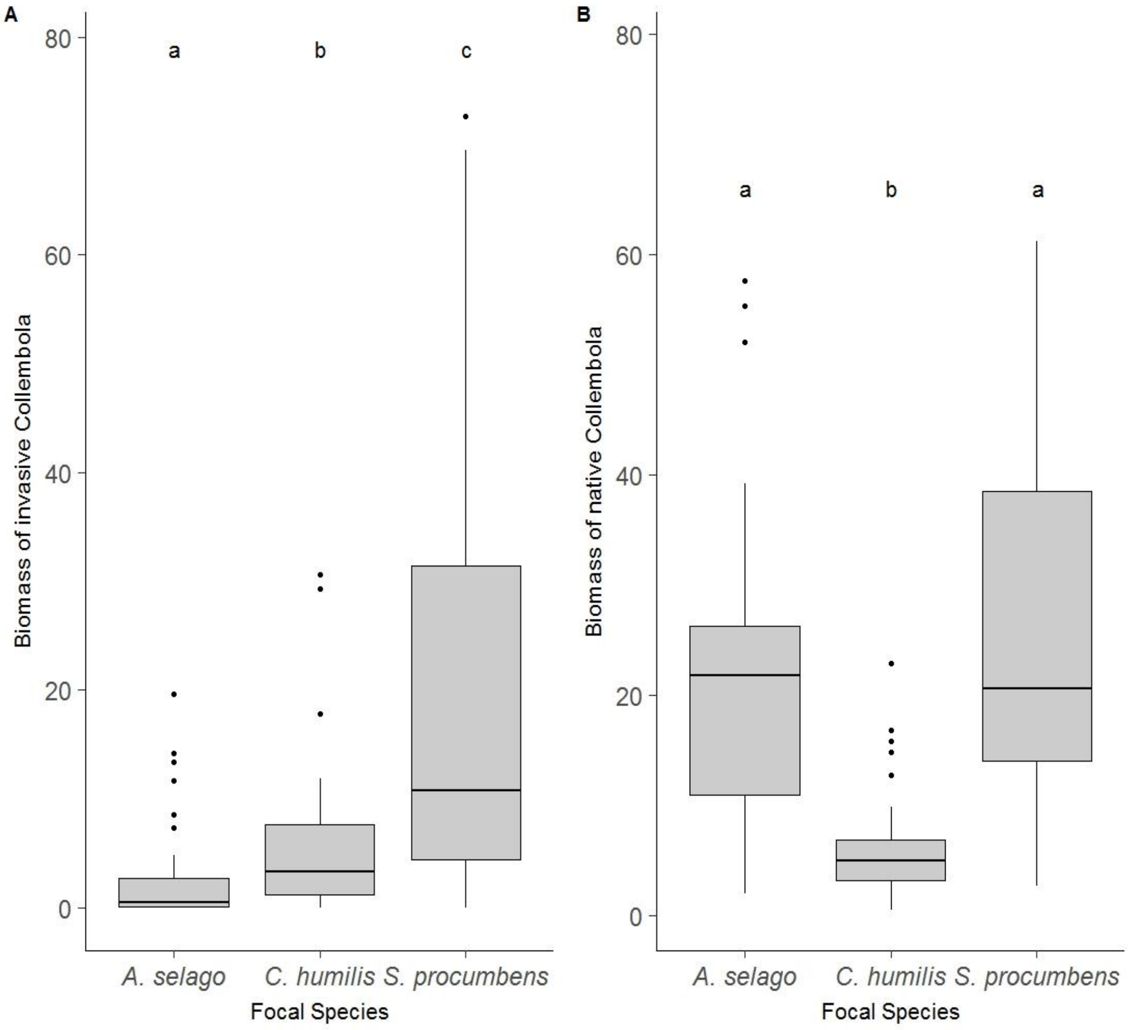

Fig. 6: Biomass of (A) invasive and (B) native Collembola species extracted from the invasive plant *Sagina procumbens* and the native focal plant species *Azorella selago* and *Clasmatocolea humilis*. The extremes of the box indicate the interquartile range, while the horizontal bar in the center of the box represents the median. The whiskers show the first and third quartile. Dots represent outliers. Different letters indicate significant statistical differences between focal plant species.

Testing whether S. procumbens has a negative impact on native taxa

There was no significant difference between the richness of native and of invasive Collembola assemblages in *S. procumbens* ($p > 0.05$; F = 0.017017; df = 1; $R^2 = 0.31\%$); however, the abundance of native Collembola was significantly higher than that of invasive Collembola ($p < 0.001$; F = 22.260; df = 1; $R^2 = 30.44\%$).

The composition of epiphytic plant communities (Fig. 7) did not differ significantly between the focal plant species. Invasive Collembola species composition differed significantly ($p < 0.001$)

between the three focal plant species (Fig. 8A). Native Collembola species composition was also significantly different between the three focal plant species ($p < 0.001$; Fig. 8B); however, species composition clustered more for invasive Collembola species (Fig. 8A) than for the native Collembola species (Fig. 8B).

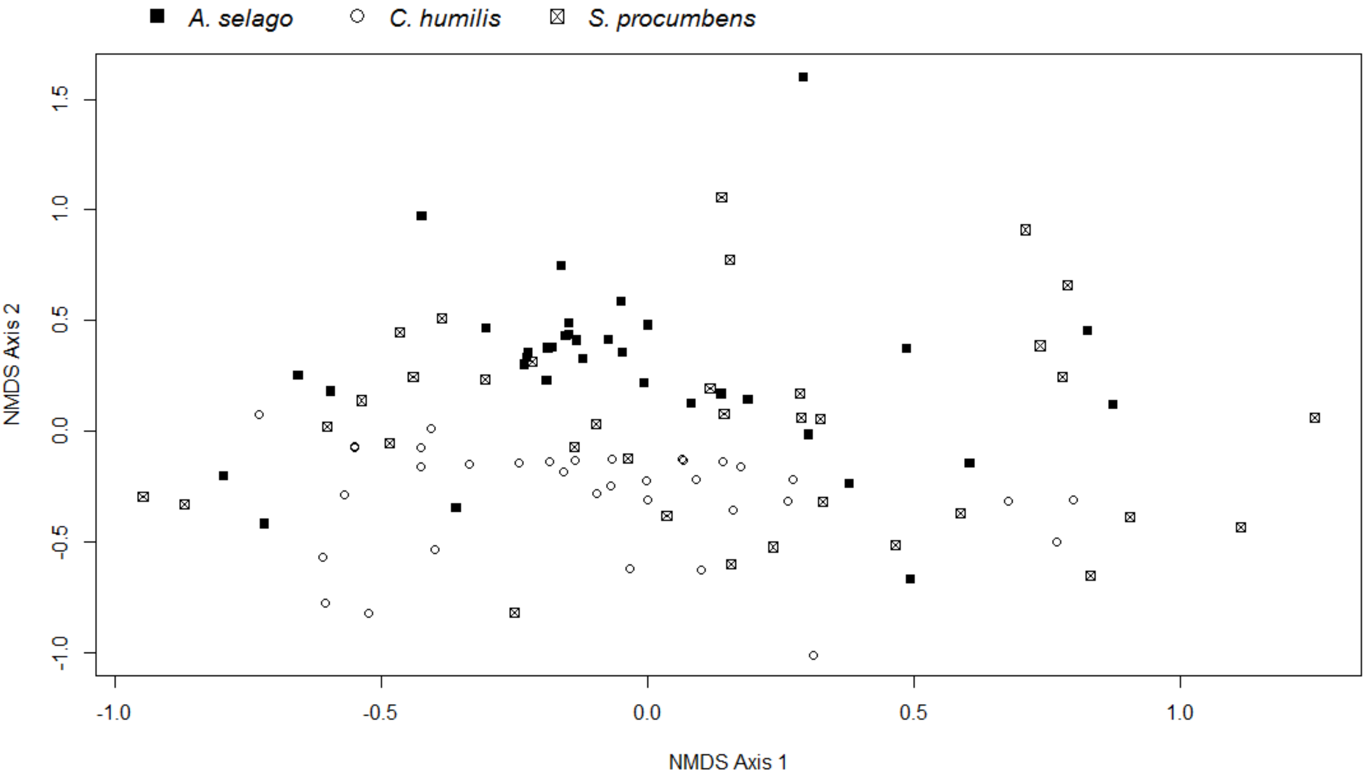

Fig. 7: NMDS ordination illustrating species composition of native plant species communities growing epiphytically on *Sagina procumbens, Azorella selago* and *Clasmatocolea humilis.* Composition of epiphyte plant communities did not differ between focal plant species (p = 0.1, Stress value = 24.2%).

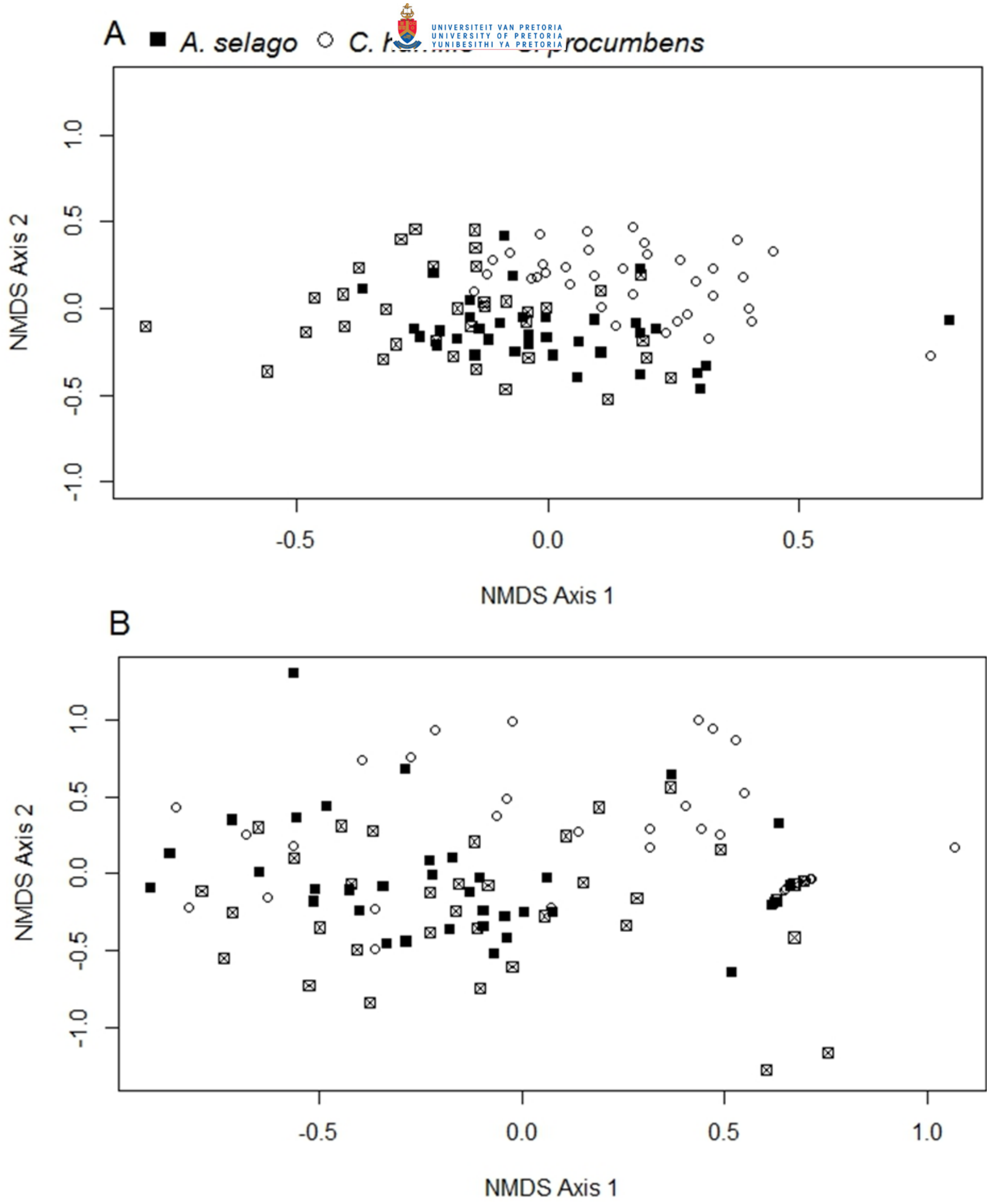

Fig 8: NMDS ordination plot illustrating species composition of (A) invasive and (B) native Collembola found in three different focal species, namely *Sagina procumbens, Azorella selago* and *Clasmatocolea humilis*. Composition of invasive and native Collembola differed significantly between focal plant species. ($p < 0.001$, Stress value = 24.7% (invasive); $p < 0.001$, stress value = 19.7% (native)).

The hierarchical clustering analysis (Fig. S1) showed no obvious pattern of clustering for any ecological habitat preference of Collembola between the three focal plant species.

Microclimatic parameters of focal plants

All descriptive temperature measurements, with the exception of mean temperature, were significantly different between the three focal plant species (Fig. 9). However, *S. procumbens* displayed an intermediate maximum, minimum and range of temperature. Maximum and range of temperature were highest in *A. selago*, followed by *S. procumbens* and then *C. humilis*. Minimum temperature was highest in *C. humilis*, followed by *S. procumbens* and then *A. selago.*

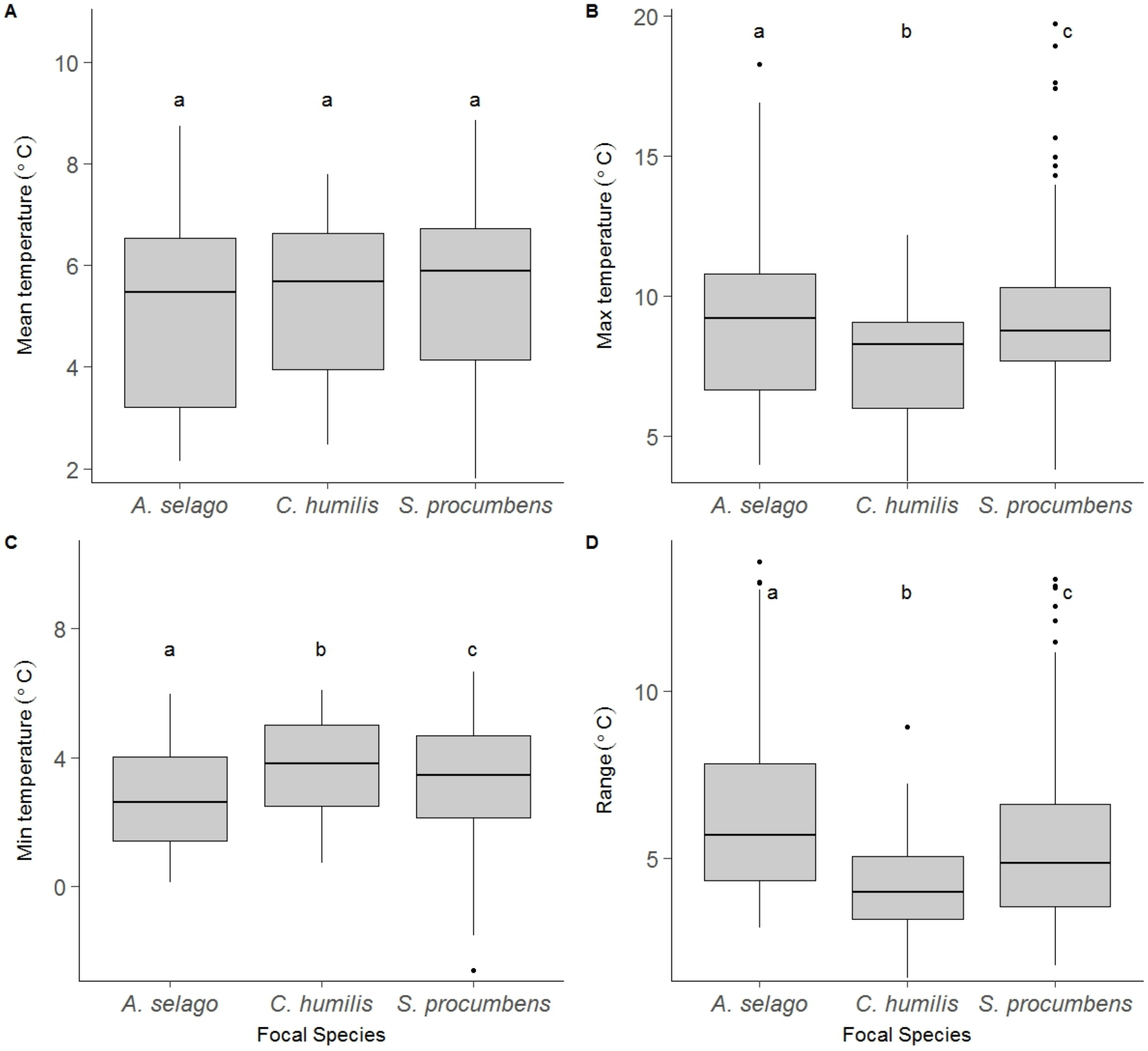

Fig. 8: Differences in thermal conditions between three focal plant species. (A) Mean, (B) maximum, (C) minimum temperature, and (D) range of temperature. The extremes of the box indicate the interquartile range, while the horizontal bar in the center of the box represents the median. The whiskers show the first and third quartile. Dots represent outliers. Different letters indicate significant statistical differences between focal plant species.

Discussion

The primary aim of this project was to assess whether the widespread and aggressive invader *S. procumbens* causes an invasional meltdown in two different taxa (Collembola and plant communities) on Marion Island. I found mixed evidence of invasional meltdown, with plants showing no evidence in support of an invasional meltdown, while Collembola provided partial support of an invasional meltdown model.

The invasional meltdown hypothesis could not be substantiated for vascular plants. There was a low number of invasive vascular plant species growing epiphytically on the focal plant species. My results suggest that there was equal facilitation across all three focal species. Indeed, on Marion Island it has been shown that *A. selago* facilitates other vascular plants (e.g. *Agrostis magellanica*; le Roux and McGeoch, 2008b, le Roux and McGeoch, 2010), although little research has looked at facilitation by other cushion- or mat-forming species on the island. Thus, invasive *S. procumbens* does not facilitate other invasive plants more than native plants. This result is in broad agreement with previous studies that found no support for the invasional meltdown hypothesis for plants (Pearson et al., 2016). Indeed, only a few studies have substantiated plant-plant invasional meltdowns (Flory and Bauer, 2014, Sheppard et al., 2018). It appears that very few studies have tested invasional meltdowns in plants (Ricciardi, 2003, Conners, 2012), despite the large number of invasive plant species occurring globally.

Invasive Collembola richness was significantly higher in *S. procumbens* than *A. selago* and *C. humilis*, while the richness of native Collembola species was not significantly different in *S. procumbens* from that of *A. selago*, nor the richness of *C. humilis*. This provides evidence in support of the invasional meltdown hypothesis because invasive species benefitted from *S. procumbens*, while native Collembola species did not.

The impact of invasive species is often a function of their abundance and can be enhanced by facilitative interactions with other invaders (Simberloff and Von Holle, 1999, Ricciardi, 2001). Additionally, biomass gives an indication of the relative strength of the invasive species' impact and can used as a measure for the impact of invasive species (Parker et al., 1999, Pearson et al., 2016). Therefore, the greater the abundance and biomass of invasive Collembola species, the greater and more pronounced their interaction will be with *S. procumbens*, and the greater their potential ecological impact will be. Hence, the abundance and biomass of invasive species are crucial metrics in the quantification of invasive species' ecological impacts (Pearson et al., 2016). Under the invasional meltdown hypothesis, the facilitation by *S. procumbens* of a higher abundance of invasive (but not native) species was expected, but was not found. However, the biomass of invasive species was significantly higher in *S. procumbens* than *A. selago* and *C. humilis* and the biomass of native Collembola was also significantly higher in *S. procumbens* than *C. humilis* but did not differ significantly between *S. procumbens* and *A. selago*, consequently, providing some evidence for the invasional meltdown in Collembola biomass in *S. procumbens*.

The invasional meltdown hypothesis emphasizes positive interactions (e.g. facilitation) rather than negative interactions (e.g. competition) among invaders (Simberloff and Von Holle, 1999, Simberloff, 2006, Jackson, 2015). Under the invasional meltdown model, positive interactions could threaten community integrity through the increase in the cumulative number of successful introductions of invasive species, which are expected to disrupt native populations, thus making the community easier to invade. Once established, some invasive species may modify habitat conditions to favor further invasions (as in the case with *S. procumbens*; Simberloff and Von Holle, 1999, Ricciardi, 2001). This creates a positive feedback system that accelerates the accumulation of invasive species and enhances their synergistic impacts (Simberloff and Von Holle, 1999).

In other studies where an invasional meltdown has been documented, invading species have acted in consort, sometimes forming so-called "synergistic juggernauts" that had more severe joint impacts than that of the several species acting separately (Simberloff and Von Holle, 1999, Ricciardi, 2001, O'Dowd et al., 2003, Green et al., 2011, Von Holle, 2011, Montgomery et al., 2012). In these studies, the synergistic impacts of the invading species devastated native populations (Simberloff and Von Holle, 1999, Montgomery et al., 2012, Neumann et al., 2014), and dominated and extirpated functionally integral native species, which modified ecosystem dynamics (O'Dowd et al., 2003, Ricciardi, 2003, Abbott and Green, 2007, Green et al., 2011). Consequently, ecosystems were modified to preferential states of invasive species, making the native community more susceptible to the establishment of previously unsuccessful invasive taxa (Bially and Macisaac, 2000, O'Dowd et al., 2003, Green et al., 2011). Ecosystem functional and structural changes induced by invasive species are particularly apparent on islands where the native functional redundancy is low, food webs were simple, and the fraction of introduced species was large (White and Harris, 2002, O'Dowd et al., 2003, Abbott and Green, 2007, Green et al., 2011, Montgomery et al., 2012, Ricciardi et al., 2013). Based on my observations, *S. procumbens* may induce direct functional changes, e.g. by overgrowing *A. selago* plants (pers. obs.) and changing associated Collembola species composition, but indirect effects through invasional meltdown are restricted to increases in the richness and biomass of invasive Collembola in *S. procumbens*. The impacts of such changes on the function of the Marion Island ecosystem remain to be determined.

The high abundance of both native and invasive Collembola species found in *S. procumbens* could possibly be explained by Collembola's preference to feed on non-arbuscular mycorrhizal fungi (Caltrans, 2011). These are present on the roots of *S. procumbens* (Frampton and Hopkin, 2001, Wang and Qiu, 2006, Caltrans, 2011), but appear to be absent from *A. selago* and *C. humilis* (Frenot et al., 2005a, Weakley, 2015). This preferential feeding of Collembola on non-arbuscular mycorrhizal fungi is a behavior which could favour the growth of *S. procumbens* by increasing nitrogen mineralization in the roots of *S. procumbens* (Gange, 2000, Frampton and Hopkin, 2001).

Ceratophysella denticulata (an invader from central Europe) was the most abundant invasive Collembola found on *S. procumbens*. It is an r-selected species (Greenslade and Convey, 2012), as it has a high dispersal ability, a short life cycle and lays a large number of small eggs (Greenslade and Convey, 2012). *Ceratophysella denticulata* belongs to the family Hypogasturidae, known for dominating areas to which it has become invasive, and impacting native biota, such as reducing native Collembola richness and abundance (Convey et al., 1999, Greenslade, 2002, Terauds et al., 2011). Based on the dominance of *C. denticulata*, a consequent decrease in the native Collembola species was expected, which would have substantiated the invasional meltdown model; however, results indicate that not to be the case. Two other invasive species (*Parisotoma notabilis* and *Isotomurus maculatus*) dominated with *C. denticulata* in *S. procumbens*, a relationship possibly driven by *S. procumbens*' facilitative ability. Apart from these two species being r-selected and considered a great risk to the sub-Antarctic based on a risk assessment done by Greenslade and Convey (2012), not much is known about their impacts on either plant or Collembola communities.

Little evidence was found of *S. procumbens* directly negatively impacting native vascular plants growing on, and native Collembola living in, *S. procumbens*, as neither the abundance nor composition of native taxa seemed to be negatively affected by *S. procumbens.* However, Simberloff (2011) warns that invasive species that show little or no impact could have greater impacts in the future.

Therefore, little evidence for direct negative impacts of *S. procumbens* on native plants and Collembola was found in this system; yet evidence for indirect negative impacts mainly associated with invasional meltdown (i.e. facilitation of invasive Collembola by *S. procumbens*) were found.

Whether these indirect impacts influence ecosystem resilience is yet to be determined. No study has assessed the functional complementarity of organisms on Marion Island; but because Marion Island is a relatively species poor system (Smith et al., 2001), one could assume that it possesses a low native species functional complementarity (i.e. no functional equivalent replacements). Maintaining this notion, with *S. procumbens* facilitating invasive Collembola, which may impact native Collembola, crucial ecosystem functions, may be lost.

Changes in the richness and abundance of plants and Collembola with *S. procumbens* do not appear to reflect the microclimatic conditions associated with *S. procumbens*. Extreme temperatures and high daily thermal oscillations are the main climatic factors determining microarthropod reproductive success and survival (Molina-Montenegro et al., 2006, Cavieres et al., 2007, Jarošík et al., 2015). The lower Collembola abundance in *C. humilis* is therefore not an indication of the microenvironment being more stressful for Collembola species as this focal plant had the least extreme and least variable thermal conditions. Although not measured, this species seemed to hold more moisture than the other two focal species (pers. obs), which could be a contributing factor for lower Collembola abundance in *C. humilis* (Marx et al., 2009).

Under further climate change, invasional meltdown effects on Collembola could worsen. Invasive Collembola on Marion Island develop faster than their indigenous equivalents, despite the alien and native species not differing in their lower developmental thresholds (Janion et al., 2010). Moreover invasive Collembola can survive higher temperatures than their native congeners (Slabber et al., 2007). As a result, further warming of the island will likely disproportionately benefit the invasive Collembola species (Chown et al., 2007). Increases in temperatures could additionally favour the spread of invasive Collembola by allowing them to colonize new habitats, enabling invasive species to expand their geographic ranges (Cannon, 1998, Gabriel et al., 2001, Robinet and Roques, 2010, Treasure, 2012).

In summary, an invasional meltdown associated with *S. procumbens* was not observed for vascular plants, although some evidence was found for Collembola. Considering the key contribution of Collembola to nutrient cycling in the sub-Antarctic (Hugo et al., 2004, Verma and Paliwal, 2010), the influence of *S. procumbens* on the richness, abundance and biomass of invasive Collembola species has the potential to affect ecosystem functioning in the region. Overall, the results from this study highlight the importance of considering the ecological impacts of species invasions across multiple taxa, especially where the invading species is a habitat-forming organism.

Supplementary data

Table SI: Model statistics of generalized linear mixed models (for richness and abundance) and general linear mixed models (for biomass) comparing richness, abundance and biomass between three focal plant species, *Sagina procumbens, Azorella selago* and *Clasmatocolea humilis*. The taxa that are compared between focal plants are indicated in the “Organism” column. The asterisks (*) next to F-values indicate significant differences between focal plants.

Measure	**Organism**	**F-value**	**Degrees of freedom**	**χ^2**	**Model R^2 (%)**
Richness	Native plants	0.15	2	0.86	0.32
Richness	Invasive Collembola	13.76***	2	$6.65x10^{-7}$	18.47
Richness	Native Collembola	2.09	2	0.12	4.55
Abundance	Invasive Collembola	1143.50***	2	$2.20x10^{-16}$	43.06
Abundance	Native Collembola	579.66***	2	$2.20x10^{-16}$	37.58
Biomass	Invasive Collembola	28.08***	2, 68	0.02	45.63
Biomass	Native Collembola	33.72***	2, 68	$2.26x10^{-15}$	14.60

Table SII: Mean and coefficient of variation of abundance of Collembola species per plant core extracted from the three focal plant species, *Azorella selago, Clasmatocolea humilis* and *Sagina procumbens*. The Collembola indicated with an asterisk (*) were introduced to Marion Island.

Collembola species	**Plant Species**		
	A. selago	***S. procumbens***	***C. humilis***
Ceratophysella denticulata*	2.200 ± 2.301	50.743 ± 1.933	7.714 ± 2.044
Tullbergia bisetosa	7.343 ± 1.176	7.914 ± 1.292	1.057 ± 2.350
Cryptopygus tricuspis	1.543 ± 2.688	0.714 ± 5.677	0.829 ± 2.475
Cryptopygus dubius	28.400 ± 8.625	36.743 ± 1.296	18.686 ± 1.152
Cryptopygus antarcticus	1.829 ± 2.621	2.429 ± 3.282	1.343 ± 2.416
Parisotoma notabilis*	1.714 ± 4.389	20.114 ± 2.183	0.057 ± 4.121
Folsomotoma marionensis	26.543 ± 1.298	41.943 ± 1.784	4.229 ± 1.118
Mucrosomia caeca	4.571 ± 2.375	4.629 ± 2.208	1.029 ± 1.951
Isotomurus maculatus*	1.143 ± 1.992	5.714 ± 1.319	1.886 ± 1.360
Pogonognathellus flavescens*	--	--	0.029 ± 5.916
Megalothorax minimus*	12.657 ± 1.325	7.7432 ± 0.021	1.171 ± 1.751
Sminthurinus granulosus	0.114 ± 4.636	0.200 ± 5.116	--
Sminthurinus tuberculatus	--	0.429 ± 4.744	--

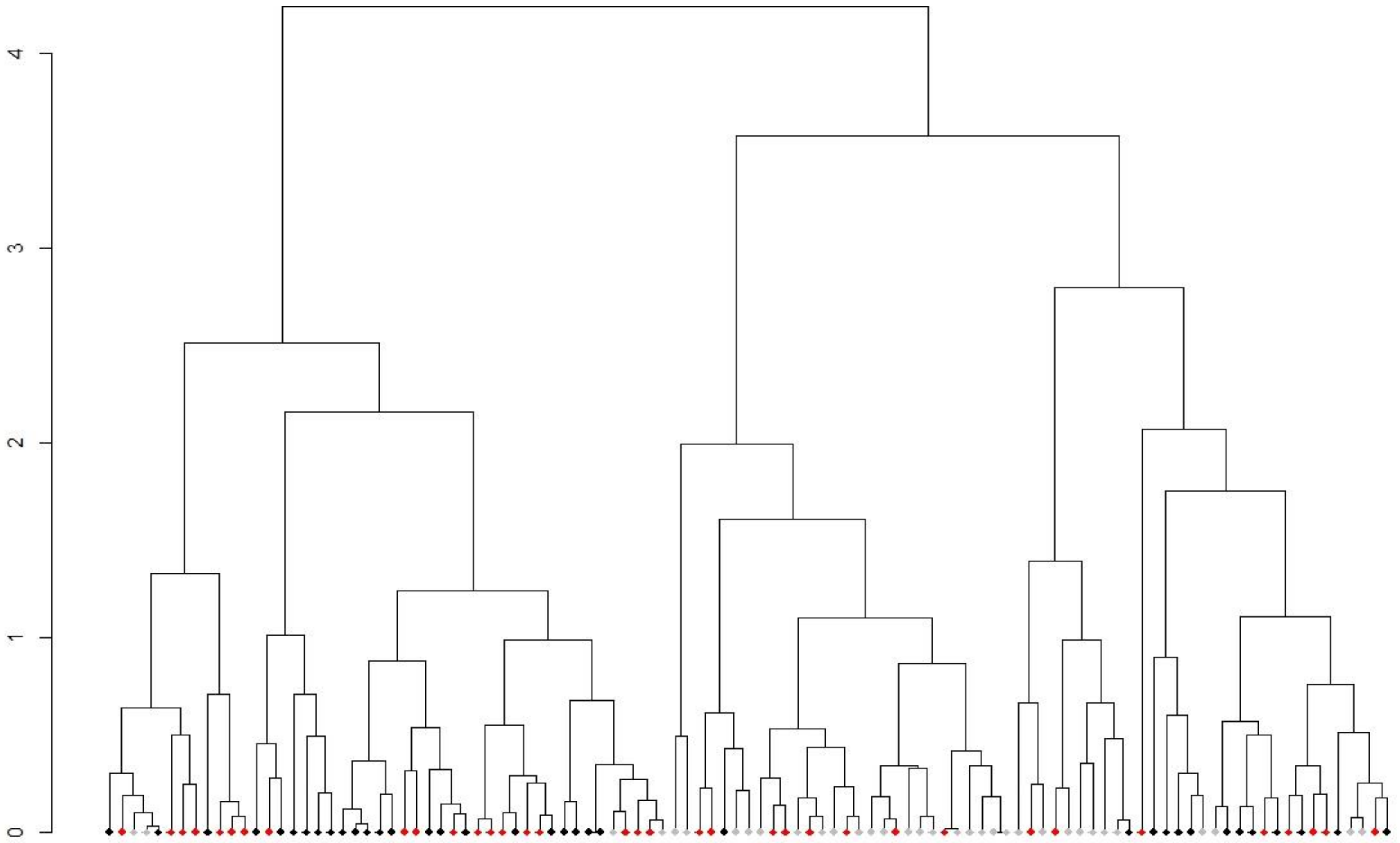

Fig. S1: Hierarchical clustering analysis of Collembola habitat preference (i.e. euedaphic or hemiedaphic) on *Sagina procumbens* (red rhombi), *Azorella selago* (black rhombi) and *Clasmatocolea humilis* (grey rhombi). Length of vertical segment indicates dissimilarity (longer vertical segments indicate less similarity than shorter vertical segments). No obvious pattern of clustering was observed for the habitat preference of Collembola for any of the three focal plant species.

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Chapter 3: General conclusion

This study examined the impacts of *Sagina procumbens* on the biota of Marion Island, by assessing whether or not *S. procumbens* causes an invasional meltdown in different taxa. Information pertaining to the impacts of *S. procumbens* (a widespread invader in the sub-Antarctic) is very limited and is often based on anecdotal evidence (Gremmen et al., 2001, Visser et al., 2010, Cooper et al., 2011). This study revealed that *S. procumbens* does not cause an invasional meltdown in plant communities but may be associated with an invasional meltdown in Collembola.

Microarthropod abundances have been found to show seasonal variation (Barendse and Chown, 2001), and therefore the specifics of this relationship may be different when sampling in multiple seasons. However, the destructive nature of the coring sampling procedure makes repeated sampling of the same plants impossible, highlighting the need for different Collembola extraction procedures, which would allow for monitoring of these microarthropods within the same substrate over longer periods. A next topic of research may be the need to identify the mechanisms through which *S. procumbens* affects the abundance and composition of Collembola. Temperature conditions experienced by Collembola in the different focal species are unlikely to have driven differences in abundance and composition of Collembola. Another microclimatic factor that could have played a role, but was not measured, is moisture content of each of the focal plants. However, the high abundance of Collembola could be also be driven by feeding preference (i.e. non-arbuscular mycorrhizal fungi; Caltrans, 2011) if Collembola indeed have a preference for non-arbuscular mycorrhizal fungi. Fairly little research exists on the microbial ecology of the sub-Antarctic islands, and little work has been done on mycorrhizal fungi of Marion Island (Smith and Newton, 1986).

This study mainly assessed the impacts of *S. procumbens* on epiphytic plants and associated Collembola communities. However, it did not consider other aspects of *S. procumbens'* impact on the Marion Island ecosystem. For example, I did not *per se* investigate whether *S. procumbens* facilitates native species. However, some evidence of positive facilitation between *S. procumbens* and native Collembola abundance was found. Therefore, a future line of investigation could test for facilitation of native species by invaders. Facilitation of native species by invasive species has been observed elsewhere (Smith and Knapp, 1999, Tecco et al., 2006). For example, some studies have found invasive species aiding in the pollination of native species (McKinney and Goodell, 2011). Facilitation is predicted to occur when functionally integral native species are replaced by, and their functional roles are taken up by invasive species (Rodriguez, 2006).

Furthermore, from field observations, the dense root system of *S. procumbens* appears to be growing over native cushion- and mat-growing plants, especially the keystone species *Azorella selago*, which is killed below a *S. procumbens* growth, with its dense root system (Fig. 10A) replacing *A. selago* stems. Additionally, *S. procumbens* has also been seen growing as a pioneer species in young volcanic ash (Fig. 10B). However, these patterns have been mainly observed at the coast and not further inland, where *S. procumbens* plants tend to be much smaller and rarer, possibly because of limiting factors such as differences in soil texture and nutrient concentrations. Thus, the mechanism of how *S. procumbens* manages to outcompete and kill native species, and under what conditions, needs further investigation. Additionally, the spread rate of *S. procumbens* at island-scale has been investigated (le Roux et al., 2013); however, the rate at which individual *S. procumbens* plants grow and dominate native species has not.

This study is only the second to have looked at the impact of an invasive plant species on the native communities of the Prince Edward Islands, with the first from Gremmen et al. (1998), assessing the impacts of *Agrostis stolonifera*. This study thus contributes to better informing on the impacts of invaders, an important research gap for the islands (Greve et al., 2017).

Several studies have predicted that climate change will affect the performance of species and alter species assemblages in the sub-Antarctic (e.g. Chown et al., 2007, le Roux and McGeoch, 2008a, Janion et al., 2010, Ansorge et al., 2014, Bergstrom et al., 2015). As both *S. procumbens* and invasive Collembola are predicted to be favoured by climate change (Chown et al., 2007, le Roux et al., 2013) (i.e. the species expand their ranges and increase in abundance), the positive interaction between *S. procumbens* and invasive Collembola could become a greater threat to the native biota of Marion Island, as well as the sub-Antarctic in general. Indeed, in a worst-case scenario, the invasional meltdown may displace native biota and alter the system to favour further establishment and spread of other invasive species (e.g. see O'Dowd et al., 2003).

Sagina procumbens is already established on eleven other sub-Antarctic islands (le Roux et al., 2013); therefore, our observations from Marion Island may also be observed on other sub-Antarctic islands. My study highlights the need and importance of stringent biosecurity procedures on the sub-Antarctic islands to minimize introductions of new species, and thus opportunities for positive interactions between invasive species, which can have an elevated potential to threaten these systems (Simberloff and Von Holle, 1999).

Fig. 10: (A) *Sagina procumbens*' dense root system killing *Azorella selago,* (B) *Sagina procumbens* growing as a pioneer species in young volcanic ash. (Photo credits (A-B) Michelle Greve)

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