Species occupancy, distribution and abundance: indigenous and alien invasive vascular plants on sub-Antarctic Marion Island

by

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DECLARATION

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ABSTRACT

Macroecological relationships have rarely been studied at wide spatial scales and across geographic ranges of species in the field in the sub-Antarctic. In this thesis I examined the occupancy, distribution and abundance, and the relationships thereof, of indigenous plants and alien species at broad (island-wide) and fine scales across sub-Antarctic Marion Island. The impacts of alien species and their interactions with indigenous plants were also investigated.

I examined the nature of the abundance structure of a cushion-forming, vascular plant, *Azorella selago*, at the island-wide scale. Moreover, the hypothesis that species reach their highest abundances at the centre of their geographic range and decline in abundance towards the range edges was tested. *Azorella selago* cushions were counted in 8 m x 8 m quadrats, placed regularly at 1 minute latitude and longitude intervals across Marion Island. Using spatially non-explicit and explicit methods, this study showed that the abundance structure of *A. selago* had a more complex pattern of high abundance patches and low abundance gaps in its island-wide distribution. Subsequently, the hypothesis of an abundant centre distribution was not supported for *A. selago* across Marion Island. Rather, there were sharp discontinuities at both the coastal and altitudinal (667 m a.s.l.) limits for the species, between which little pattern in altitudinal abundance structure existed.

Mice (*Mus musculus*) have recently been found to cause extensive structural damage to *A. selago*. The structural influence of mice on vegetation structure at the landscape scale has largely been overlooked on many sub-Antarctic islands. I mapped the distribution of evidence of mouse damage within the cushions of *A. selago* across the island using systematic (at 1 minute latitude and longitude intervals) and opportunistic sampling. Approximately 40 % of the systematically sampled sites had evidence of mouse damage to *A. selago*. Furthermore, a third of cushions in opportunistically sampled sites was damaged. Mouse damage was high in sites of low *A. selago* abundance, emphasizing that impacts of mice may be greater in low cushion abundance areas. This damage sometimes led to the disintegration of entire cushions. Given that *A. selago* acts as a nurse plant and supports high abundances of indigenous invertebrates, the impacts of mice on this keystone species may have significant ecological implications.

Studies on interactions between alien and indigenous plants are limited within the sub-Antarctic. I examined the fine-scale distributions and co-occurrences of alien plants, *Agrostis stolonifera* and *Sagina procumbens*, and the indigenous *Acaena magellanica* (in 2 m x 2 m plots, subdivided into 0.25 m x 0.25 m quadrats) along rivers on Marion Island. Environmental variables were important for the occurrence of these species. In particular, 42.95 % and 24.82 % of the deviance in the occurrence of *A. stolonifera* and *S. procumbens*, respectively, was explained by environmental variables, compared to 17.35 % for *A. magellanica*. Furthermore, the co-occurrence of *A. magellanic*a with *A. stolonifera* was significantly influenced by environmental variables. Significant positive spatial associations between *A. magellanica* and *A. stolonifera* were found, while the interactions of either species with *S. procumbens* were either spatially dissociated or random. Therefore, this study highlighted that alien species are responding to different environmental variables and conditions on Marion Island. *Sagina procumbens* seems to be less sensitive to the island's environmental conditions and may thus be affecting biodiversity at broader ranges. This thesis provides unparalleled data on the distributions and interactions of indigenous plants and alien species for Marion Island. Alien species are undoubtedly posing significant threats to indigenous plants on the island and this thesis presents insight into interactions of species, specifically plants, an approach underrepresented in the sub-Antarctic to date

OPSOMMING

Makro-ekologiese verhoudings is selde bestudeer op wye ruimtelike skale en oor geografiese gebiede van spesies in die veld in die sub-Antarktiek. In hierdie tesis het ek die digtheid, bewoning, verspreiding en die verhoudings daarvan, van inheemse plante en uitheemse spesies ondersoek op breë (eiland-wyd) en smal skale oor sub-Antarktiese Marion Eiland.

Die impakte van uitheemse spesies en hul interaksies met inheems plante is ook ondersoek. Ek het die aard van die digtheidstruktuur ondersoek van 'n kussing-vormende, vaatplant, *Azorella selago*, op die eiland-wydte skaal. Bowenal is die hipotese dat spesies hul hoogste digtheid bereik in die sentrum van hul geografies gebied en afneem in digtheid na die grense van die gebied getoets. *Azorella selago* kussings is getel in 8 m x 8 m kwadrante, wat eweredig geplaas is op 1 minuut breedte- en lengtegraad intervalle oor Marion Eiland. Deur gebruik te maak van ruimtelik nie-eksplisiete en eksplisiete metodes, het hierdie studie getoon dat die digtheidstruktuur van *A. selago* ‘n meer komplekse patroon van hoë digtheidslaslappe en lae digtheidsgapings in sy eiland-wyd verspreiding het. Vervolgens is die hipotese van 'n digte sentrum verspreiding nie gesteun vir *A. selago* oor Marion Eiland nie. Daar was eerder skerp diskontinuïteite by beide die kus- en hoërliggende (667 m bo seespieël) grense vir die spesie, waartussen daar ’n oneweredige patroon in digtheidstruktuur bestaan het.

Onlangs is bevind dat muise (*Mus musculus*) uitgebreide struktuele skade aan *A. selago* veroorsaak. Die struktuele invloed van muise op plantegroei struktuur op landskapskaal is grootliks oor die hoof gesien op baie sub-Antarktiese eilande. Ek het die verspreiding van die bewyse van muisskade binne die kussings van *A. selago* oor die eiland gekarteer deur gebruik te maak van sistematiese (tot 1 minuut breedte- en lengtegraad intervalle) en opportunistiese opnames. Ongeveer 40 % van die sistematiese opname kwadrante het bewyse van muis skade aan *A. selago* vertoon. Verder, ‘n derde van die kussings in die opportunistiese opname kwadrante was beskadig. Muisskade was hoog in plotte met lae *A. selago* volopheid, wat beklemtoon dat impakte van muise groter mag wees in lae kussing digtheid gebiede. Hierdie skade het partykeer gelei tot die verbrokkeling van hele kussings. Gegewe dat *A. selago* as 'n verpleegsterplant optree en ’n hoë digtheid van inheemse invertebrata ondersteun,

mag die impakte van muise op hierdie hoeksteen spesie beduidende ekologiese implikasies tot gevolg hê.

Studies oor interaksies tussen uitheemse- en inheemse plante is beperk in die sub-Antarktiese gebied. Ek het die smal-skaal verspreidings ondersoek en medevoorkoms van uitheemse plante, *Agrostis stolonifera* en *Sagina procumbens*, en die inheems *Acaena magellanica* (in 2 m x 2 m kwadrante, subverdeel in 0. 25 m x 0. 25 m kwadrante) langs riviere op Marion Eiland. Omgewingsveranderlikes was belangrik vir die voorkoms van hierdie spesies. In besonder, 42.95 % en 24.82 % van die afwykings in die voorkoms van *A. stolonifera* en *S. procumbens*, onderskeidelik, is verduidelik deur omgewingsveranderlikes, vergeleke met 17.35 % vir *A. magellanica*. Verder, die medevoorkoms van *A. magellanica* saam met *A. stolonifera* is beduidend beinvloed deur omgewingsveranderlikes. Beduidende positiewe ruimtelike assosiasies tussen *A. magellanica* en *A. stolonifera* is gevind, terwyl die interaksies van beide spesies met *S. procumbens* was of ruimtelik nie-geassosieerd of lukraak. Daarom het hierdie studie uitgelig dat uitheemse spesies reageer op verskillende omgewingsveranderlikes op Marion Eiland. *Sagina procumbens* blyk minder sensitief te wees tot die eiland se omgewingsomstandighede en mag dus moontlik biodiversiteit op breër vlakke beïnvloed. Hierdie tesis voorsien ongeewenaarde data oor die verspreiding en interaksies van inheems plante en uitheemse spesies vir Marion Eiland. Uitheemse spesies hou ongetwyfeld 'n beduidende bedreiging in vir inheems plante op die eiland, en hierdie tesis bied insig in die interaksies van spesies, spesifiek plante – 'n benadering wat swak verteenwoordig was in die sub-Antarktiese gebied tot op hede.

DEDICATION

This thesis is dedicated to my late grandfather, Jeremiah Matare Dziba (Manzini)

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Chapter 1

GENERAL INTRODUCTION

"*Macroecological patterns constitute a basic description of facets of the distribution of life across the Earth, and the primary goal of macroecology is to explain their existence*." – Gaston & Blackburn, 1999 (*Oikos*, **84**, 356).

Macroecology is the study of ecological patterns and processes at broad spatial and temporal scales, and is dependent on observational and inferential hypothesis tests (Scheiner 2003; see also Brown 1999). Recently, interest has increased in understanding macroecological patterns (Brown 1999), and specifically the relationships between abundance and distribution (Hengeveld & Haeck 1982; Brown 1984; Wright 1991; He & Hubbell 2003), abundance and occupancy (Hartley 1998; Holt *et al*. 2002, McGeoch & Gaston 2002; Warren *et al*. 2003; Freckleton *et al*. 2006), and occupancy and scale (Kunin *et al*. 2000; He & Gaston 2000a; McGeoch & Gaston 2002; Hui *et al*. 2006). Understanding these relationships may offer the ability to determine common mechanisms linking the changes in macroecological patterns and processes across various spatial scales (Gaston & Blackburn 2000; Freckleton *et al*. 2006).

Abundance is a measure of the total population size of a given species in a community. It can be viewed as the spatial distribution of individuals in habitat patches or mapped grid squares in which the species is present (see Gaston 1994; Brown 1995; Hartley 1998); and occupancy is the total number of patches or grid squares that are occupied (Hartley 1998). The distribution of a species defines the localities of where the species is found through space and time (Coomes *et al*. 1999). The shape of the distribution of a species' geographic range can be classified into three patters of distribution: random (at seemingly random locations with no particular arrangement), uniform (under-dispersed with an even or regular distance between the species), and aggregated (over-dispersed or clumped together across an area) (Coomes *et al*. 1999; Hui *et al*. 2006). Here, the distribution of species will be referred to as the measure of aggregation.

Relationship between occupancy, aggregation, abundance, and sampling scale

Measures of species occupancy, aggregation, and abundance are interdependent (He & Gaston 2003). In addition, measures of these variables and the relationships between them are highly scale dependent (Guo *et al*. 2000; He & Gaston 2000a; McGeoch & Gaston 2002). Both of these insights have led to major advances in attempts to predict species abundance from measures of their occupancy (He & Gaston 2000b; Kunin 1998; Kunin *et al*. 2000). However, the success of models that have been used to predict abundance from occupancy has been varied (Warren *et al*. 2003). Reasons for this include difficulties in accurately describing the relationship between occupancy, aggregation, and abundance, and that the majority of models exclude information on the spatial distribution of occupancy values (Hui *et al*. 2006). For example, uncertainties remain on the form of the relationship between occupancy and scale for common and rare species, and on the relationship between species aggregation, abundance and occupancy (McGeoch & Gaston 2002).

It is well documented that there is a positive correlation between abundance and occupancy (Gaston 1994; Warren *et al*. 2003) as well as between occupancy and aggregation (He & Hubbell 2003), however, the interrelationship between these variables has not been studied over a range of spatial scales, i.e. from a local scale to the geographic range of species (Brown 1984; Sagarin & Gaines 2002a). Moreover, there are only a few studies that have systematically investigated the characteristics of these relationships at broad spatial scales over the entire geographic range of any given species (Gaston 1994, 2003). Sampling scale is an essential element for studying macroecological patterns (Blackburn & Gaston 1998). Grain and extent are the most commonly used components of scale (Scheiner *et al*. 2000), and together they define the lower and upper spatial limits of the area where the species has been recorded (Gaston 1994, 2003). The scale at which the sampling area is divided can have a significant impact on investigations of these patterns (Scheiner 2003) and plays a major role in determining the shape of the observed occupancy distributions of species (He & Gaston 2000a). Macroecological studies at broad spatial scales may give an overview of distribution patterns of species across study systems, while fine scale studies are important for identifying the basis for the observed patterns (Wiens 1989; Gaston & Blackburn 1999).

In trying to understand the distribution of species, the shape of the abundance structure of species has been studied widely (Whittaker 1967; Hengeveld & Haeck

1982; Gaston 2003; Samis & Eckert 2007). It is generally assumed that the distribution of species abundance follows a Gaussian distribution within their geographical range, i.e. the abundant centre hypothesis (Grinnell 1922; Whittaker 1967; Brown 1984; Maurer 1994; Brown 1995). Despite the fact that there is good evidence that species range distributions may be non-Gaussian (Sagarin & Gaines 2000a), there have only been a few studies that have quantified abundance structure over wide geographic ranges, involving the entire range of any particular species (e.g. Brewer & Gaston 2002, 2003). However, most studies of abundance and species range are partial, only involving a small portion of the geographic range of the species concerned, with only a few comprehensive studies (i.e. performed at continental or oceanic scales) (Gaston & Blackburn 1996; Gaston *et al*. 1997).

The relationships between occupancy, aggregation, and abundance are frequently studied by placing a grid over a study area and enumerating the individuals of the species concerned in each cell of the lattice (He & Hubbell 2003). Species with low local abundance tend to have restricted distributions, whereas those with high local abundance occur more widely (Brown 1984; Warren & Gaston 1997; He & Gaston 2000a; Holt *et al*. 2004). In general, the structure of the distribution of species should be in equilibrium within their natural range. However, when considering alien species or species that are expanding their distributions, range structure may not be in equilibrium (Wilson *et al*. 2004). Although there are similarities in the scaling patterns of abundance and distribution for both alien and indigenous species, alien species are expected to differ as they tend be aggregated at local scales (Labra *et al*. 2005). Furthermore, alien species demonstrate a more even abundance-distribution relationship, probably due to their broad tolerances of environmental changes, resulting in their successful establishment and further spread (Labra *et al*. 2005). Thus, the species abundance-distribution patterns for alien species should be indicative of substantial expansion because these species are still expanding their range whereas indigenous species have been in their native environment for much longer and have established relatively constant populations within their ranges (Brown *et al*. 1995; Rodríguez & Delibes 2002).

However, owing to the poor knowledge of the complete distributions of species abundances within their geographic ranges, abundance and distribution patterns are still not well understood (Sagarin & Gaines 2002a). A key contributor to the paucity in understanding these patterns is the inaccessibility of entire geographic ranges

(Gaston 1994, 2003). Because most species inhabit large geographical ranges, it is often logistically difficult to consistently sample abundance throughout their range (Gaston 1994; Sagarin & Gaines 2002b; Gaston 2003). Also, factors such as the size of the species and its ability to disperse make it difficult to gain the maximum representation of a species optimal sample size unit of occupancy distribution patterns (McGeoch & Gaston 2002).

Here, some of these issues are addressed across the geographic range of a sub-Antarctic island, Marion Island. While the altitudinal limits of indigenous vascular plants are known for the island (Huntley 1970; Hedding 2006; le Roux & McGeoch, in press), and the localities of where most alien plant species occur are generally known (Gremmen 1975; Gremmen & Smith 1981; Gremmen *et al*. 1998; Gremmen & Smith 1999), their patterns of aggregation have not been explored at broad and fine spatial scales across the island's range.

Biological invasions and the sub-Antarctic

Alien invasive species are naturalized species (species that form self-regulating populations for at least ten years) that when introduced to an environment, are able to produce viable offspring that can disperse away from the site of introduction with the potential to broaden their area of invasion (Richardson & Pyšek 2006). Invasion is seen as a balance of local and regional processes (Siemann & Rogers 2003), and thus the invasibility of an environment and the invasion potential of a species are of fundamental importance in understanding the ability of an invasive species to establish itself in a new habitat (Frenot *et al*. 2001).

Alien species, whether intentionally or accidentally introduced, usually spread rapidly to become the most common species in a number of environmental conditions (Pimentel 2002). Consequently, alien species can decrease species richness and diversity in the communities they invade, making them one of the main drivers of global environmental change (Byers *et al*. 2002; Sala *et al*. 2000; Vermeij 2005). The establishment of an introduced species is dependent on the number of individuals introduced and inherent characteristics such as the capacity at which the species can disperse as a seed, juvenile, or adult (Maina & Howe 2000). Furthermore, the successful establishment of alien species in non-native environments is partially a consequence of the lack of natural enemies (MacArthur & Wilson 1967; Maron & Vilà 2001; Colautti *et al*. 2004; Vermeij 1991; Vilà *et al*. 2005). Islands possess a vast abundance of resources and most lack natural enemies that could possibly suppress aliens and may thus favour the introduction and successful establishment of alien species (Sax & Brown 2000; Courchamp *et al*. 2003; Daehler 2003).

The invasion of plant communities by non-indigenous species resulting in habitat alteration, as well as climate change and human disturbance are some of the major concerns in conservation biology (Vitousek *et al*. 1997; Maron & Vilà 2001; Chown & Gaston 2000; Miller *et al*. 2002). The relatively recent increase in human travel has made biological invasions a widespread and significant component of environmental change (Vitousek *et al*. 1996; Vitousek *et al*. 1997; Prinzing *et al*. 2002; Blackburn & Gaston 2005). Specifically, while sub-Antarctic islands remained relatively free of human disturbance until recently, the arrival of humans (eventually leading to the establishment of research stations on several islands), has subsequently resulted in the escalation of introduced species because the number of people (initially sealers and whalers, and then researchers and tourists) visiting these islands has increased (Chown *et al*. 1998; see also Gremmen 1997; Frenot *et al*. 1999; Frenot *et al*. 2001; Frenot *et al*. 2005; Vidal *et al*. 2003; Chown *et al*. 2005). Also, when compared to other parts of the world, the sub-Antarctic is experiencing rapid climate change (Smith 2002; Chapuis *et al*. 2004; le Roux & McGeoch 2008) and as a result, it is expected that the number of alien species will increase and existing alien species will spread more rapidly increasing their distribution ranges (see Smith & Steenkamp 1990; Bergstrom & Chown 1999).

Because of their isolation, poor species composition and high endemism, sub-Antarctic islands are, therefore, ideal for examining how species will respond (spatially) to global climatic change (Bergstrom & Chown 1999). These islands are undergoing rapid environmental change caused by alien species as well as global climatic change and can thus provide useful settings for understanding macroecological patterns and processes involving interactions between indigenous and introduced species (Bergstrom & Chown 1999; Chapuis *et al*. 2000; Chown *et al*. 2002; Chapuis *et al*. 2004). Hence, examining macroecological patterns on sub-Antarctic systems may aid in the investigation of processes involving the introduction, establishment and dispersal of non-indigenous species, as well as changes to community structure caused by the alien species (Chevrier *et al*. 1997; Hennion & Walton 1997a, b). Moreover, it is expected that with climate change (which has resulted in an increase in available ground; see Sumner *et al*. 2004 for an example on

Marion Island), the colonisation and establishment of non-indigenous species will increase (Frenot & Gloaguen 1994; Convey 1997). In consequence, these species may become dominant species among sub-Antarctic biota, dramatically changing these pristine, previously undisturbed ecosystems (Frenot *et al*. 2001). For example, it is predicted that with the changing climate, alien plant species, such as *Agrostis stolonifera*, that rarely produce seeds in the sub-Antarctic, but spread vegetatively, may flourish and possibly start to produce viable seeds (Gremmen 1997). Sub-Antarctic islands can thus be used as models for invasion biology as well as in a variety of studies concerning modern ecology and the evolution of species distributions (Bergstrom & Chown 1999; Frenot *et al*. 2001).

STUDY LOCATION

The research for this study was conducted on sub-Antarctic Marion Island (46°54´S 37°45´E) from April 2005 to May 2006 and April 2007 to May 2007. Marion Island covers 290 km^2, rising to 1230m a.s.l. with a 72 km coastline, and forms one of two islands in the Prince Edward Island group (Fig. 1). Prince Edward Island (44 km^2) is situated 22 km to the north of Marion Island (Smith 1976, 1987). These islands are of volcanic origin and are situated in the Southern Indian Ocean, just north of the Antarctic convergence, approximately 1800 km south of Port Elizabeth, South Africa (see van Zinderen Bakker *et al*. 1971; Chown & Froneman 2008 for general information on the climate, geology, biota of Marion Island). These islands were discovered in the 1800s and were frequently visited by sealing vessels until their annexation by South Africa (1947 for Marion Island and 1948 for Prince Edward Island) (Hänel & Chown 1999). A research station was established on Marion Island in 1948 where continuous biological research has been conducted since 1965 (Hänel & Chown 1999). While Prince Edward Island is uninhabited, Marion Island hosts small, annually rotated groups of researchers, meteorologists and support staff staying at the island’s weather station (Gremmen *et al*. 2003).

Marion Island has a typical sub-Antarctic climate, characterised by low annual air temperature, high precipitation, a high degree of cloudiness, high relative humidity, and strong predominantly westerly winds (Smith 1977a, b; Smith 1987). The island has experienced rapid climate change over the last fifty years with the annual mean temperature increasing by nearly 1.5 °C (Smith 2002; le Roux & McGeoch 2008). In addition, le Roux & McGeoch (2008) showed that annual rainfall decreased from about 3,000 mm per year in the 1960s to just above 2,000 mm per year in the 1990s. Furthermore, between the 1960s and 1990s the mean and maximum duration of consecutive days without rainfall increased and maximum daily rainfall decreased, while an increase in the variability in daily rainfall was observed (Smith 2002; le Roux & McGeoch 2008). With the observed increase in the number of dry days as well the warmer temperatures, it is expected that the island's biota will undergo drastic changes, so altering ecosystem functioning (Smith & Steenkamp 1990; Smith 2002; le Roux & McGeoch 2008).

Because of its isolation and the low energy availability, Marion Island's biota is species poor (Chown *et al*. 1998; Chown *et al*. 2005; see also Huntley 1972; van Zinderen Bakker 1978; Smith 1987). Forty-two vascular plant species have been recorded on Marion Island (of these eighteen are considered introduced, six of which no longer occur) (Gremmen 1997). The vegetation of the island was first classified based on floristic composition by Huntley (1971) and later by Gremmen (1981). The island's vegetation was then reclassified based on floristic composition and soil chemistry by Smith & Steenkamp (2001). Smith & Steenkamp (2001) classified the islands vegetation into seven habitat complexes, namely: coastal salt-spray, fellfield, slope, biotic grassland, biotic herbfield, mires, and the polar desert. These habitat complexes comprise a total of twenty-three different vegetation communities. The coastal salt-spray complex is limited to the island's shore zone and is dominated by *Crassula moschata* and *Cotula plumosa*, but *Azorella selago* is co-dominant in the coastal fellfield habitat. Fellfield is the dominant vegetation complex on the island and is mainly found on ridges and plateaus exposed to strong winds. Fellfield vegetation is generally made up of bare rock or scoria and is dominated by the cushion plant, *Azorella selago*, while in certain fellfields *Agrostis magellanica* and *Blechnum penna-marina* may co-occur. The slope complex is overwhelmingly dominated by the fern, *B. penna-marina* and often, *Brachythecium* mosses and the dwarf shrub *Acaena magellanica* co-occur. The slope complex is mainly found on lowland slopes up to *c*. 300 m a.s.l. The slope drainage line habitat, where *Agrostis stolonifera* is the main alien plant species, belongs to this complex. The biotic grassland complex is also influenced by seabirds and occurs close to the coast and inland up to approximately 150 m a.s.l. where the soils are influenced by burrowing birds. *Poa cookii* is the dominant species in this complex, while in the coastal tussock grasslands and around king penguin rookeries, *Callitriche antarctica*, *Montia fontana*, *Cotula plumosa* and

Poa annua are the dominant co-occurring species. The biotic herbfield complex is found mainly near coastal areas influenced by manure deposits and trampling of the soils and vegetation by seabirds and seals. This complex is dominated by *Cotula plumosa*, and *P. cookii*. Other species found in this complex are *Callitriche antarctica*, *M. fontana* and *P. annua*. The mire complex covers extensive parts of the lowlands and the vegetation is usually dominated by mosses, liverworts, grasses and sedges. The last complex is the polar desert where vascular plants are absent, although *Azorella selago* may occur in low cover at altitudes below 650 m. Non-vascular plants such as lichens and mosses, are the main plants that occur on most of the polar desert. See Huntley (1971), Gremmen (1981), Smith & Steenkamp (2001), Smith *et al.* (2001), and Smith & Mucina (2006) for the detailed classifications of these complexes and their respective habitats.

Two species of terrestrial mammals have been introduced by humans, namely, the house mouse (*Mus musculus domesticus*; Jansen van Vuuren & Chown 2007), probably introduced through ship wrecks and sealer expeditions (Skinner *et al.* 1978), and the recently eradicated (Bester *et al.* 2000) feral house cat (*Felis catus*). There are no indigenous terrestrial mammals on the island.

STUDY SPECIES

This study examined the distribution of two indigenous vascular plant species, *Azorella selago* Hook. (Apiaceae) and *Acaena magellanica* Lam. Vahl. (Rosaceae), and three alien species, two of them plants: *Agrostis stolonifera* L. (Poaceae) and *Sagina procumbens* L. (Caryophyllaceae) and the third, a mammal, the house mouse, *Mus musculus* L. (Muridae), at different spatial scales depending on the species.

Azorella selago

The cushion plant *Azorella selago* Hook. (Apiaceae) is an important constituent of sub-Antarctic plant communities and is considered a keystone species on Marion Island (Hugo *et al.* 2004; le Roux *et al.* 2005). It is a long-lived perennial (le Roux & McGeoch 2004) and a pioneer species of fellfield communities and deglaciated areas (Huntley 1970; Frenot *et al.* 1993). On Marion Island, the species has been shown to influence geomorphological processes by stabilising loose substrates (Holness & Boelhouwers 1998; Boelhouwers *et al.* 2000). It is also one of the major contributors to the aerial cover and standing crop of Marion Island's vegetation (Smith 1977b).

Azorella selago is common in all habitat complexes on the island (Huntley 1972), occurring from sea level to approximately 840 m a.s.l. (Hedding 2006). It frequently serves as a nurse plant with at least sixteen vascular and seventeen non-vascular plants having been found growing epiphytically on *A. selago* cushions (Huntley 1972; Gremmen 1981; McGeoch *et al*. 2008). In addition, the cushions also form an important habitat for some indigenous invertebrate species on the island (Barendse & Chown 2001; Hugo *et al*. 2004; McGeoch *et al*. 2006; McGeoch *et al*. 2008).

Acaena magellanica

Acaena magellanica is the most widely distributed species in the genus, occurring from South America (25° S) to all sub-Antarctic islands (Walton 1976, 1977, 1979). In sub-Antarctic vegetation, the species is considered a dwarf shrub and is able to tolerate a wide range of edaphic conditions (Walton 1976). The species generally inhabits humid vegetation areas, particularly borders of water bodies (Walton 1977). *Acaena magellanica* thrives in well-drained sites that are rich in minerals with minimal exposure to salt-spray and also sheltered from strong winds (Huntley 1971; Walton 1977). On Marion Island, *A. magellanica* is dominant in most vegetation communities and is also the main species occurring in the slope drainage-line communities along rivers (Walton 1977; Gremmen *et al*. 1998; Smith *et al*. 2001). It has been shown that this plant is threatened by alien species, particularly *Agrostis stolonifera*, which has the potential to displace this species in drainage-line communities on the island (Gremmen 1981; Gremmen *et al*. 1998).

Agrostis stolonifera

The bent-grass, *A. stolonifera*, is widely distributed in the Northern Hemisphere and is considered and invasive in the Southern Hemisphere (Walton 1975; Gremmen & Smith 1981). It is a widespread naturalized alien plant species on Marion Island (Watkins & Cooper 1986). This grass was first recorded close to the meteorological station on Marion Island in 1965 and is thought to have been introduced in the 1950s or early 1960s (Gremmen & Smith 1981; Gremmen 1982; Gremmen 2004). The species occurs largely on the northern and eastern coast of the island and has also been recorded around two field huts, i.e. Mixed Pickle Cove and Kildalkey Bay on the western and south eastern sides of the island, respectively (Smith *et al*. 1986; Gremmen *et al*. 1998; Gremmen & Smith 1999). *Agrostis stolonifera* is a fast growing, patch-forming grass that, when detached from the parent plant, spreads by means of stolons (Grime *et al*. 1990). Unlike most alien plant species it is able to invade undisturbed communities (Watkins & Cooper 1986). The species is also able to invade a wide range of habitats and on Marion Island and has a high impact on drainage-line communities where it has become one of the dominant species (Gremmen & van der Meijden 1995; Gremmen *et al*. 1998).

Sagina procumbens

The procumbent pearlwort is indigenous to the Northern Hemisphere and is an aggressive alien plant in the Southern Hemisphere (Walton 1975; Gaston *et al*. 2003). *Sagina procumbens* is believed to have been introduced near Marion Island's research station in the late 1950s or early 1960s and was first collected in 1965 (Gremmen 2004). This small herb is able to regenerate both by the dispersal of seeds and by vegetative means (Grime *et al*. 1990; Gremmen *et al*. 2001). The seeds of the plant are freeze tolerant (Salisbury 1962) and the species is thought to be both phenotypically plastic and genotypically variable (Grime *et al*. 1990). Seeds are produced in abundance and are able to lie dormant in seed banks in the soil (Grime *et al*. 1990; Gremmen *et al*. 2001). The species appears to invade natural vegetation communities where there has been a great deal of disturbance and where there is uncolonized bare soil (Watkins & Cooper 1986; Gremmen *et al*. 2001).

Mus musculus

House mice (*Mus musculus*) are widespread in the sub-Antarctic and are thought to have been accidentally introduced to Marion Island *c*. 200 years ago, from a Scandinavian population through sealing expeditions (Watkins & Cooper 1986; Chown & Cooper 1995; Hänel & Chown 1999). On Marion Island, mice are one of the major contributors to ecosystem change and have been shown to prey on invertebrate fauna which are major contributors of nutrients (Crafford 1990; Chown & Smith 1993; see also Chown & Cooper 1995). This has resulted in a decrease in the lesser sheathbill population, which also preys on the invertebrate fauna of the island (Huyser *et al*. 2000). Lately, mice are showing to have an impact on the cushion plant *A. selago* by causing extensive structural damage to the cushions, often leading to the disintegration of the plants (personal observation). Furthermore, in the results of a study conducted by Avenant & Smith (2003) it was reported that in vegetations where

A. selago was not the dominant plant species, more than 50 % of mouse burrows occurred on *A. selago*, in habitats where the plant was not the dominant species.

Thus, all these species play dominant roles in the structure and functioning of the terrestrial habitat of Marion Island, and their roles will be dealt with in the respective chapters of this thesis.

THESIS OUTLINE

The main objectives of this research are to examine and test predictions relating to the relationship between occupancy, abundance, aggregation, and scale on Marion Island. Additionally, the impact of terrestrial invasive species on indigenous plant species is investigated, and particularly how they interact with the indigenous plants and each other.

The thesis is split into five chapters, with the first chapter being a general introduction to topics of species abundance and distribution patterns as well as alien species in the sub-Antarctic. In chapter two, the generality of the abundant centre hypothesis (Brown 1984) is tested by examining the geographic abundance structure of *Azorella selago* at an island-wide scale. In the third chapter, the impact of alien house mice on *A. selago* as well as the spatial variation in structural damage to *A. selago* by mice is investigated at a landscape scale. The fourth chapter focuses on the distribution and spatial patterns of two alien vascular plant species, *Agrostis stolonifera* and *Sagina procumbens*, and the indigenous *Acaena magellanica* and how they interact with each other along rivers. In the fifth and final chapter, the general findings for each chapter (chapters 2-4) are summarised and synthesised, and the possible implications and influences of the alien species on macroecological patterns of Marion Island's indigenous biota are discussed.

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FIGURE

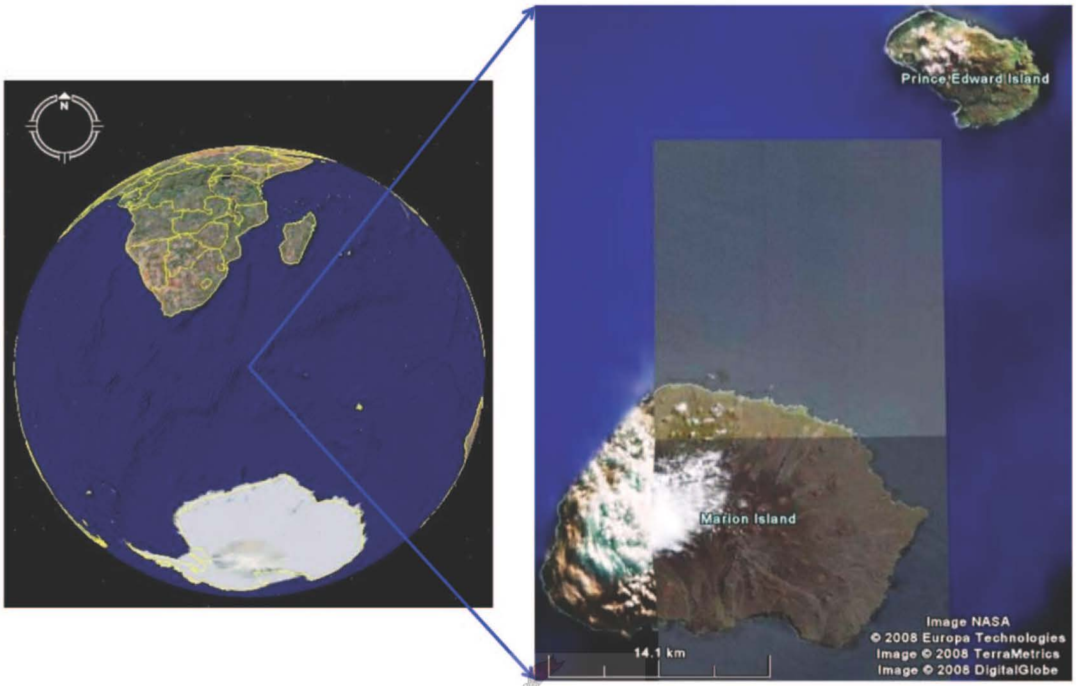

Figure 1 The geographic location of the study site, Marion Island (with its neighbour, Prince Edward Island). Images obtained from Google Earth, (www.earth.google.com, accessed on 22 August 2008).

Chapter 2

TESTING THE ABUNDANT CENTRE HYPOTHESIS ON AN ISLAND-WIDE SCALE: ABUNDANCE AND DISTRIBUTION OF *AZORELLA SELAGO* ON SUB-ANTARCTIC MARION ISLAND

INTRODUCTION

Two of the most fundamental ecological characteristics of any species are its distribution and abundance. Much of ecology, and especially macroecology, has been focussed on understanding not only the determinants of species abundances and their spatial variation, but also how these translate into occupancy and eventually the distribution ranges that characterise all species (MacArthur 1972; Hengeveld 1990; McGeoch & Gaston 2002; Gaston 2003). Early theory suggested that spatial variation in abundance typically assumes a Gaussian form, such that a species reaches its highest densities at the centre of its geographic range with density gradually declining towards the range edge, more or less evenly in all directions (Grinnell 1922; Whittaker 1967; Hengeveld & Haeck 1982; Brown 1984; Maurer 1994; Guo *et al.* 2005). Later work has questioned this idea, now known as the 'abundant centre hypothesis', demonstrating that complex environmental gradients result in a spatially variable abundance structure, which is not typically Gaussian (e.g. Brewer & Gaston 2002, 2003; Sagarin & Gaines 2002a; Klok *et al.* 2003; McGeoch & Price 2004). Indeed, two relatively recent reviews found that of the investigations that directly tested the hypothesis, fewer than half found support for it (Sagarin & Gaines 2002b; Gaston 2003), with the remainder either rejecting the hypothesis or being inconclusive.

Nonetheless, the number of studies that has sought to test the abundant centre hypothesis over broad spatial and temporal scales is relatively small (e.g. Brewer & Gaston 2002, 2003; Murphy *et al.* 2006; Samis & Eckert 2007). Moreover, several of these studies are complicated either by the use of presence/absence data only (Buzas *et al.* 1982; Rondinini & Boitani 2006; Zhou & Griffiths 2007), or by the use of relatively indirect, rather than survey methods (discussion in Sagarin & Gaines 2002b; Sagarin *et al.* 2006). Moreover, work has typically been limited to continental situations and in a small number of regions globally (Sagarin & Gaines 2002b). In consequence, the extent to which the assumption of an abundant centre distribution applies remains something of an open question. Indeed, Sagarin *et al*. (2006) argued that the field remains '*observation limited*'. Such a situation is unhelpful because geographic patterns in species abundance form an important basis for understanding population and community-level dynamics in space and time (Sagarin & Gaines 2002a; Gaston 2003), and for taking appropriate conservation actions (e.g. Channell & Lomolino 2000).

In this study I contribute to present understanding of the abundance structure across environmental gradients (see also McGill *et al*. 2006) by quantifying the distribution and abundance of a vascular plant species across an entire, self-contained area within its overall geographic range. Specifically, I examine the abundance structure of the cushion-forming dicot *Azorella selago* Hook. (Apiaceae) across sub-Antarctic Marion Island. Whilst the analysis is partial in the sense that it does not cover the full range of *A. selago* (which occurs on several Southern Ocean islands) (Huntley 1970; Martinez 1989; Frenot *et al*. 1993), it is complete in the sense that it covers the full local distribution of the species on an island typically separated by hundreds of kilometres from the nearest patches of the same species (with the exception of the 22 km distant and adjacent Prince Edward Island – see Chown & Froneman 2008). Specifically, I determine whether the species is (i) evenly or patchily distributed across the entire island, (ii) whether its abundance is highest at the geographic centre of its range on the island and declines in abundance toward the range edges (Brown 1984), assuming that its range might incorporate the entire island, or (iii) whether its abundance structure shows a more complex pattern, such that abundance is highest in the centre of the species' realised range, declining towards high and low elevations and forming an almost torus-like shape, perhaps a more realistic interpretation for the abundant centre distribution on a mountainous island. Other variations on these abundance structure themes are also plausible, but these largely involve more threshold-like or more gentle alterations in abundance over the torus-like space and are not further considered.

MATERIALS AND METHODS

Study site and species

Field work was conducted on Marion Island (46°54′S, 37°45′E) (for information on the climate, biota and ecosystems of the island see Chown & Froneman 2008) from April 2005 to May 2006. Marion Island's biota is comparatively species poor, the severity of the climate prevents the growth of trees and shrubs (Gremmen 1981), and only seven habitat complexes (subdivided into twenty-three vegetation communities) have been recorded on the island (Gremmen 1981; Smith *et al*. 2001).

Azorella selago Hook. (Apiaceae) is an important constituent of sub-Antarctic plant communities and is considered a keystone species on Marion Island (Hugo *et al*. 2004; le Roux *et al*. 2005). It is a long-lived perennial (le Roux & McGeoch 2004) and a pioneer species of fellfield communities and deglaciated areas (Huntley 1970; Frenot *et al*. 1993), where it stabilises loose substrates (Holness & Boelhouwers 1998; Boelhouwers *et al*. 2000). It is also one of the major contributors to the aerial cover and standing crop of Marion Island's vegetation (Smith 1977, 1978), and is common in all habitat complexes on the island (Huntley 1972a), occurring from sea level to approximately 840 m a.s.l. (Hedding 2006). *Azorella selago* frequently serves as a nurse plant, and at least sixteen vascular and seventeen non-vascular epiphytic plants are associated with it (Huntley 1972b; Gremmen 1981; McGeoch *et al*. 2008). In addition, the cushions also form an important habitat for many invertebrate species on the island (Barendse & Chown 2001; Hugo *et al*. 2004; McGeoch *et al*. 2006).

Azorella selago has two distinct growth forms, discrete cushions and large, continuous mats (Frenot *et al*. 1993, Mortimer *et al*. 2008). In both growth forms, the leaves and stems of the plant typically grow tightly against each other to create hard, compact surfaces varying in height and diameter (le Roux & McGeoch 2004). In the discrete cushion growth form, cushions grow as spatially isolated individuals that are mainly surrounded by bare ground and rocks (le Roux & McGeoch 2004; le Roux *et al*. 2005). The mat growth form comprises flat, continuous expanses of plant material and often, though not exclusively, occurs in association with seepages as well as drainages (Huntley 1972b; Gremmen 1981). Single, continuous mats may extend over areas as large as 30 m x 40 m. Genetic evidence suggests that mats might either be single, continuous cushions or a series of cushions that have merged (Mortimer *et al*. 2008). The species is slow-growing (Huntley 1972b; Frenot *et al*. 1993; le Roux & McGeoch 2004), and cushion age has been estimated to be between 30 and 80 years for single cushions of *c*. 40 cm in diameter (le Roux & McGeoch 2004).

Sampling

Count data for *A. selago* were obtained based on a system of grid cells (He & Hubbell 2003). Gridline intersection points were identified on a minute-by-minute basis for Marion Island, with a total of 124 sampling points across the entire island (Fig. 1). Each gridline intersection was used as a sampling point and an 8 m x 8 m plot (sub divided into sixteen 2 m x 2 m quadrats) was placed at the intersection and the number of *A. selago* cushions was counted in the 2 m x 2 m quadrats. Although this method provides a measure of cushion density (number of plants per 64 m^2 plot), for convenience from here on I refer to cushion abundance. Intersection points were pre-programmed into a hand-held GPS (Garmin E-trex Vista-C® with a barometric altimeter which was calibrated at least once a day at known altitudes). At each point, the following were noted: GPS co-ordinate (4 m accuracy), volcanic lava type or substrate (see Boelhouwers *et al*. 2008), habitat complex (according to Smith *et al*. 2001), and topography (slope and aspect). Of the 124 sites, 110 were physically surveyed. Of the remaining 14 sites, anecdotal data were obtained for three based on observations by geomorphological researchers, and the remainder were surveyed using oblique aerial photographic pictures taken from 50 m above the ground. The slope and aspect of the sites that were not physically visited were estimated using a topographic map (obtained from the Chief Directorate: Surveys and Mapping, Cape Town). The altitudes of these sites were estimated to the nearest 10 m using the Marion Island digital elevation model (originally from the Chief Directorate: Surveys and Mapping; corrected by Hedding 2006).

Data analyses

The GPS co-ordinates as well as abundance data were converted to shapefiles and plotted in ArcGIS™ 9.1 to produce a map of the distribution and abundance of *A. selago* across Marion Island. Kriging (discussed in detail below) was then used to interpolate data for sites that were not physically surveyed for the purpose of illustration only. Because observed abundance data were not normally distributed and to approximate normality, the data were log-transformed. The island was then divided into eight sub-quadrants to determine whether a difference in the abundance frequency distribution of *A. selago* exists between the northern, north eastern, eastern, south eastern, southern, south western, and north western sides of the island. An abundance-occupancy scatterplot and least squares linear regression of $\log_{10}$ abundance on occupancy was used to examine the relationship between abundance and occupancy. Unless stated, all statistical analyses were performed using Statistica 7.0 (StatSoft 2004, Tulsa, Oklahoma, USA).

To quantify the association between the presence of the two growth forms of *A. selago* (discrete cushions and mats) and habitat characteristic states (Table 1), including the different sides of the island (i.e. north, east, south, and west), chi-square (χ^2) test statistics were calculated using exact nonparametric inference statistics (StatXact 7; Cytel Software © 2005). The exact inference method provides accurate p-values when using small sample sizes (Lynch *et al*. 1991; Anonymous 2005). Furthermore, analyses of variance (ANOVA) were used to test for significant differences in *A. selago* abundance between the different states for each of the four habitat characteristics measured (Table 1).

The distribution of a species within its geographic range can be classified into three patterns: random, uniform, or aggregated (Coomes *et al*. 1999). To determine whether the distribution of *A. selago* across Marion Island was random, even, or aggregated, I quantified the patterns of aggregation using three approaches, i.e. Morisita's index (spatially implicit), Moran's autocorrelation index (spatially semi-explicit), and geostatistical prediction (spatially explicit, *sensu* Veldtman & McGeoch 2004). Morisita's index (I_m), a spatially implicit approach, is independent of total count, mean abundance, and number of grid squares sampled, but is dependent on the mean number of samples in the sampled area (Veldtman & McGeoch 2004). The significance of the deviation of I_m from 1 was assessed by calculating the chi-square statistic. A high χ^2 value, greater than the critical value at the specified degrees of freedom, indicates that the value for Morisita's index is statistically significant from 1 (Hamill & Wright 1986). Moran's autocorrelation index (I), is a spatially semi-explicit approach (Dale *et al*. 2002) used for estimating the degree of spatial autocorrelation between the number of observations and the distance separating them (SAAP v4.5; Wartenberg 1989). Geographical positions were used to compute a Euclidean distance matrix (Wolf 2005). The number of distance classes was determined by following Sturge's rule (Legendre & Legendre 1998), and a fixed distance *c*. 2.8 km (actual geographic distance was *c*. 2.3 km) was used. Distance classes that contained less than 1 % of the total number of point pairs were considered unreliable and were omitted (Legendre & Fortin 1989; Legendre & Legendre 1998) and for this reason the correlogram was drawn for distances class 1-10. Moran's autocorrelation index is greater than 1 for positive autocorrelations (aggregated), 0 for no autocorrelation (random), and less than 0 for negative autocorrelations (approximating an even distribution) (Moran 1950; Cocu *et al*. 2005).

The geostatistical prediction of spatial autocorrelation is a spatially explicit approach regularly used in ecological analyses for the detection and quantification of spatial pattern by means of interpolation across a sampling area (Cressie 1986; Lin *et al*. 2007). The most widely used method in geostatistics is the prediction of spatial pattern by the means of kriging, a linear interpolation process based on the values of the neighbouring sample points weighted by distance and the degree of autocorrelation among measured points separated by similar distances elsewhere in the sample area (Zimmerman & Zimmerman 1991; Legendre & Legendre 1998). Kriging is used for producing interpolated maps by determining the level of spatial autocorrelation of the variable being analysed and also provides a way of predicting abundances at unsampled sites (Rossi *et al*. 1992; Aubry & Debouzie 2000). Here, universal kriging (Zimmerman & Zimmerman 1991) was used to identify areas of high and low *A. selago* abundance. The interpolation was performed using ArcGIS™ 9.1 Geostatistical Analyst.

Several suggestions have been made for the ways in which tests for an abundant centre distribution should be undertaken. For example, Sagarin *et al*. (2006) suggested that the balance point of the range should be sought, rather than the intersection of the longest perpendicular axes as suggested by Brown (1984). Sagarin & Gaines (2002b) argued against the use of simple linear regression to examine the hypothesis when sampling is not uniform, and suggested other methods for examining the hypothesis. Here, I calculated the balance point of the range, but with the realization that for a two-dimensional distribution across a steep environmental gradient such a null model is unlikely to be realistic. The more reasonable hypothesis for an abundant centre distribution would be much more torus-like, with low abundances at the altitudinal limits and high abundances in the centre. Should such a distribution be collapsed to a single dimension, a quadratic, unimodal relationship with altitude might be expected. The more complex, two dimensional distribution should readily be visible as a mid-altitude band of high abundance.

To test these assumptions I not only plotted the interpolated distribution, obtained after kriging (see above) but also used a Generalised Linear Model regression (GLM, with log link function, Type 3 model and a correction for over-dispersion) to examine the relationship between the abundance of *A. selago* and altitude and the linear and quadratic terms for latitude (Lat) and longitude (Long). Akaike's Information Criterion (AIC) and Akaike weights, w_i, were used to identify the best model (Burnham & Anderson 1998; Johnson & Omland 2004). Because altitude tends to be collinear with spatial variables (see also Körner 2007), it was omitted from a second set of models, especially given its specific colinearity here with longitude ($r = -0.335$; $p < 0.05$). The best model excluding altitude was selected as above.

RESULTS

A total of 3578 discrete *A. selago* cushions was recorded and the estimated mean cushion density was 0.81 cushions.m^{-2} (± 0.08 SE) in sites occupied by discrete cushions. Of the occupied (83) sites, 83 % were occupied by discrete cushions and 17 % by mats (Fig. 2a). The species was absent in the centre of the island (Fig. 2b). Discrete cushion abundance ranged from 1 to 208 cushions per plot with an altitudinal range of between 37 and 667 m a.s.l. Three sites had abundances greater than 150 cushions per plot, situated on the south-east and north sub-quadrants of the island (Fig. 2a).

Most plots included 1 to 50 cushions (Fig. 3a), and the abundance frequency distribution (at the plot scale) was clearly right-skewed (Shapiro-Wilk $W = 0.7648$; $p < 0.0001$; skewness = 1.7558; kurtosis = 3.1328). Log-transforming the data did not fully normalize the data, and indeed the distribution became left-skewed (Fig. 3b). In addition, the distribution of *A. selago* abundance was not normally distributed on any of the eight sub-quadrants of the island (Shapiro-Wilk test, $p < 0.003$ in all cases). A left-skewed frequency distribution was observed for the occupancy of *A. selago* across Marion Island (Shapiro Wilk $W = 0.7604$; $p < 0.0001$; skewness = -0.0156; kurtosis = -1.8605). Of the occupied sites, 34% lay within the 15 to 16 occupancy class (Fig. 4a). Log-transforming the occupancy data had little effect on the occupancy-frequency distribution (Shapiro Wilk $W = 0.7207$; $p < 0.0001$; skewness = -0.3141; kurtosis = -1.8166). The relationship between abundance and occupancy was significant and positive. This relationship was found to be strong at abundances below 32 cushions per plot, becoming weaker with an increase in the number of cushions per plot (Fig. 4b). In addition, cushion abundance of 32 cushions per plot and above was likely to result in occupancy of between 69 % and 100 %.

With the exception of island side, the occurrence of the two *Azorella selago* cushion growth forms was not significantly associated with the different habitat characteristics. The mat growth form was more prevalent on the western side of the island (χ^2 = 12.6000; df = 3; p = 0.0055; Fig. 2a). Assessments of the influence of habitat characteristics on *Azorella selago* abundance revealed that abundance differed significantly among characteristic states only in the case of habitat complex ($F_{(5, 69)}$ = 3.2742, p = 0.0104). However, the differences among habitat complexes were not consistent, except for low abundance in the coastal salt-pray complex.

Morisita's index was significantly greater than 1.0 (I_m = 1.72) and the calculated χ^2 value was greater than the critical value at $p < 0.05$. Thus, the abundance of *A. selago* abundance was significantly aggregated across sites. No significant spatial autocorrelation in cushion abundance was found across the island at the measured scale, i.e. 8 m x 8 m plots on a minute-by-minute basis (Fig. 5). The spatially explicit, geostatistical description of *A. selago* abundance, however, demonstrated clear patchiness in the distribution and abundance of *A. selago* across Marion Island and thus, centres of high and low *A. selago* abundance (Fig. 2b). The balance point of the range was found to be at approximately 46°54.300′S, 37°45.300′E (arrow in fig. 2a).

A sharp, stepped decline in *A. selago* abundance was observed at both coastal and altitudinal (at 667 m a.s.l.) range edges (Fig. 6). *Azorella selago* abundance and altitude showed a significant, but weak negative relationship. However, when the sites above the 667 m threshold were excluded the relationship was not significant (p = 0.2848). Latitude and longitude did not explain the distribution pattern of *A. selago*, and no significant patterns were observed for the relationship between these variables and *A. selago* abundance (Latitude: p = 0.4677; Longitude: p = 0.2334).

The best subset model based on Akaike's Information Criterion (AIC), was the model that included all of the quadratic terms of latitude and longitude (AIC = 4695.20; w_i =0.819; Table 2). Therefore, all the predictor variables in the model, with the exception of Lat*Long, were found to be significant descriptors of the observed *A. selago* abundance patterns across Marion Island (Table 2).

DISCUSSION

This study provides the first quantification of the abundance structure for a plant species, *Azorella selago*, across its entire geographic range on a small sub-Antarctic island. *Azorella selago* was absent at the centre of the island and abundance was consistently high below a threshold altitude of 667 m. Moreover, no gradual increase or decline in abundance with altitude is present. Rather, a sharp increase in abundance was observed at the coastal range edge and an abrupt stepped decline at 667m a.s.l.

(Figs 2b and 7). More typically, *A. selago* showed patches of high abundance, most commonly at exposed low to mid-elevational areas, and large areas of low abundance or absence (at the highest elevations). These findings were entirely inconsistent with either a balance point of range expectation (see Sagarin *et al*. 2006), or the expectation of a mid-elevational peak if the two-dimensional torus expectation were to be collapsed into one dimension. Even the two-dimensional kriging interpolation did not match the torus-like expectation. In consequence, these findings provide no support for an abundant centre distribution hypothesis for *Azorella selago* on Marion Island. Therefore, this study of the island-wide distribution of a species is similar to most previous findings that have failed to find evidence for an abundant centre distribution, either on linear or two dimensional gradients in continental situations (see summaries in Sagarin & Gaines 2002b; Gaston 2003; Sagarin *et al*. 2006, and more recent work by e.g. Samis & Eckert 2007). Rather, like many other species, *A. selago* displays complex patterns of high and low abundance across its range.

In defence of the abundant centre hypothesis, it might be argued that the abundance and distribution characteristics of this species across a relatively small, mountainous island are unusual. However, two lines of evidence suggest that this is not the case. First, both the abundance and occupancy frequency distributions were typical of what has been found for many continental species across a wide range of taxonomic groups (see Gaston & Blackburn 2000; van Rensburg *et al*. 2000; McGeoch & Gaston 2002; Gaston 2003). Second, a strong, positive intraspecific relationship between abundance and occupancy was found, which is also typical of many species across a wide range of scales (Gaston 1999; He & Gaston 2000; Hui & McGeoch 2007). In consequence, in most other ways the macroecology of *A. selago* is typical, therefore supporting the strength of the evidence concerning the absence of an abundant centre distribution.

What environmental factors might be responsible for the complex patterns shown by *A. selago* is not entirely clear. The distribution and availability of suitable habitat attributes are important factors underpinning species abundance and distribution patterns (Brown 1984; Caughley *et al*. 1988; Holt & Keitt 2000; Fortin *et al*. 2005; Borges & Júnior 2006). Species are often non-randomly distributed in their geographic ranges and are rather patchily distributed in accordance with patchy habitat characteristics (Hamill & Wright 1986), as was the case here. Although some association with grey lava fellfield areas (see Verwoerd 1971) is evident, formal tests of such associations showed little significance. At lower elevations it seems likely that salt-spray limits the distribution of the species and its abundance at coastal sites. It has long been observed that areas exposed to salt-spray on the island support separate communities dominated by halophilic species such as *Crassula moschata* and *Cotula plumosa* (Gremmen 1981; Smith *et al*. 2001). Thus, it seems highly likely that *A. selago* is unable to tolerate the high marine salt load typical of these areas, as is the case for many other species on the island (Gremmen & Smith 2008).

The sharp, stepped decline in the abundance of *A. selago* with an increase in altitude is likely a consequence of changing temperature and perhaps snow cover. At present this would seem unlikely given a gradual decline in temperature with elevation (see e.g. Deere *et al*. 2006) and the virtual absence of a snow line (Sumner *et al*. 2004). However, the island has undergone rapid climate change over the last 40 years with mean annual temperature increasing by nearly 1.5°C (Smith & Steenkamp 1990; Smith 2002; le Roux & McGeoch 2008a). In the 1960s, the permanent snow line was found at approximately 650 m a.s.l., although by the late 1970s it had already receded to *c*. 950 m a.s.l. (Hall 1980). At present, the permanent snow line no longer exists and the stationary glacier (ice plateau) that existed above 1000 m a.s.l., has also disappeared (Sumner *et al*. 2004). However, the permanent snow line of 650 m in the 1960s is consistent with the present distribution of *Azorella selago* found in this study.

This finding would suggest that *A. selago* is incapable of surviving severely reduced light conditions. Indeed, experimental work at lower elevations, which included shading, suggested that under low light conditions the plant becomes etiolated, disrupting the wind and temperature resistant cushion-shape (Huntley 1972b), ultimately leading to cushion death (le Roux *et al*. 2005). Although, the highest altitude recorded for *A. selago* is currently 840 m (Hedding 2006), its abundance and distribution is relatively sparse above 650 m. Moreover, the species is slow growing and likely recruits only under a relatively restricted set of conditions (le Roux & McGeoch 2004). In addition, substrate movement is considerable at high elevations as is the occurrence of freeze-thaw cycles (Boelhouwers *et al*. 2003; Holness 2003), which could inhibit seedling establishment (Heilbronn & Walton 1984). In concert, these factors likely account for the inertia between exposure of the high elevation areas and colonization of the species. Although it seems plausible to argue that this difference in habitat availability and the elevational limit of *A. selago*'s distribution will gradually be reduced, the increasing frequency of clear sky evenings

(Smith & Steenkamp 1990; le Roux & McGeoch 2008a), and therefore of soil frost and needle ice conditions might preclude colonization for some time (Heilbronn & Walton 1984). Moreover, colonization rates are likely to differ among island sides especially because the western side of the island has more temperate, less variable conditions (Rouault *et al*. 2005; Nyakatya & McGeoch 2008). These island-side differences in climatic conditions likely also account for the more frequent occurrence of mats on the western than on the eastern side of the island.

Of course, although a threshold in the abundance of species may indicate a sudden change in abiotic conditions (Caughley *et al*. 1988), thresholds may also arise along shallow gradients where other factors such as competition come into play (Case & Taper 2000). However, with the possible exception of small scale competition along drainage lines at lower elevations, and in warm, moist areas that favour mire formation (see Gremmen 1981; Scott 1985; Yeloff *et al*. 2007), competition between *A. selago* species and other plants on Marion Island seems unlikely. At least at high elevations and in exposed areas, the converse seems to be true, with *A. selago* facilitating the establishment of other species which grow epiphytically on the cushions (Huntley 1972b; le Roux & McGeoch 2008b; McGeoch *et al*. 2008). Moreover, at the highest elevations, virtually no epiphytes are found (le Roux & McGeoch 2008b) and no other plant species are evident except for a very poorly developed interstitial cryptogam flora (Gremmen 1981). Similarly, although one weevil species feeds on live *A. selago*, the only herbivore known to use live material of this species, its abundance and consumption rates are too low to effect a reduction in plant viability (Crafford *et al*. 1986; Chown & Schlotz 1989; Crafford & Chown 1991). In consequence, abiotic controls on the elevational limits of the distribution and abundance of *A. selago* seem most likely. Why the species has not evolved to overcome these barriers is also a significant question, and various hypotheses have been proposed in this context for other organisms (Hoffmann & Blows 1994; Gaston 2003; Blows & Hoffmann 2004). However, addressing these questions is beyond the scope of this largely mensurate study.

In conclusion, this study has demonstrated, at the island-wide scale, that the abundance structure of a keystone vascular plant species, the cushion-forming *A. selago*, does not show evidence of an abundant centre distribution. Rather, its internal abundance structure across the island is much more like that typically documented for other species: complex patches of high and low abundance occur within the overall range limits of the species.

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TABLES

Table 1 The list of habitat characteristics and their different states used as relational variables for understanding the distribution of *A. selago* across Marion Island.

Substrate	Habitat complex	Slope	Aspect (abbr.)
Full vegetation cover	Coastal salt spray	Flat	Flat
Grey lava	Fellfield	Undulating	North (N)
Black lava	Slope	Slight	North East (NE)
Scoria	Mire	Moderate	East (E)
Other[1]	Other[2]	Steep	South East (SE)
-	-	-	South (S)
-	-	-	South West (SW)
-	-	-	North West (NW)

[1] A combination of grey lava, black lava, and scoria

[2] A transition between fellfield and slope complex

Table 2 The best subset model of the quadratic polynomial describing observed *A. selago* abundance and distribution patterns based on the lowest AIC and highest w_i values (AIC = 4695.20; $w_i = 0.819$; L. ratio $\chi^2 = 1460.14$; $p < 0.0001$) resulting from a GLM regression assuming a Poisson error distribution (log link function, Type 3 model) (Lat = latitude, Long = longitude).

Model	Predictor variables in the model	χ^2	p-value
GLM	Lat (-),	4.70175	0.0301
	Long (-),	30.0512	< 0.0001
	Lat*Long (+),	0.12108	0.7279
	Lat^2 (+),	10.516	0.0012
	Long^2 (+)	27.5977	< 0.0001

FIGURES

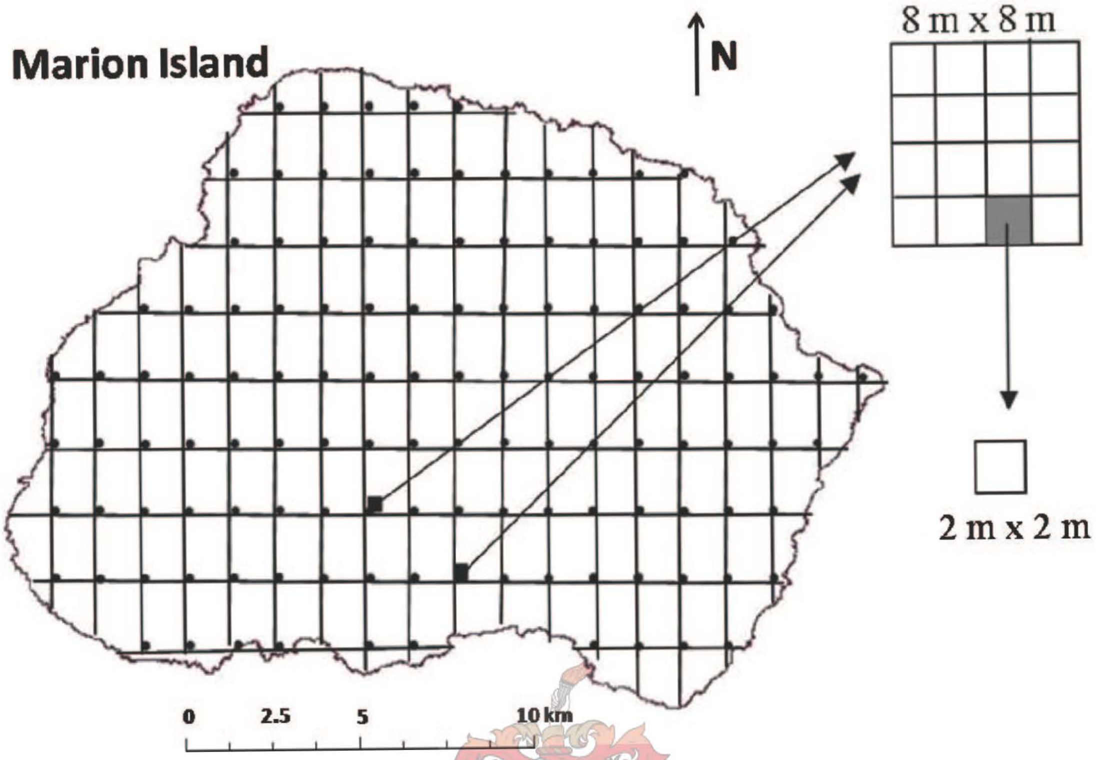

Figure 1 Sampling design illustrating the gridline intersection points; ■ = 8 m x 8 m grid (subdivided into sixteen 2 m x 2 m quadrats) placed at grid intersection points.

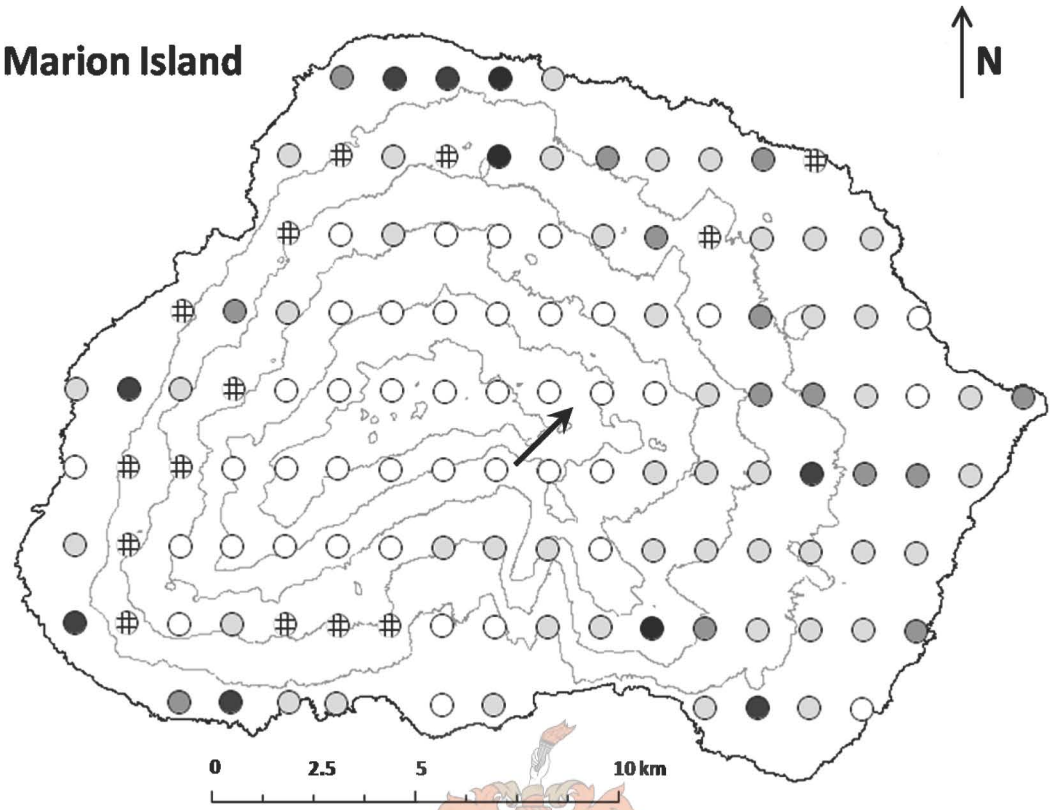

Figure 2 a The distribution of *Azorella selago* abundance and mat cushions across Marion Island. The white circles represent areas where *A. selago* was absent; ◌ = cushion abundance between 1 to 50 cushions per plot; ◍ = 51 to 100 cushions; ◉ = 101 to 150 cushions; and ● = 151 to 210 cushions per plot. The squares within white circles indicate sites with cushion mats. The arrow indicates the balance point of the range.

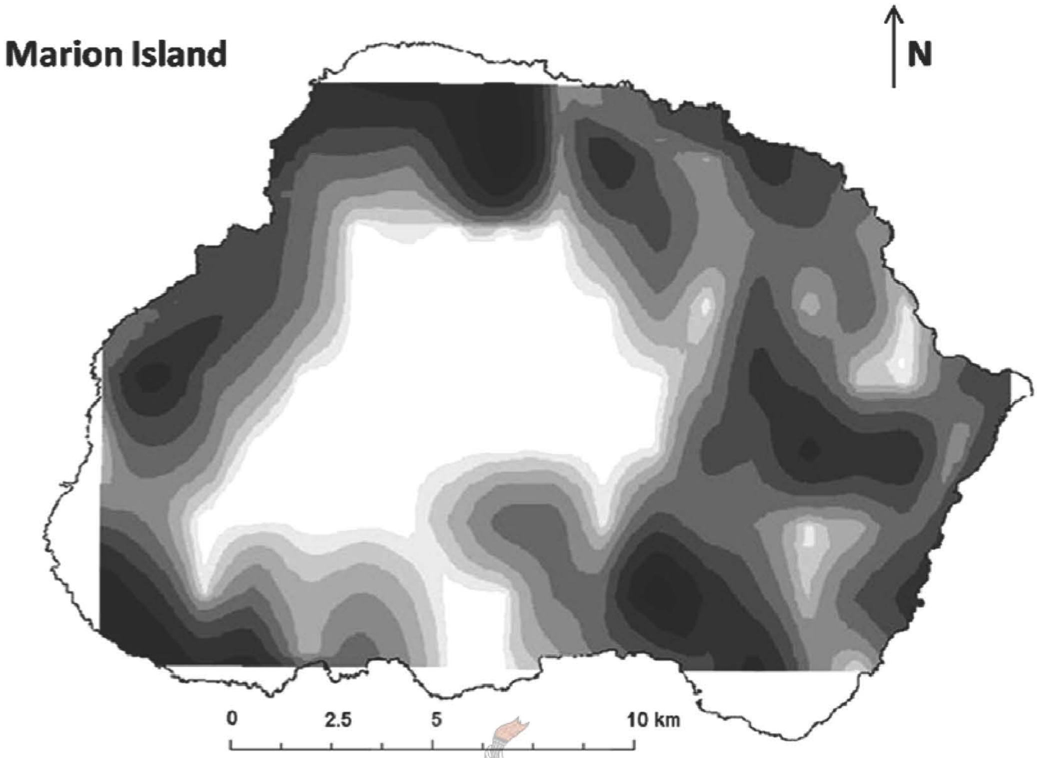

Figure 2 b The interpolated pattern of spatial autocorrelation and the distribution of the abundance of *Azorella selago* across Marion Island. The white areas are sites where *A. selago* was absent and the black areas represent sites where cushion abundance was > 150 cushions per plot.

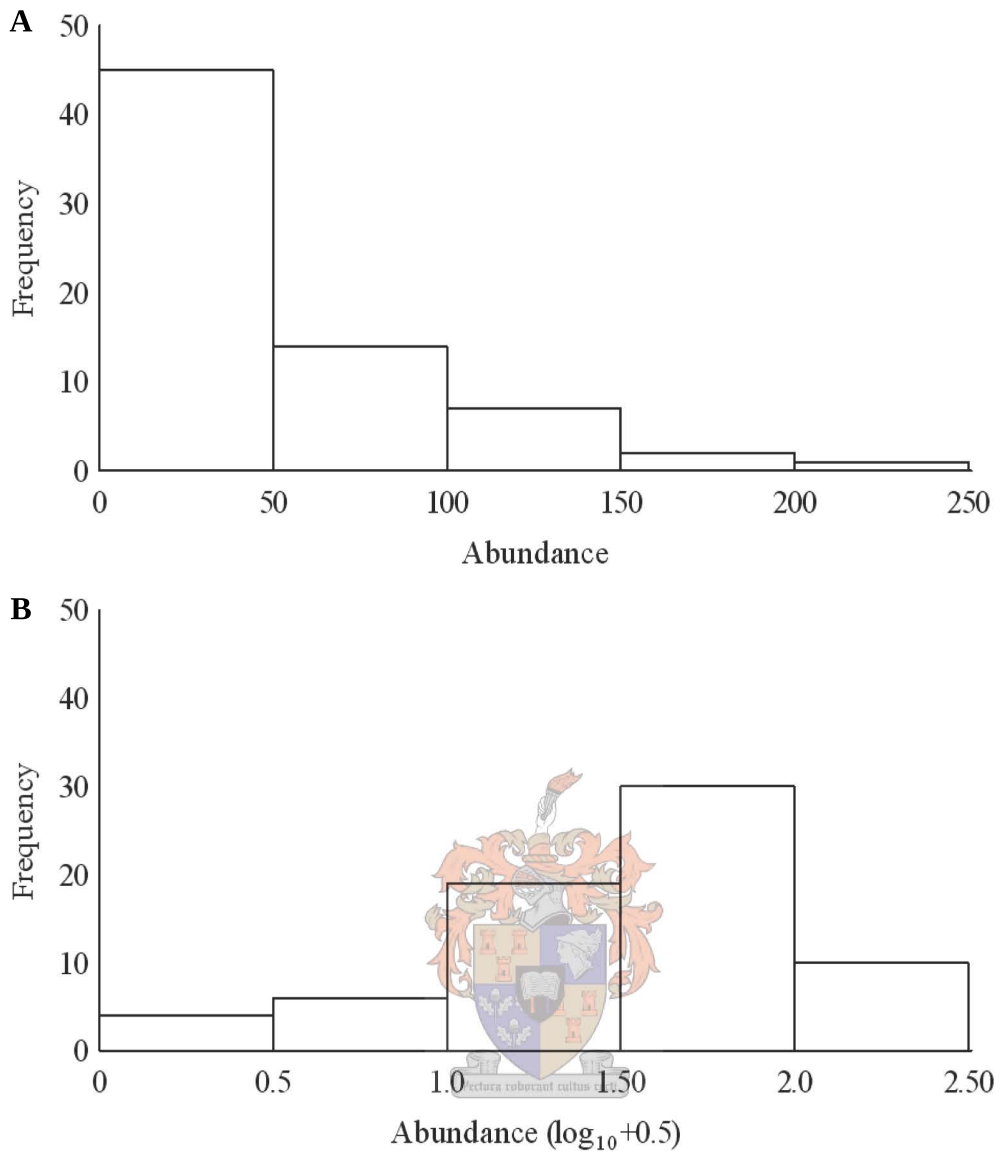

Figure 3 a The abundance (density per 8 m x 8 m plot) frequency distribution of *Azorella selago* on Marion Island; **b** the log of abundance ($\log_{10}$ density per plot) frequency distribution pattern for *Azorella selago* across Marion Island.

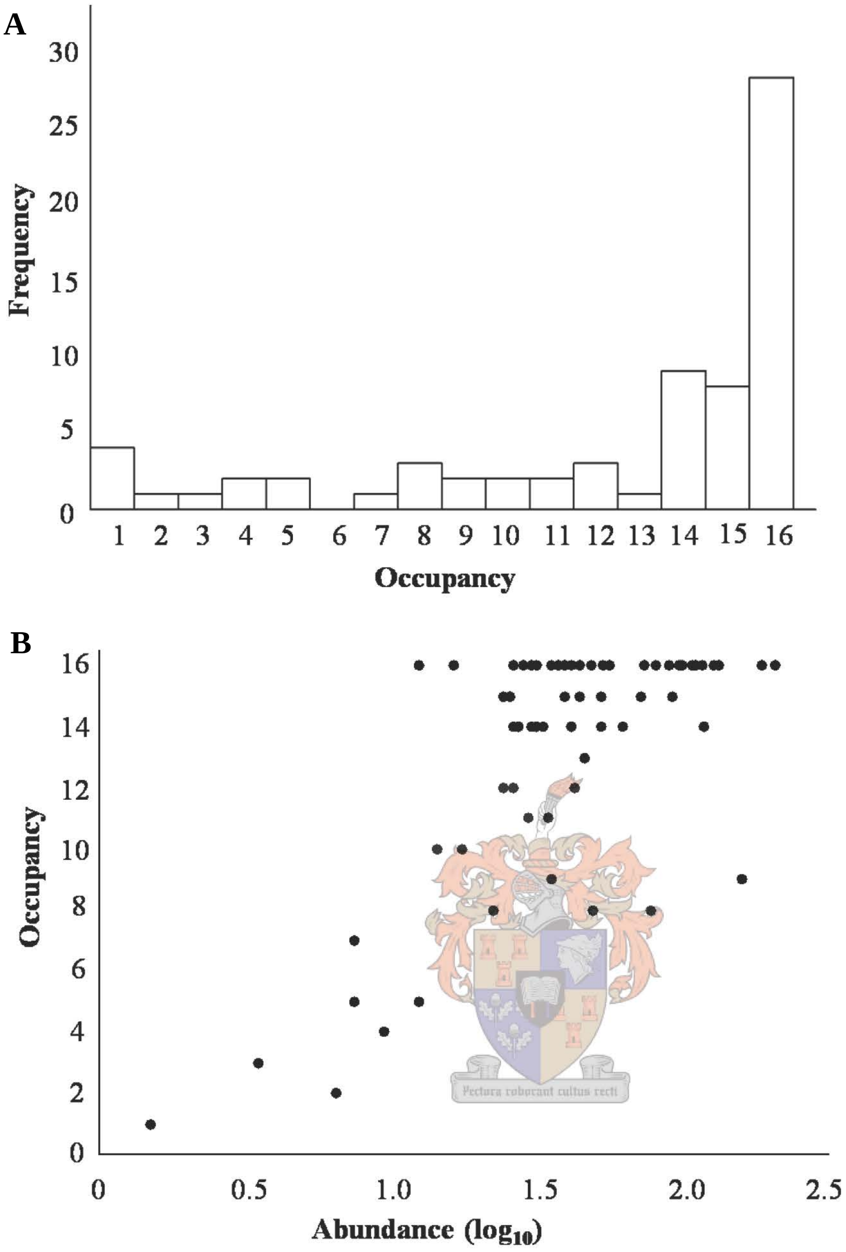

Figure 4 a The occupancy frequency distribution for the number of 2 m x 2 m quadrats occupied per plot (with 16 indicating 100 % occupancy). **b** The relationship between the occupancy and abundance ($\log_{10}$ density per plot) of *Azorella selago* across Marion Island ($r^2 = 0.8964$; $p < 0.0001$; $y = 1.9563 + 6.9734*x$).

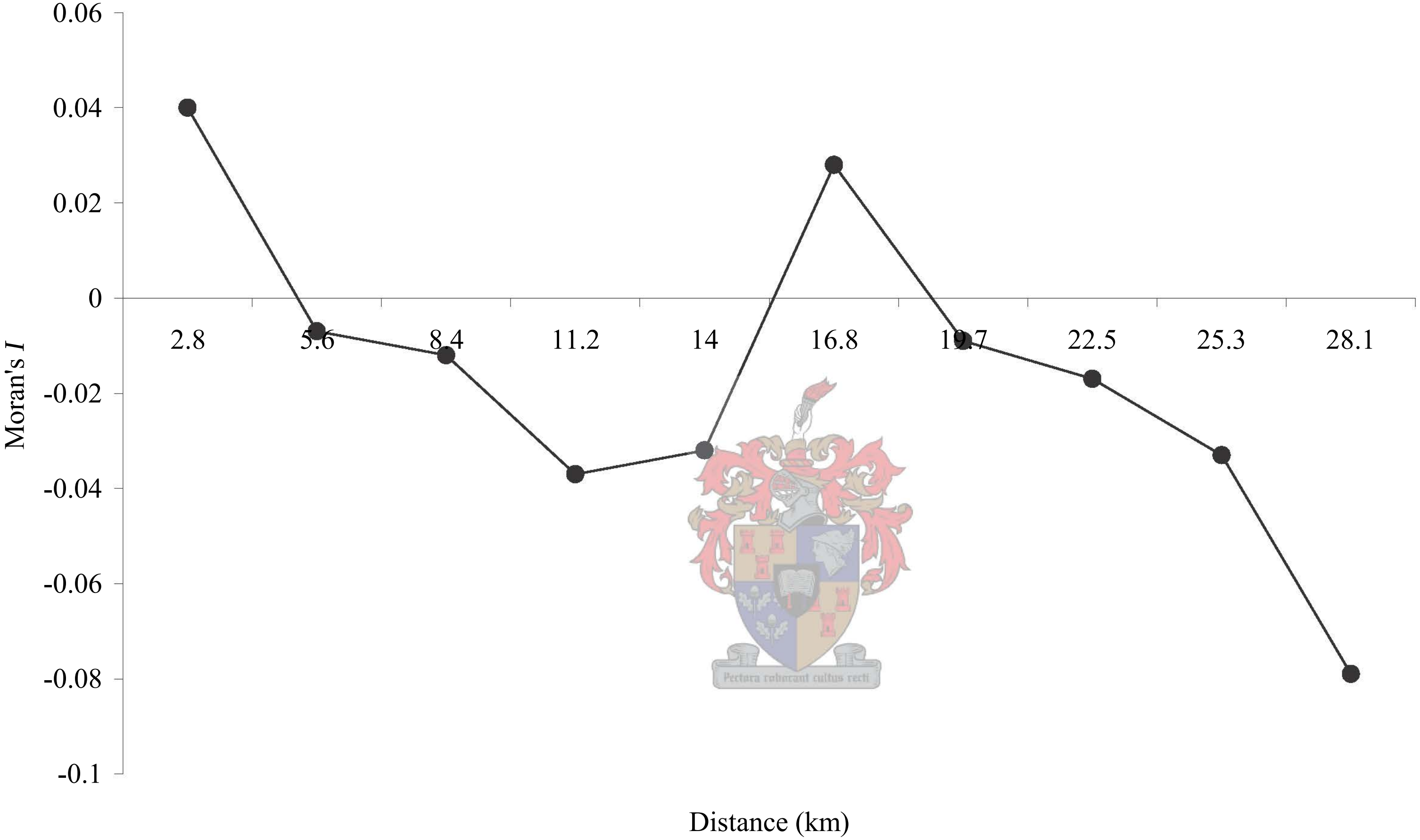

Figure 5 Correlogram of Moran’s autocorrelation coefficient for the spatial distribution of *Azorella selago* abundance across Marion Island (p > 0.05 at all distance classes).

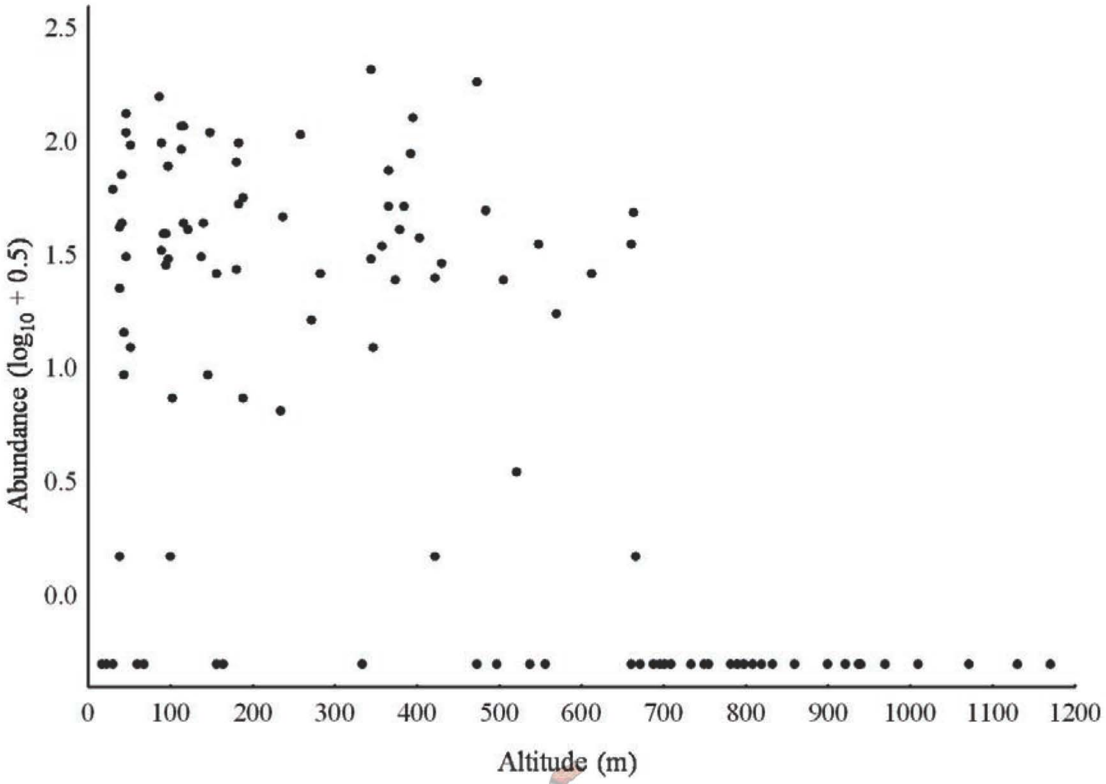

Figure 6 The relationship between *Azorella selago* abundance ($\log_{10}$ density per plot) and altitude ($r^2 = 0.3727$; $p = 0.0001$; $y = 1.5761 - 0.0018*x$).

Chapter 3

SPATIAL VARIATION IN STRUCTURAL DAMAGE TO A KEYSTONE PLANT SPECIES IN THE SUB-ANTARCTIC: INTERACTIONS BETWEEN *AZORELLA SELAGO* AND INVASIVE HOUSE MICE

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INTRODUCTION

The house mouse, *Mus musculus* L., is one of the most successful mammal invaders on Southern Ocean islands, having established on at least eight of them (Frenot *et al*. 2005). On several of these islands the impacts of this rodent are now clear. Mice consume large numbers of indigenous invertebrates, including important keystone species such as flightless moth caterpillars on Marion Island (Crafford 1990; Chown & Smith 1993; Smith *et al*. 2002); earthworms, weevils and aphids on Guillou Island in the Kerguelen Archipelago (le Roux *et al*. 2002); and several invertebrate species on Macquarie Island (Copson 1986). The effects of mice also extend beyond direct influences on the populations of their prey species, and these include alterations of nutrient dynamics (Smith & Steenkamp 1990, 1992), changes in the distribution of prey given mouse habitat preferences (Jones *et al*. 2003), and indirect effects on indigenous predators as a consequence of competition for the same food resources (Huyser *et al*. 2000). More recently, mice have been found to feed on live albatross and petrel chicks, so posing a considerable threat to species that are in many cases already impacted by long-line fishing activities at sea (Wanless *et al*. 2007). In consequence, the significance of the introduced house mouse in the terrestrial ecosystems of Southern Ocean islands is now widely appreciated (Frenot *et al*. 2005).

However, one aspect of their activities has, to date, been under-investigated: the direct impact that the species might have on plants, and the secondary landscape level effects that might arise as a consequence. Whilst many studies have documented the presence of seeds and other plant remains in the stomach contents of mice, food items which may have both a high percentage occurrence (> 75 %) (e.g. le Roux *et al*. 2002) and percentage contribution (at times > 50 %) (Smith *et al*. 2002), few investigations have sought to determine the impact that this level of consumption might have on the plants. Only Chown & Smith (1993) have shown that by consuming seeds of the sedge *Uncinia compacta*, mice may be restricting its range expansion as a consequence of drying conditions on Marion Island. Nonetheless, high levels of mouse activity and consumption may well have broader effects, especially by transporting alien species (e.g. *Taraxacum* on Kerguelen – le Roux *et al*. 2002), or by changing the landscape through seed harvesting or burrowing (Avenant & Smith 2003).

The latter seems especially likely on Marion Island, where Avenant & Smith (2003) found that more than 50 % of mouse burrow entrances occurred in *A. selago* cushions at sites where the species was not the dominant plant. Their findings suggest that *A. selago* might be the preferred species for burrow entrances in habitats where it is present. Given the significance of this plant as a keystone species, especially in fellfield areas (Barendse & Chown 2001; McGeoch *et al*. 2008), and its effects on landscape structure (Holness & Boelhouwers 1998; Boelhouwers *et al*. 2000), mouse activity in *A. selago* could potentially have considerable, landscape level implications for ecosystem functioning on the island. Therefore, in this study I examine the extent and spatial distribution of disturbance to *A. selago* cushions by mice using systematic and *ad hoc* sampling of cushions at an island-wide scale. I do so especially to determine the extent to which the house mouse may be having impacts on the landscape: a level of impact previously not investigated for this species on the islands to which it has been introduced.

MATERIALS AND METHODS

Study site and species

Marion Island (46°54′S, 37°45′E), is situated just to the north of the Antarctic Polar Frontal Zone, and together with neighbouring Prince Edward Island makes up the Prince Edward Island (PEI) group. The island has an area of 290 km^2 and rises to 1230 m a.s.l with a 72 km coastline (Verwoerd 1971). It has undergone rapid climate change over the last five decades, with mean annual temperature increasing by nearly 1.5°C (Smith 2002; le Roux & McGeoch 2008; see also Chown & Froneman 2008 for further information on the island's ecosystems). Because of its low temperature and geographic isolation it has relatively low species richness (Chown *et al*. 1998; Chown & Froneman 2008). The island's vegetation has been classified into seven vegetation complexes containing twenty-three habitats (Huntley 1971; Gremmen 1981; Smith *et al*. 2001; Smith & Steenkamp 2001).

The house mouse was introduced to Marion Island over 200 years ago (Watkins & Cooper 1986), probably from Scandinavia (Jansen van Vuuren & Chown 2007). Following the successful eradication of feral cats (Bester *et al*. 2000), it is now the only naturalized terrestrial alien invasive mammal on Marion Island. Its population is thought to have increased over the last thirty years as a consequence of climatic amelioration. Nonetheless, the temporal demographic picture is complex with both temperature and population density acting in concert to affect population levels (Smith & Steenkamp 1990; van Aarde *et al*. 1996; Ferreira *et al*. 2006; van Aarde & Jackson 2007). Although the eradication of cats might have affected mouse densities, mice were never an important prey item for cats and cat predation likely did not limit the mouse population (Ferreira *et al*. 2006). At present, lowland mouse densities are in the region of 100-260 mice.ha^{-1}, depending on vegetation type, with peak densities occurring in April/May, and the lowest densities in October to December (Ferreira *et al*. 2006). The species has also increased its altitudinal range on the island. Anderson & Condy (1974) estimated that high mouse densities were found only below 300 m a.s.l. Later, Gleeson (1981) estimated that at 450 m a.s.l. mice were surviving close to their physiological limits on the island. Mice are now active, but not abundant, close to 800 m a.s.l. (in the Katedraalkrans field hut; personal observation) and sightings of dead mice have been reported from close to 1200 m a.s.l. (Avenant & Smith 2003).

Azorella selago Hook. (Apiaceae) is a cushion-forming plant and is an important constituent of sub-Antarctic plant communities (Huntley 1972). On Marion Island it is one of the five vascular plant species dominating the aerial standing crop (Smith 1978), and it is the only vascular plant that occurs in all vegetation complexes on the island (Smith *et al*. 2001), ranging from sea level to approximately 840 m a.s.l., so also setting the altitudinal limits for vascular plants on the island (Huntley 1972; Hedding 2006). The leaves and stems of individual *Azorella selago* plants grow tightly together to form hard, compact surfaces of various shapes and sizes, resulting in two distinct growth forms – discrete cushions, and large, continuous mats (Orchard 1989; Frenot *et al*. 1993). The discrete cushions are spatially isolated individuals that are often surrounded by bare soil and rock, while the mat growth form is characterized by flat, continuous expanses of multiple plants (Mortimer *et al*. 2008), often associated with seepages (Huntley 1972; Gremmen 1981). Continuous mats of *A.*

selago may extend over areas as large as 1200 m^2. The species is a slow growing perennial (Huntley 1972; Frenot *et al*. 1993; le Roux & McGeoch 2004), with cushion age estimated to be between 30 and 80 years for cushions of 40 cm diameter (le Roux & McGeoch 2004).

Sampling

Since most studies have examined the ecology and the impacts of mice on invertebrates at low altitudes (e.g. Gleeson & van Rensburg 1982; Crafford 1990; Chown & Smith 1993; Avenant & Smith 2003; Ferreira *et al*. 2006) and to avoid bias towards paths, the abundance and distribution of *A. selago*, and damage to it by mice across its entire, island-wide range was quantified. That is, the extent of the sampling covered the entire island. Owing to the island's considerable size, the resolution of the sampling was chosen as 1 x 1 minute. These one minute lat/long gridline intersection points resulted in a total of 124 points sampled across the island. They were located in the field using a handheld GPS receiver unit, and at each sampling point a 64 m^2 grid was placed and the total number of *A. selago* cushions (cushion density) and number of mouse burrows and/or excavated *A. selago* cushions (burrow density) were counted in each plot. Thus, the extent of the sampling was 290 km^2, the resolution was 1 x 1 minute, and the sample unit size was 64 m^2 (see McGeoch & Gaston (2002) for additional discussion of this terminology). The sampling protocol was adopted after careful consideration of the total island area to be covered relative to the spatial variation in cushion densities that had been recorded previously (where present, *c*. 0.14 to 1.55 cushions.m^{-2}, McGeoch *et al*. 2008).

In addition to the systematic sampling, twenty-six, 150 m^2 plots (randomly located at low altitudes, below 300 m a.s.l.) at several locations around the island (see Fig. 1) were also surveyed. In these plots *A. selago* density, the number of mouse burrows (occurring in both *A. selago* and the surrounding vegetation), the number of *A. selago* cushions which had been burrowed into, and the number of mouse burrows occurring in each *A. selago* cushion were recorded.

Data analyses

Global positioning system point localities were converted to shapefiles and the distribution of *A. selago* cushions, including those that had signs of mouse damage, was mapped (ArcGIS™ 9.1 ArcMap), for both the systematic and *ad hoc* sampling.

Universal kriging (ArcGIS™ 9.1 Geostatistical Analyst), a method used for producing interpolated maps by determining the level of spatial autocorrelation of the variable being analysed and for the prediction of abundances at unsampled sites (Zimmerman & Zimmerman 1991), was used to interpolate the distribution of *A. selago* density, recorded in the 124, 64 m^2 plots, across Marion Island. The proportion of mouse-damaged *A. selago* cushions per 64 m^2 plot (only plots with cushions that were burrowed into) was also interpolated by means of kriging. For both sampling approaches I also re-expressed the data on the basis of the number of burrows per cushion surface area using median cushion diameter estimates (given a right-skew in the frequency distribution) obtained from three different areas of the island (0.53 m, see le Roux & McGeoch 2004), and the assumption of an approximately spherical cushion shape.

RESULTS

Opportunistic field observations showed that mouse damage to *Azorella selago* was almost continuous along coastal and inland paths on Marion Island (Fig. 1). In the twenty-six, 150 m^2 *ad hoc* plots, the number of burrow entrances in cushions ranged from one to four (Table 1), and in some cases entire cushions were excavated by burrowing, causing the disintegration of the plant (Fig. 2).

In the *ad hoc* plots, a mean of 18 *A. selago* cushions was found per plot (a mean density of 0.12 cushions.m^{-2}) (Table 1). Of a total of 19.7 mouse burrows per plot, approximately 11.4 burrows were found in *A. selago* cushions, the remainder being found in other vegetation (Table 1). Based on a median cushion diameter of 0.475 m (le Roux & McGeoch 2004), and the assumption of a roughly spherical cushion (giving a median area of 0.746 m^2), the density of mouse burrows per cushion surface area was estimated as 0.85 burrows.m^{-2} on average, ranging from a minimum estimate of 0.44 burrows.m^{-2} of cushion area to a maximum estimate of 3.0 burrows.m^{-2} of cushion area.

In the systematic sampling (the 124, 64 m^2 plots), *A. selago* was recorded in 83 of the 124 plots, between 37 m and 667 m a.s.l. (Figs 3 and 4a). Cushion density ranged from 0.016 to 3.25 cushions.m^{-2} (mean ± SE: 0.81 ± 0.08 cushions.m^{-2}), excluding coalesced, mat-like cushions which were found in 14 of the 83 plots. Mouse burrows were found in 32 of the 83 plots (39 %) and in cushions up to 548 m a.s.l. (Fig. 3). In these, mostly higher elevation plots, the number of burrows per *A. selago* cushion was low (mean ± SE: 0.13 ± 0.04), and 28 plots had < 15 % of their *A. selago* cushions affected by mice (Fig. 4b). Areas that had high *A. selago* densities tended to have a lower proportion of mouse-damaged cushions (compare Figs 4a and b).

DISCUSSION

To date, investigations of the impacts of house mice on Southern Ocean ecosystems have been concerned largely with their direct effects on invertebrates and seabirds, and indirect effects on nutrient cycling. By contrast, little attention has been given to their impacts on plant populations (beyond documenting the inclusion of plant material in the diet) and certainly not at a landscape scale. This study makes it clear that neglect of such landscape-scale impacts will lead to an underestimate of the significance introduced mice in Southern Ocean island ecosystems. Structural damage by mice to *A. selago* is widespread on Marion Island, being found nearly across the full range of the cushion plant and up to 548 m in elevation, close to the elevational limit of cushions (667 m a.s.l.) identified in the systematic sampling. In addition, *c.* 39 % of plots sampled contained mouse damage, and within these plots damage was sometimes extensive, although more typically fewer than 15 % of cushions were affected.

In lowland areas, the *ad hoc* sampling revealed a mean density of *c.* 0.85 burrows.m^{-2} of cushion surface area. Moreover, it can be assumed that *A. selago* cushions constitute *c.* 5 % of overall surface area at these typically lower elevations, given that other plant species dominate the lowland vegetation (Gremmen & Smith 2008). At higher elevations, the percentage surface area covered by cushions ranges from 7 to 33 % with a mean of *c.* 20 % (Nyakatya *et al.* unpublished data; see also Barendse & Chown (2001) who found a value of 8.7 %). On this basis, an estimate of *c.* 425 mouse burrows per hectare can be made (0.85 burrows.m^{-2} x 500 m^{2} of cushion.ha^{-1} = 425 burrows.ha^{-1}), which is in keeping with the 340 to 1000 burrow.ha^{-1} recorded by Avenant & Smith (2003) in other lowland vegetation types. At the mostly higher elevation, systematic sampling plots, mean cushion density was high, at 0.81 cushions.m^{-2}, and burrow density was low, typically 0.13 burrows per cushion or 0.16 burrows.m^{-2} of cushion surface area. Assuming a mean surface area covered by *A. selago* cushions of *c.* 20 % of the total surface area available (see above), burrow density at these mostly higher elevations amounts to *c.* 320 per ha, a value also in keeping with the lower end of those found by Avenant & Smith (2003) for coastal areas. These estimates provide grounds for a whole-island first estimate of mouse impact on *A. selago*. If it is assumed that at low elevations (200-400 m) 0.85 burrows are found per m^2 of cushion surface, that 5 % of surface area is covered by *A. selago* cushions, and that the total surface area of these elevations is 6705 ha (Meiklejohn & Smith 2008), approximately 2.8 million burrows are likely. At the higher elevations (400 to 600 m, 5206 ha), by similar calculation, *c*. 1.7 million burrows are present. In total, 4.5 million mouse burrows are likely to have been present at the time of sampling. These values appear extraordinarily high, but on closer assessment are not unrealistic. By using the digital elevation model surface area data provided by Meiklejohn & Smith (2008) and the lowest (0.12 cushions.m^{-2}) and highest (2.81 cushions.m^{-2}) cushion density estimates for all studies of this species (Hugo 2006; Nyakatya 2006; this study), the estimated total number of cushions on the island, between 200 and 600 m a.s.l., varies between 11.4 and 267 million cushions (acknowledging that much spatial variation is present (Fig. 4b), and in many areas cushions coalesce to form mats (Gremmen 1981; Mortimer *et al*. 2008)). These numbers provide an estimate of 0.02 to 0.4 mouse burrows per cushion, which encompasses the recorded value of 0.13 burrows per cushion in the systematic sampling plots.

Given that mice are clearly capable of causing total disintegration of cushions, that *A. selago* cushions are in the order of 30 to 80 years old on average (le Roux & McGeoch 2004), and that special, and currently unknown, conditions appear to be required for seedling establishment (McGeoch *et al*. 2008), this level of ‘standing damage’ is substantial and of considerable concern for a species of which the population dynamics and turnover are so poorly known. Certainly it appears that impacts in fellfield systems may be much more significant than previously thought (e.g. Gleeson & van Rensburg 1982). However, establishing the real significance of these impacts will require an estimate of annual mouse damage to cushions as well as recruitment to the *A. selago* population because it is the interaction of these two rates that will provide the most meaningful estimate of impact. Such estimates will require long-term studies of both mouse and *A. selago* populations in a spatially explicit fashion. The spatial detail will be especially necessary because mouse damage to cushions is not uniformly distributed across the island, as is clear from the landscape-scale variation in the proportion of cushions affected by mouse burrowing (Fig. 4b) relative to cushion density (Fig. 4a). High cushion density areas are less affected by mice than low cushion density areas. It seems likely that, given temperature and density regulation of mouse abundances (Ferreira *et al*. 2006), this spatial asynchrony may well be a consequence of a surplus of cushion resources in high cushion density areas. However, only further, detailed demographic studies will reveal its cause. At present, explicit demographic work of this form is not being undertaken on the island, although several long-term plots to assess *A. selago* population dynamics have been established (McGeoch *et al*. 2008).

Of course, it is not simply direct impacts on the *A. selago* population that may be ecologically significant. *Azorella selago* serves as a nurse plant for many epiphyte species, so increasing the altitudinal range of a variety of them, and also houses high densities of invertebrates, acting as a keystone species especially in fellfield landscapes (Barendse & Chown 2001; le Roux *et al*. 2005; Hugo *et al*. 2004; McGeoch *et al*. 2008). In this way it significantly influences the structure and dynamics of fellfield systems, also contributing substantially to successional patterns found on Marion Island (Scott 1985; Yeloff *et al*. 2007). By damaging cushions, and in some cases by causing their disintegration, mice might, to an unknown and quite likely large extent, be affecting this keystone role that is played by *A. selago*. Moreover, because warming and drying on the island (le Roux & McGeoch 2008) are predicted to have deleterious effects on cushions and their associated biota (le Roux *et al*. 2005; McGeoch *et al*. 2006), and because further climate change is predicted to lead to greater impacts by mice (Smith & Steenkamp 1990), the landscape level impacts of mice on ecosystem functioning, as a consequence of their predilection for *A. selago* cushions, might be larger than presently estimated.

In addition to quantifying levels, distribution and rates of impact, understanding the reasons for the selection of cushions by mice is also important. It seems likely that a combination of thermally stable environments and significant food resources may prompt mice to select cushions for burrowing and for nest construction. Cushions act as a thermal buffer (Huntley 1971; Chown & Crafford 1992; Nyakatya & McGeoch 2008) and the difference in temperature between the plant surface and 10 cm below it may be as high as 2 °C in summer. In winter, cushions are thermally stable. Overall, cushion interiors experience less extreme and less variable temperatures than the surface of the plants, irrespective of where they occur on the island (Nyakatya & McGeoch 2008). Cushions also house high densities of arthropods (Barendse & Chown 2001), including the species on which mice feed. For instance, weevils of the genus *Ectemnorhinus* are among the preferred prey of mice (Smith *et al*. 2002), and the biomass of weevil larvae in *A. selago* cushions is more than double that found in mire communities at similar elevations, and peaks during the winter months when resources may most be required to survive harsh conditions (Chown & Scholtz 1989). Moreover, large weevil adults, preferred by mice (Chown & Smith 1993) are also abundant on *A. selago* cushions (Chown 1990). Therefore, both milder temperatures and greater food availability in cushions may have provided mice with a means of colonizing high altitudes as climates have ameliorated in these areas (see Smith 2002; le Roux & McGeoch 2008).

The present results have added to a growing list of the impacts that the house mouse has on Southern Ocean island species and ecosystems (Copson 1986; Crafford 1990; Smith & Steenkamp 1990; Huyser *et al*. 2000; Chown *et al*. 2002; le Roux *et al*. 2002; Jones *et al*. 2003; Wanless *et al*. 2007). Indeed, it is clear that this species constitutes a significant conservation challenge in the region, as do other rodent species, such as rats, that occur on several Southern Ocean islands (see e.g. Chapuis *et al*. 1994; Frenot *et al*. 2005). In a report concerning the possibility of eradicating mice from Marion Island, Chown & Cooper (1995) stated that the eradication of mice from Marion Island is both "*desirable and feasible*". Rodents, including house mice, have been successfully eradicated from several New Zealand islands (reviewed by Towns & Broome 2003; see also Howald *et al*. 2007), but most of these islands are smaller in area (Towns & Broome 2003) than is the *c*. 290 km^2 Marion Island. Nonetheless, given their significant, and probably growing impacts, the eradication of mice from Marion Island is indeed desirable and should be made a priority during the implementation of the new Environmental Management Plan for the Prince Edward Islands (see Davies *et al*. 2007).

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TABLE

Table 1 Summary statistics for the number of *Azorella selago* cushions and the numbers of mouse burrows per plot and per cushion in the 26, 150 m^2 plots.

	n	Mean ± SE	Min.	Max.
No. *A. selago* cushions per plot	26	18.00 ± 1.46	5.00	34.00
Cushion density (m^{-2})	26	0.12 ± 0.01	0.033	0.227
No. mouse burrows per plot	26	19.65 ± 2.96	3.00	53.00
No. burrows overall found in *A. selago* cushions	26	11.38 ± 1.55	3.00	32.00
No. *A. selago* cushions containing burrows	26	6.12 ± 0.74	1.00	18.00
No. burrows per cushion	26	2 ± 0.2	1	4

FIGURES

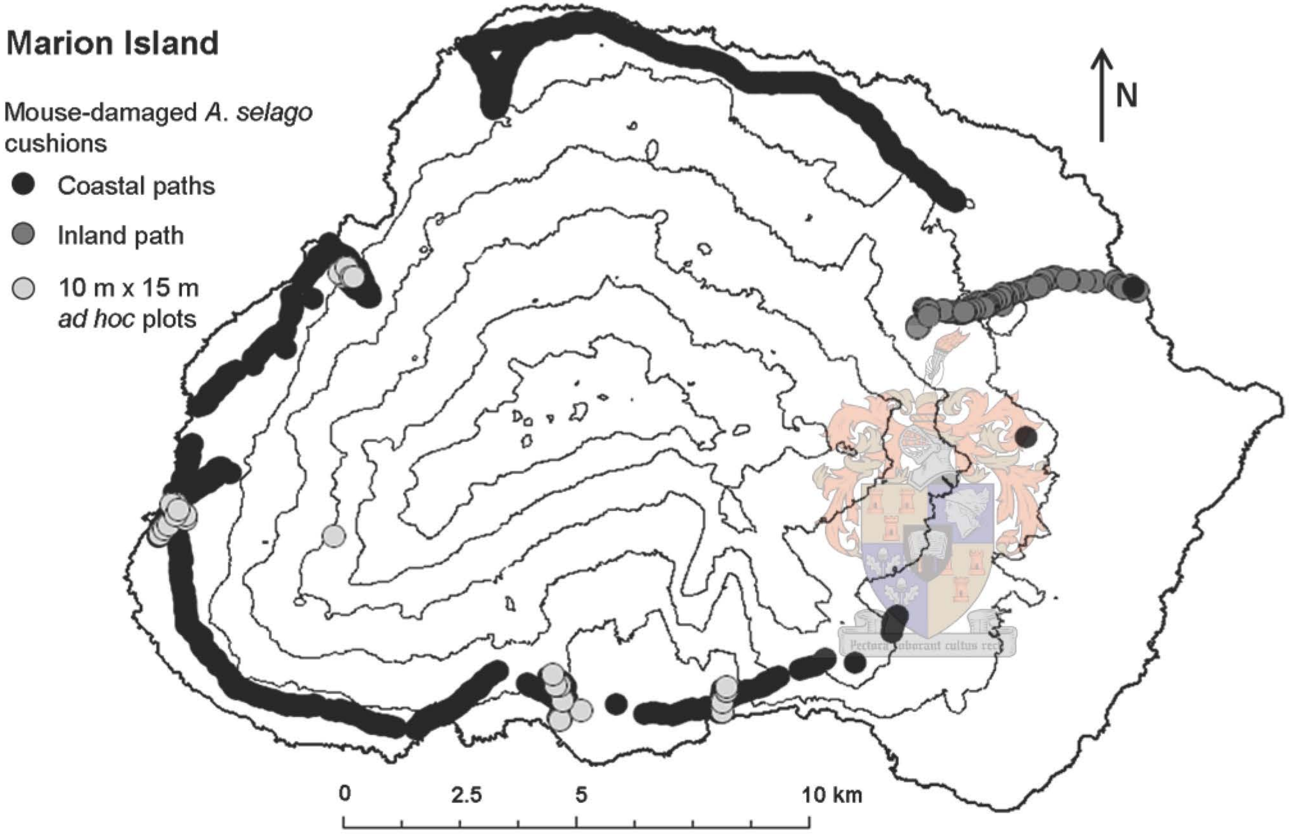

Figure 1 *Ad hoc* observations of mouse activity (damage) in *Azorella selago* cushions along coastal and inland paths on Marion Island, as well as for the twenty-six *ad hoc* 10 m x 15 m plots.

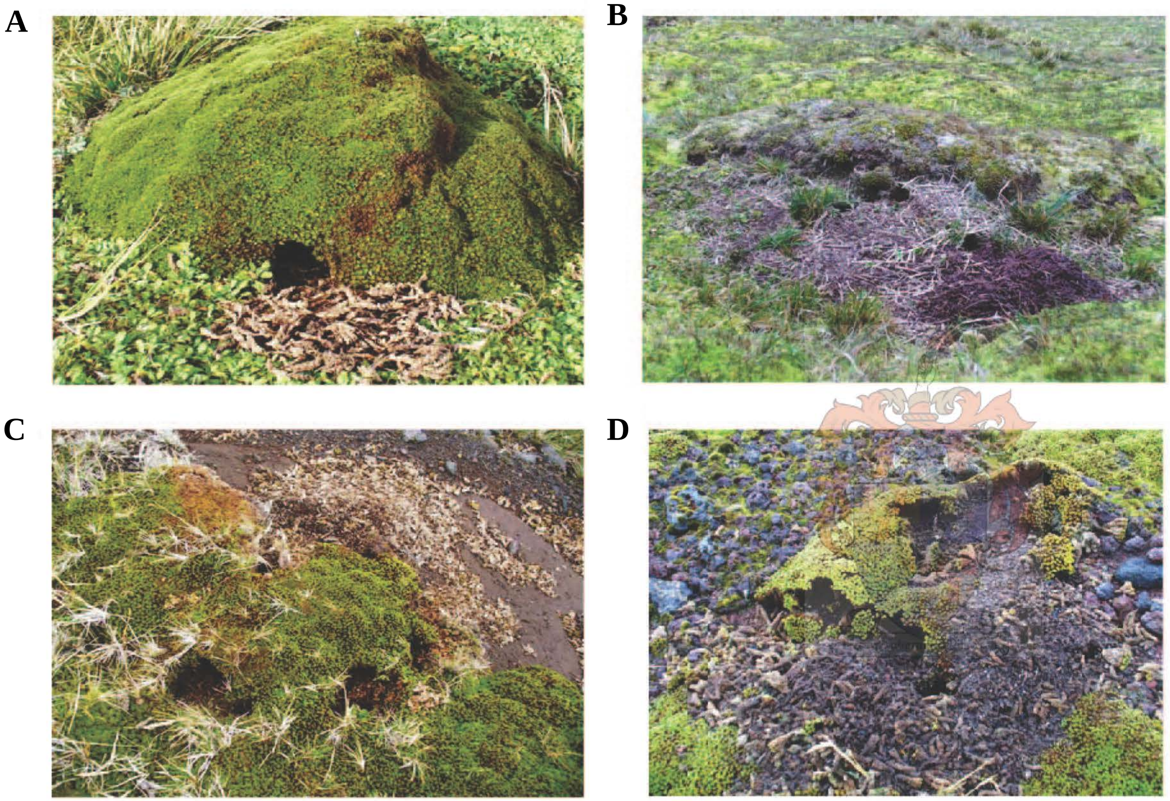

Figure 2 The observed mouse damage to *Azorella selago* cushions along paths and across Marion Island (in systematic and *ad hoc* plots). *Azorella selago* with **a** a single burrow entrance, **b** multiple burrow entrances, **c** multiple burrow entrances and partial disintegration, and **d** a disintegrated cushion where mouse burrow entrances are barely visible.

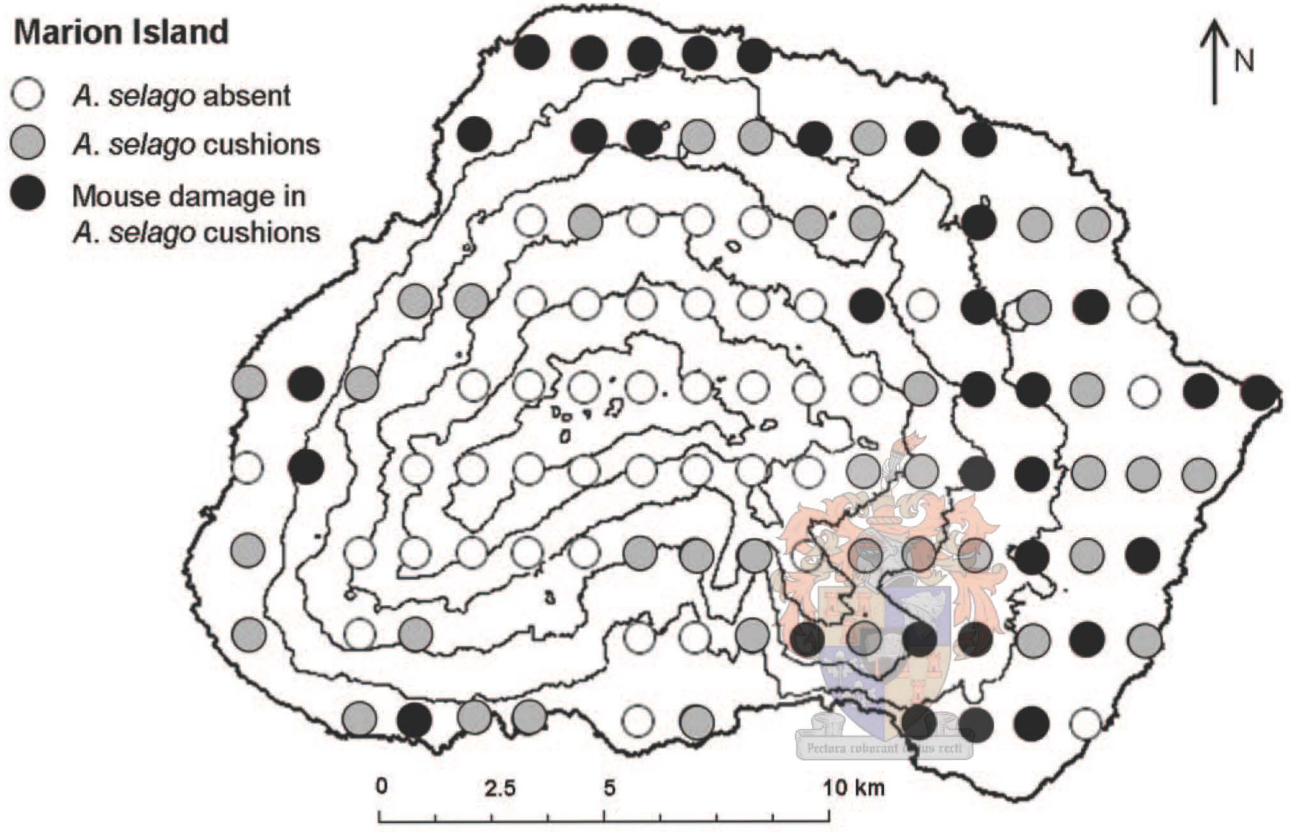

Figure 3 The distribution of *Azorella selago* recorded on a minute-by-minute basis across Marion Island. The white circles indicate areas where *A. selago* is absent. The grey circles show areas where *A. selago* is present, but no mouse damage was found, while the black circles are indicative of *A. selago* cushions that had signs of mouse damage.

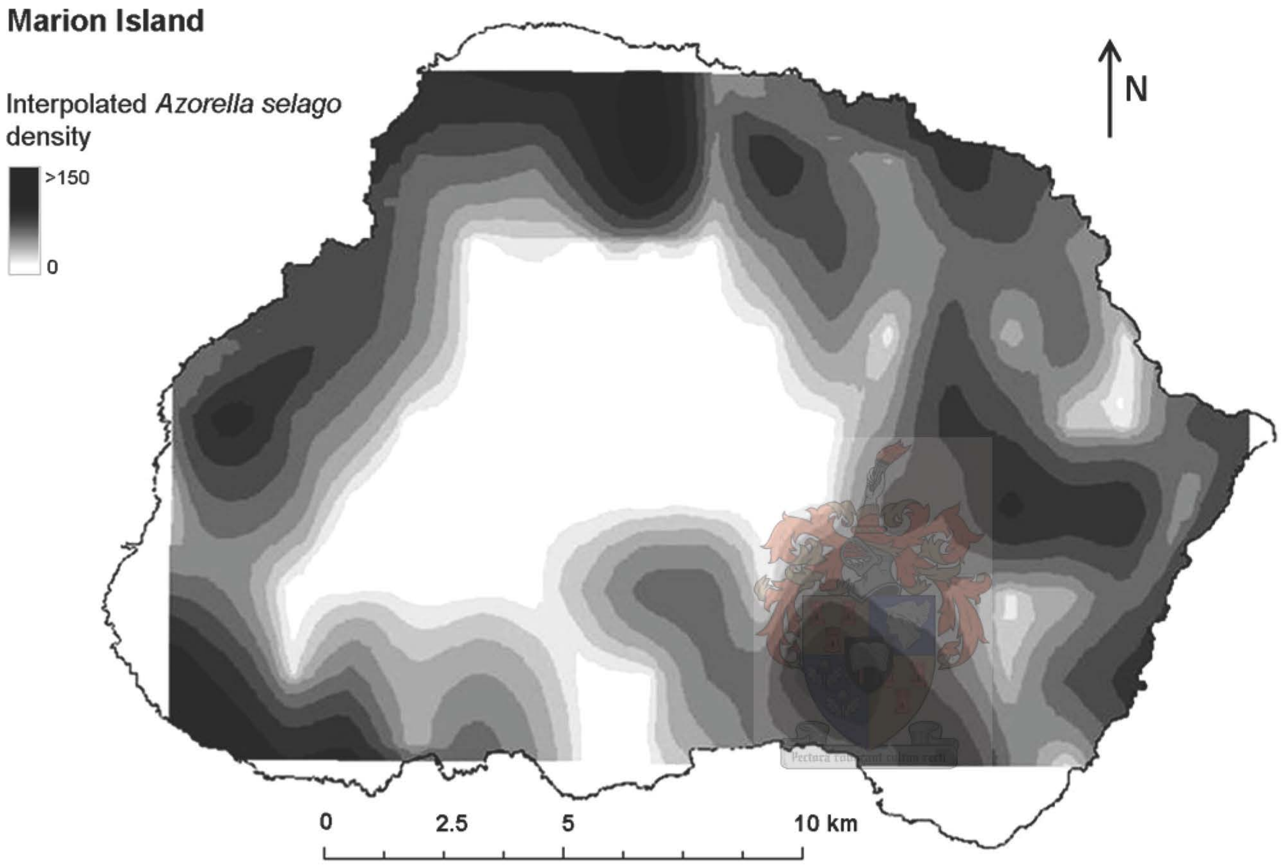

Figure 4 a Interpolated *Azorella selago* cushion density in 64 m^2 plots on a minute-by-minute basis across Marion Island. White areas indicate sites where *A. selago* is absent and the black areas represent high *A. selago* densities (> 150 cushions per plot).

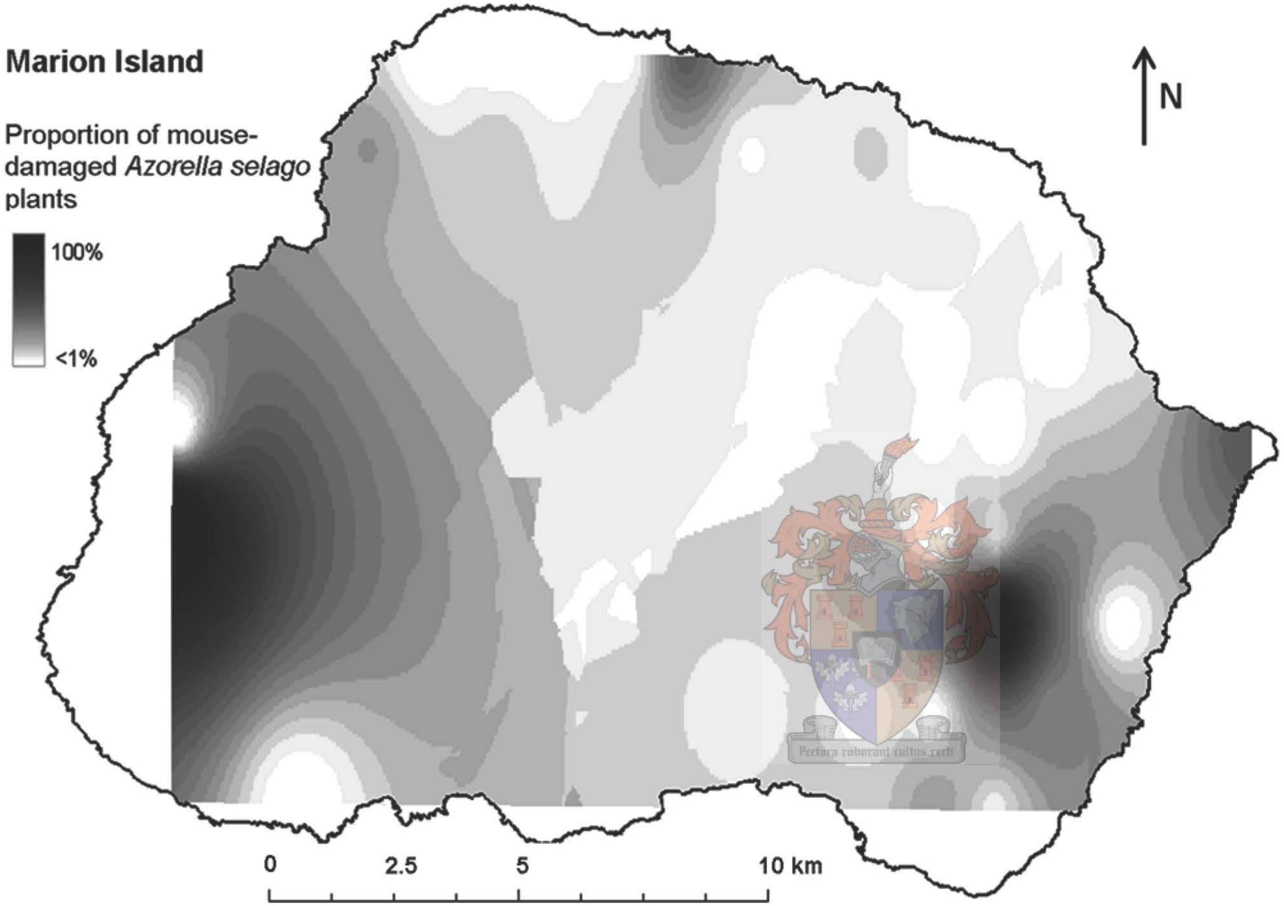

Figure 4 b Interpolated proportions of mouse-damaged *Azorella selago* cushions in 64 m^2 plots based on the thirty-two plots where *A. selago* was damaged or burrowed into by mice with mouse damage ranging from <1 % (white areas) to 100 % (black areas).

Chapter 4

INTERACTION BETWEEN INDIGENOUS AND ALIEN PLANT SPECIES ALONG RIVERS ON MARION ISLAND

INTRODUCTION

Interspecific interactions between plants are well documented (see reviews by Goldberg & Barton 1992; Goldberg *et al*. 1999; Brooker *et al*. 2008). Moreover, interactions between alien and indigenous species as well as the habitats they occur in are of considerable interest (e.g. Gerry & Wilson 1995; Callaway & Walker 1997; Osunkoya *et al*. 2005; Garcia-Serrano *et al*. 2007). Interspecific relationships between alien and indigenous species may affect ecosystem functioning and energy flow, ultimately modifying the abundances and characteristics of indigenous species (Mack & D'Antonio 1998; Osunkoya *et al*. 2005; see Bergstrom & Chown 1999; Brooker 2006 for reviews). Alien plant species often interact directly with indigenous species by competing for space and resources (Stoll *et al*. 2002). The distribution of plants can thus be seen as a reflection of positive and negative interactions between co-occurring species in response to local abiotic and biotic conditions (Stoll *et al*. 2002; Boyden *et al*. 2005; Tirado & Pugnaire 2005; Miriti 2007). Depending on the severity of environmental conditions, interactions between co-occurring species may switch between facilitation (positive) and competition (negative) (Hunter & Aarssen 1988; Bertness & Callaway 1994; Tirado & Pugnaire 2005; le Roux & McGeoch 2008a; but see Maestre *et al*. 2006). Therefore, documenting the spatial structure of alien species relative to indigenous ones provides valuable insight not only into alien species distributions, but also into alien-indigenous species interactions and factors facilitating and limiting alien species range expansion (Brooker 2006).

The invasion process starts with the introduction of viable propagules leading to the colonization of the new habitat (Mack *et al*. 2000; Richardson *et al*. 2000; Gammon & Maurer 2002; With 2002; Richardson & Pyšek 2006). After colonization, a species may become established and disperse away from the parent plant to form invasive populations (Mack *et al*. 2000; Richardson *et al*. 2000; Sakai *et al*. 2001; Gammon & Maurer 2002; With 2002; Richardson & Pyšek 2006). The invasion process is dependent on the number of introduced viable propagules (i.e. propagule pressure) and inherent species characteristics such as dispersal capacity (Mack *et al*. 2000; Maina & Howe 2000; Sakai *et al*. 2001). Moreover, some alien species have broad environmental tolerances, and once they have become successfully established, they are often capable of rapidly expanding their range (Richardson 1998; Sakai *et al.* 2001; Daehler 2003).

The introduction of alien species to intact habitats is one of the major causes of environmental change (Vitousek *et al.* 1996; Chapin *et al.* 2000; Mack *et al.* 2000). On sub-Antarctic islands, alien species are contributing to considerable changes in biodiversity (Crafford 1990; Gremmen *et al.* 1998; Bergstrom & Chown 1999; Frenot *et al.* 2005). This is largely attributed to their substantial impacts at a range of levels (Frenot *et al.* 2005), and their increasing numbers owing to increases in the number visitors to these isolated ecosystems (Chown & Gaston 2000; Chown *et al.* 2005). The latter has led to increased likelihood of the introduction of species that would not have been able to reach these remote ecosystems without the aid of anthropogenic transport (Vermeij 1996; Chown *et al.* 1998; Chown & Gaston 2000; Frenot *et al.* 2001; Chown *et al.* 2005; Vermeij 2005). As with global trends (e.g. Yelenik *et al.* 2004; see review by Mack & D'Antonio 1998), alien species are now one of the main drivers of modifications to ecosystem functioning and have directly or indirectly affected the spatial distribution of many indigenous species on these islands (e.g. Gremmen *et al.* 1998; Frenot *et al.* 2001; Courchamp *et al.* 2003; Gremmen 2004).

Although 108 alien plant species occur in the sub-Antarctic (Frenot *et al.* 2005), few studies have investigated the interactions between indigenous and alien plant species in this region (e.g. Gremmen *et al.* 1998; Lee *et al.* 1991). For example, on sub-Antarctic Marion Island there have only been two studies that have discussed possible consequences of alien plants on indigenous vegetation (see Huntley 1971; Gremmen *et al.* 1998). While the distribution of naturalized alien plant species (able to maintain a stable population for at least ten years; Richardson & Pyšek 2006) is approximately known for Marion Island (Gremmen 1975; Gremmen & Smith 1981; Bergstrom & Smith 1990; Gremmen *et al.* 1998; Gremmen & Smith 1999), the way in which they interact with indigenous plant species and each other on the island is not well understood.

While invasions occur in various habitats on Marion Island (Gremmen 1997; Gremmen & Smith 1999), this study focuses on river communities. There are several intermittent and permanent streams and only three perennial rivers on the island (Hänel & Chown 1999; Smith 2008) (for convenience, all streams and rivers in this study will be referred to as rivers). Because of their high moisture content, nutrients, and constant disturbance (by humans, animals, and natural phenomena such as flooding), rivers are often favourable sites for the establishment of alien species (Hood & Naiman 2000; van Wilgen *et al*. 2001; van Wilgen *et al*. 2007; Foxcroft *et al*. 2007; Richardson *et al*. 2007). Furthermore, regular water flow makes them potential down-stream dispersal agents for propagules, exacerbating the colonization of disturbed areas and competition with indigenous species (Richardson *et al*. 2007).

Among the eighteen vascular plant species that have been introduced to Marion Island, two species in particular, *Agrostis stolonifera* L. (Poaceae) and *Sagina procumbens* L. (Caryophyllaceae), are of great conservation concern (Gremmen & Smith 1999). Both species are classified as naturalized alien species on the island (Gremmen 1997). They are widespread and dominant in a number of habitat complexes and are able to modify both undisturbed and disturbed habitats (Gremmen 1997; Gremmen *et al*. 1998; see also Gremmen *et al*. 2001). Furthermore, *A. stolonifera*, predominantly found in drainage-line vegetation communities (Gremmen & van der Meijden 1995), has been shown to displace indigenous flora and associated fauna, often becoming the dominant vascular plant (Gremmen *et al*. 1998; Gremmen & Smith 1999). *Sagina procumbens* has invaded six of the seven habitat complexes, and is also often a dominant vascular plant in the communities it has invaded (Gremmen 1997). Fresh water systems (including rivers) are important for the recycling and dissemination of nutrients on the island (Smith 2008). Therefore, the distribution of both these species, as well as other alien species, and their interactions with indigenous plants is important to quantify along Marion Island's rivers.

The objective of this study is to provide the first quantification of the distribution of two major alien plants, *A. stolonifera* and *S. procumbens*, and the indigenous *Acaena magellanica* (Lam.) Vahl. (Rosaceae) along the rivers of Marion Island. In addition, I examine fine-scale spatial distribution patterns of the three species to infer how they interact with each other, particularly interactions between the alien species and *A. magellanica*. I also investigate the relationships between various environmental variables and the independent distribution of each species and where they co-occur. It is predicted that the alien species will be more spatially aggregated than the indigenous species because *A. magellanica* has been in its habitat longer, and *A. stolonifera* and *S. procumbens* are likely to be still expanding their distribution ranges on the island (Wilson *et al*. 2004). The way in which the alien species interact with *A. magellanica* is expected to differ. *Agrostis stolonifera* has the potential to displace *A. magellanica* in drainage-line communities (Gremmen 1981; Gremmen *et al*. 1998). Therefore, in plots where these species co-occur, without *S. procumbens*, negative interactions are predicted. On the other hand, *S. procumbens* is abundantly distributed across various habitats and has not been documented to interact negatively with any plant species on the island. This species is thus not predicted to interact negatively with *A. magellanica* in plots that contain both species without *A. stolonifera*. The co-occurrence of more than two species often results in the facilitation or suppression of one or more species (Callaway 1995; Levine 1999; Brooker *et al*. 2006). Thus, in plots where the three species simultaneously co-occur, there may be evidence of competitive exclusion (or indirect facilitation).

MATERIALS AND METHODS

Study site

Sub-Antarctic Marion Island (46º 54´S, 37º 45´E), situated approximately 2300 km south east of Cape Town, South Africa, was the study site for this research. The island is 290 km^2 in area and rises to 1230 m a.s.l. with a 72 km coast line. Its neighbour Prince Edward Island (44 km^2) is 22 km north-north east of the island and together they form the Prince Edward Island archipelago (see van Zinderen Bakker *et al*. 1971; Chown & Froneman 2008 for further information).

There are twenty-two indigenous vascular plants on Marion Island. Five, including *A. magellanica*, form part of the dominant vascular plants of the island's aerial crop (Smith 1977, 1978). The island's vegetation has been classified into seven vegetation complexes and twenty-three habitats found within these complexes (Huntley 1971; Gremmen 1981; Smith & Steenkamp 2001; Smith *et al*. 2001). In this study, vegetation along the rivers was only identified to the complex level and only the complexes that were recorded along the rivers were included in the analyses, i.e. coastal, fellfield, slope, mire, and the biotic complexes (see Smith & Steenkamp 2001; Smith *et al*. 2001 for detailed classifications). Because some habitat complexes had too few categories, similar complexes such as the biotic ones were grouped together for statistical analyses.

Study species

Acaena magellanica

Acaena is a Southern Hemisphere genus containing at least 100 species (Lloyd *et al*. 2002). The plants of the genus are low-growing, mat-forming, with creeping semi-woody stems that readily produce roots at the nodes (Conner 1987). The fruit are morphologically variable with some species having barb-tipped spines that attach to animals for dispersal (Lee *et al*. 2001). *Acaena magellanica* is the most widely distributed species in the genus, occurring from South America (25° S) to all sub-Antarctic islands (Walton 1976, 1977, 1979). In sub-Antarctic vegetation, this perennial species is considered a dwarf shrub and is able to tolerate a wide range of edaphic conditions (Walton 1976; Huntley 1971). The species generally inhabits humid, well-drained vegetation, and particularly borders of water bodies (Walton 1977). Also, this species thrives in sites that are rich in minerals with minimal exposure to salt-spray and also sheltered from strong winds (Huntley 1971; Walton 1977). On Marion Island, *A. magellanica* is dominant in most vegetation communities and is also the main species occurring in the slope drainage-line communities including riverbanks (Walton 1977; Gremmen *et al*. 1998; Smith *et al*. 2001).

Agrostis stolonifera

The bent-grass, *Agrostis stolonifera*, is a fast growing, perennial of 8-40 cm in height (Hubbard 1984; Grime *et al*. 1990). It is a patch-forming grass that, when detached from the parent plant, spreads by means of stolons (Hubbard 1954; Grime *et al*. 1990; Edgar & Forde 1991). It is widely distributed in the Northern Hemisphere where it is commonly used as lawn grass or cultivated as a turf grass for golf courses (Odland 1930; Stuckey & Banfield 1946; McCann & Huang 2008). It is considered an invasive in the Southern Hemisphere (Walton 1975; Gremmen & Smith 1981). The species is persistent and grows as thick dense mats with vigorous growth rates (Levy 1924) and can therefore rapidly colonize large areas. On Marion Island, *A. stolonifera* is a widespread naturalized alien plant species (Watkins & Cooper 1986). It is generally found in sheltered areas associated with mire water tracks, stream- and riverbanks, and along edges of ponds and lakes (Gremmen 1981). This grass was first recorded close to the meteorological station on Marion Island in 1965 and is thought to have been introduced in the late 1950s or early 1960s (Gremmen & Smith 1981; Gremmen 1982, 2004). The species occurs largely on the northern and eastern coast of the island and has also been recorded around two field huts (Mixed Pickle Cove and Kildalkey Bay) on the western and southeastern sides of the island, respectively

(Smith *et al*. 1986; Gremmen *et al*. 1998; Gremmen & Smith 1999). Although the plants of this species occasionally produce seeds on Marion Island (Gremmen 1997), the rate at which it spreads is estimated to be between 100-400 m y^{-1} (Gremmen *et al*. 1998; Gremmen & Smith 1999).

Sagina procumbens

Sagina is a genus of about 15 species of annual and perennial herbs (Crow 1979). The plants of *Sagina* grow as low matted herbs with glabrous stems and leaves arranged in opposite pairs (Vivian 1942). The genus is indigenous to cool, temperate Northern Hemisphere climates and is an aggressive invasive alien plant in the Southern Hemisphere (Walton 1975; Crow 1979). The procumbent pearlwort, *Sagina procumbens* was first collected in 1965 near the research station on Marion Island and is also thought to have been introduced in the late 1950s (Gremmen *et al*. 2001; Gremmen 2004). *Sagina procumbens* is a small herb that is able to spread both by seed dispersal and vegetative means (Grime *et al*. 1990; Gremmen *et al*. 2001). In the Northern Hemisphere, self-pollinating flowers occur from May to September and seeds are released from June to October (Clapham *et al*. 1987; Grime *et al*. 1990); phenology on Marion Island is not well known. The seeds of the plant are freeze tolerant (Salisbury 1962) and once germinated, it only takes a few months for the plants to start producing viable seeds (Gremmen *et al*. 2001). The plants of the species grow rapidly to form large, dense mats (Vivian 1942; Gremmen *et al*. 2001) and the rate of spread of *S. procumbens* on Marion Island is estimated at approximately 100-300 m y^{-1} (Gremmen & Smith 1999).

Sampling

Field work was conducted along the rivers on Marion Island between March and May 2006 as well as April and May 2007. Seventeen rivers, including a total of 616 plots, were sampled around the island. Rivers were identified by walking along the coast of Marion Island and locating the river mouth. Each river was named following the Marion Island Provisional map (May 2005 version, obtained from the Chief Directorate: Surveys and Mapping, Cape Town) and rivers that did not have names were named from the closest landmark or field hut. At each river, the first two sampling plots were adjacent to each other (i.e. at the opposite riverbanks of the same river) and were recorded as 0 m from the coast and 0 m from the riverbank (Fig. 1).

The following were noted at each plot: GPS position, altitude, distance from the riverbank and coast (for subsequent plots along the river), habitat complex, and the moisture status of the river (i.e. whether the river was flowing or dry). At each plot, a 2 m x 2 m grid (subdivided into sixty-four 0.25 m x 0.25 m quadrats) was used for measuring the presence-absence of each species (i.e. *A. magellanica*, *A. stolonifera*, *S. procumbens*) using a cover-abundance scale (percentage cover) independently of each other. Percentage cover of each species in each sampling plot was 0 where the species was absent in a 0.25 m x 0.25 m quadrat, 1 where it covered <50% of the quadrat, and 2 for cover that was >50%. The grid was then moved 25 m away from the 0 m plot such that the two plots were perpendicular to each other (Fig. 1). From the 25 m plot, the grid was moved a further 25 m, such that the next sampling plot was 50 m away from the 0 m plot (Fig. 1). The method was repeated every 250 m to 1 500 m upriver on both riverbanks of the same river. Some rivers were not sampled up to 1500 m because they were either too short or there were topographical barriers such as very steep inclines.

Data analyses

Species occurrence and spatial aggregation patterns along rivers

The data for all rivers were pooled together to determine the mean (± SE) occupancy for each species. Mean (± SE) occupancy for each species was then quantified for individual rivers. To determine whether the three species were individually spatially random, aggregated, or segregated in individual 2 m x 2 m plots, an index of aggregation (I_a) and the associated probability of I_a (p_a) were obtained using the spatially explicit approach, Spatial Analysis by Distance IndicEs (SADIE) (Perry 1995). The I_a was calculated for the individual species, independent of the other two co-occurring species. Each quadrat in the plots was treated as a spatial position within the plot (such that the bottom left quadrat would, for example, be labelled as “1; 1” and the adjacent as “1; 2”, etc). The Red-Blue Batch Analysis Runner (version 0.5 © 2003; Kelvin F. Conrad and Rothamsted Research), was used to quantify I_a and p_a in SADIE (Perry 1995; Perry & Dixon 2002). Because the data were not normally distributed, the non-parametric option was selected for the analyses (Perry & Dixon 2002). For spatially random patterns I_a = 1, while I_a > 1 would suggest that the species was spatially aggregated, and I_a < 1 when the spatial pattern for the species was segregated (Perry 1995; Perry *et al*. 1999).

Spatial association and co-occurrence patterns

To compare whether species pairs, i.e. *A. magellanica* and *A. stolonifera* (*AcAg*), *A. magellanica* and *S. procumbens* (*AcSa*), and *A. stolonifera* and *S. procumbens* (*AgSa*) were spatially associated or dissociated with each other where the species co-occurred in individual plots, I used an Association Analysis Batch Runner (version 0.6 © 2002; Kelvin F. Conrad and IACR-Rothamsted) (Perry 1998). This extension of SADIE uses clustering results (v_i and v_j) obtained from the aggregation index output to test for spatial association between any species pair occurring in the same plot (Perry *et al*. 1999; Perry & Dixon 2002). The null hypothesis is that no spatial association exists between any given species pair (Perry & Dixon 2002). SADIE quantifies the overall measure of spatial association, χ, and estimates the sample size from a Dutilleul adjustment to generate critical values for χ. For a two-tailed test with a Dutilleul adjusted probability, $p \leq 0.025$ for positive associations and $p \geq 0.975$ for negative associations (dissociation) (Perry & Dixon 2002). Significant positive χ values between the pairs would suggest facilitation or show that the species prefer similar abiotic conditions that are positively associated with both species (Miriti 2007). Similarly, negative spatial associations suggest interspecific competition or differences in the tolerance of abiotic conditions (Miriti 2007).

To determine which environmental variables explained the observed spatial association levels (i.e. association, no association, and dissociation) between species pairs, cumulative ordinal logistic regression modelling (PROC LOGISTIC procedure in SAS; SAS Institute Inc. Cary, New York) was used (Guisan & Harrell 2000). The association level (+1 for association, 0 for no association, and -1 for dissociation) was the dependent variable with the following as independent variables: distance from the coast (k =7, df = 6), distance from the riverbank (k = 3, df = 2)), habitat complex (k = 4, df = 3), altitude (continuous), and the moisture status of the river (k = 2, df = 1). The relationships between the environmental variables were examined for collinearity by using Pearson's product-moment correlations and the Variance Inflation Factor (VIF) (Legendre & Legendre 1998). The significant correlations between the predictor variables were disregarded because VIF < 10 in all cases (Legendre & Legendre 1998). Therefore,

$$\text{logit } y = \text{distance from coast} + \text{distance from riverbank} + \text{altitude} + \text{habitat complex} + \text{moisture status} \quad (1),$$

where y is the spatial association (χ) level.

To examine whether the three species were spatially more random, aggregated, or segregated than expected by chance where they co-occurred, I used the spatially implicit variance ratio (VR) and C-score tests (Schluter 1984; Bell 2005). Schluter's variance ratio (VR), which compares the observed variance of occupancy in individual plots, assuming that the variance of the occurrence of each species was independent of the other two species (Schluter 1984; Gotelli 2000; Sfenthourakis *et al*. 2005), was calculated for each of the species combinations (i.e. *A. magellanica* and *A. stolonifera* (*AcAg*, n = 47), *A. magellanica* and *S. procumbens* (*AcSa*, n = 44), *S. procumbens* and *A. stolonifera* (*AgSa*, n = 24), and all three species together (*AcAgSa*, n = 22)). The variance ratio (VR) is made up of the ratio of two variances, i.e. the variance of species richness per site and the sum of the variances of species co-occurrences across sites (Schluter 1984; Bell 2005). Therefore,

$$VR = R_T^{\ 2} / \sum \sigma_i^{\ 2} \quad (2),$$

where T is the total number of species in sample i. In plots where there is strong competition between the species, the observed VR should be significantly smaller than expected by chance (Gotelli & Entsminger 2001). Furthermore, a positive VR (> 1) illustrates positive covariation, a negative VR (<1) is indicative of negative covariation between the species, and VR = 1 where there is no association or covariation between the species (Schluter 1984). The calculated VR was then multiplied by the number of plots (N) to determine the value of W (the test statistic) with a chi-square distribution at N degrees of freedom (Schluter 1984; McGeoch & Chown 1997; Gabriel *et al*. 2001).

The C-score index measures the average number of checkerboard units (CU) for each species pair (Stone & Roberts 1990; Sfenthourakis *et al*. 2005). For any given species pair CU is calculated as:

$$\text{CU} = (R_i - R_{ij})\,(R_j - R_{ij}) \quad (3),$$

where R_i is the range of species i and R_j is the joint range of both species i and j. Because C-score is dependent on the number of sites sampled, sites that contained joint absences were omitted from the analyses (Bell 2005). In sites where the species compete with each other the C-score value should be greater than expected by chance (Gotelli & Entsminger 2001). Both the C-score and VR were calculated in Ecosim 7.0, with 5000 iterations, fixed rows and equiprobable columns (Gotelli & Entsminger 2001). Alpha-inflation corrections were not applied to the obtained significance levels (p-values) for the spatial aggregation and association indices as well as co-occurrences because these aspects of the study were largely exploratory and not hypothesis testing (see Moran 2003; Garcia 2004 for discussion on the application of alpha-inflation corrections in ecological studies).

Effects of environmental variables on species occurrences and co-occurrences

To determine which environmental variables were significantly associated with the observed distribution and co-occurrence patterns of the three species and because the distribution of the data were binary, a logistic regression model with a logit link, binomial distribution, and scaled deviance (PROC GENMOD procedure in SAS; SAS Institute Inc. Cary, New York) was used (Collette 1989). The following were used as predictor variables: distance from the coast, distance from the riverbank, habitat complex, altitude, and the moisture status of the river. Therefore, the basic model (Model 1a) was:

$$\text{logit}(p_i) = \text{distance from coast} + \text{distance from riverbank} + \text{altitude} + \text{habitat complex} + \text{moisture status} \quad (4),$$

where

$$p_i = \frac{\text{occupancy of species } x}{64 \text{ (i.e. number of quadrats)}} \quad (5).$$

To examine the effects of the alien species on *A. magellanica*, the $\log_{10}$ of *A. stolonifera* and *S. procumbens* occupancies were added to the model as independent variables (Model 2a and b), i.e.

logit (p_i) = $\log_{10} Ag$ or $\log_{10} Sa$ + distance from coast + distance from riverbank + altitude + habitat + moisture status (6).

Finally, to examine the effects of both invasive species on *A. magellanica*, both species were included in the model (Model 3), i.e.

logit (p_i) = $\log_{10} Ag$ + $\log_{10} Sa$ + distance from coast + distance from riverbank + altitude + habitat + moisture status (7).

RESULTS

Species occurrence and spatial aggregation along rivers

The indigenous *A. magellanica* was present along all 17 rivers (Fig. 2). Of these rivers, 35% were uninvaded (Fig. 2). *Acaena magellanica* had by far the highest occupancy, followed by *A. stolonifera*, then *S. procumbens* (Table 1). The alien species were mainly recorded along rivers from Log Beach to Kildalkey (Fig. 2, clockwise from Log Beach on the eastern side of the island). With the exception of Mixed Pickle, where *A. stolonifera* co-occurred with *A. magellanica*, neither of the alien species was recorded along rivers between Storm Petrel and Watertunnel (Fig. 2, anti-clockwise from Storm Petrel). *Agrostis stolonifera* was found along 53% of the rivers, while *S. procumbens* occurred along 41% of the rivers (Fig. 2). *Agrostis stolonifera* (on its own) co-occurred with *A. magellanica* along 24% of the rivers (Fig. 2) and another 12% of the rivers contained *S. procumbens* and *A. magellanica* (Fig. 2). All three species co-occurred, simultaneously along 29% of the rivers between Log Beach and Kildalkey where 67% of the flowing rivers were located (Table 1).

The mean index of aggregation for each species showed that all species had aggregated distributions, i.e. $I_a > 1$ (*A. magellanica*: $I_a = 1.669 \pm 0.039$, *A. stolonifera*: $I_a = 1.942 \pm 0.084$, and *S. procumbens* = 1.719 ± 0.054) and none were spatially segregated or randomly distributed (Fig. 3; see Appendix A for a summary of the percentage of aggregated distributions for each species along individual rivers). The aggregation index (I_a) for *A. magellanica* ranged from 0.80 to 2.93 and of these 69.85% were significantly aggregated at $p < 0.05$ (Fig. 3a). For *A. stolonifera*, I_a varied from 0.81 to 2.96 with 79.17% being significantly aggregated (Fig. 3b). The I_a

for *S. procumbens* ranged from 0.91 to 2.85 with 82.81% representing significant aggregation (Fig. 3c).

Spatial association and co-occurrence patterns

The spatial association index, χ, showed that most of the associations between species pairs were random, i.e. not significant ($0.975 < p > 0.025$). More dissociations (negative interactions; $p > 0.975$) than associations (positive interactions; $p < 0.025$) were observed for both the *AcAg* and *AcSa* species pairs, while the *AgSa* pair had more associations than dissociations (Fig. 4). The spatial association index (χ) for the *AcAg* pair ranged from -0.87 to 1.00 with 34.88% of the associations being negative (dissociation), 37.27% showed no association and 27.91% were positively associated (Fig. 4a). The χ for the *AcSa* pair also ranged from -0.87 to 1.00 and showed that 43.24% were dissociated, 45.95% showed no association and 10.81% were positively associated (Fig. 4b). For the *AgSa* pair, χ varied from -0.81 to 1.00 and there were 21.05% of dissociations, 42.11% of no association, and 37.84% of positive associations (Fig. 4c). The cumulative ordinal logistic regression showed that the observed associations between the *AcAg* species pair were significantly associated with altitude, habitat complex, and moisture status (Table 2). Conversely, none of the environmental variables were significantly associated with the observed spatial associations for the *AcSa* and *AgSa* species pairs (Table 2).

The variance ratio (VR) and C-score showed that the majority of the co-occurrences of the species combinations were not significantly different from random (i.e. VR and C-score were significantly greater and smaller than expected by chance, respectively). All the significant VR and C-score values suggested negative interactions (or competition) between species pairs (i.e. VR and C-score were significantly smaller and greater than expected by chance, respectively) in all species combinations, i.e. *AcAg*, *AcSa*, *AgSa*, and *AcAgSa* (Table 3 shows the percentage of the significant VR and C-score for all species combinations and see Appendix B for significant results for individual plots along individual rivers). On the whole, more negative than positive instances of covariation were observed for the *AcAg*, *AcSa*, and *AcAgSa* species combinations. The *AgSa* species combination showed more positive than negative instances of covariation (Table 3). The *AcAgSa* species combination showed equal (1:1) instances of negative and positive covariation (Table 3).

Effects of environmental variables on species occurrences and co-occurrences

According to the logistic regression models (Model 1a), *A. magellanica* occurred consistently along rivers with no significant differences with increasing distance from the coast (Table 4; Fig. 5a (i)). The occurrence of both alien species (Models 1b and c) was significantly affected by the distance from the coast (Table 4). There was a decrease in the mean number of quadrats occupied by both species with increasing distance from the coast (Fig. 5a (ii and iii); see Appendix C for the change in mean occupancies of the three species along individual rivers). While distance from the riverbank was significantly associated with the occurrence of *A. magellanica* and *A. stolonifera*, it had no effect on the occurrence of *S. procumbens* (Table 4). With increasing distance from the river, there was a decrease in the mean occupancies for *A. magellanica* and *A. stolonifera*, whereas *S. procumbens* was relatively unaffected (Fig. 5b; see Appendix D for the change in mean occupancies of the three species along individual rivers). *Acaena magellanica* was not restricted by habitat complex although mean occupancy remained highest in the slope habitat complex (Fig. 5c (i)). Both *A. stolonifera* and *S. procumbens* occupancy were significantly related to habitat complex (Table 4). Mean occupancy for *A. stolonifera* was highest in the slope complex, while *S. procumbens* occupied more sites in the coastal complex (Fig. 5c (ii and iii)). *Acaena magellanica* and *A. stolonifera* demonstrated similar patterns in the shape of their mean occupancies in the different habitat complexes, with the mean occupancies at the coastal, mire and fellfield habitat complexes being lower than the slope habitat complex (taking into consideration that *A. magellanica* still occupied far more quadrats than *A. stolonifera*) (Fig. 5c (i and ii)). The occurrences of *A. magellanica* and *S. procumbens* were not affected by the moisture status of the rivers (Table 4; Fig. 5d). Conversely, *A. stolonifera* occurrence was significantly linked to the moisture status of rivers, with occupancy being significantly higher along flowing rivers (Table 4; Fig. 5d (ii)). Altitude was significantly associated with the occurrence of the alien species, but not with the indigenous species (Table 4). Both alien species exhibited high occupancies below 100 m a.s.l., while *A. magellanica* occupancy was consistent at all altitudes (Fig. 5e). When *A. stolonifera* was added to the logistic regression model (Model 2a), a positive, but non-significant relationship was observed between the species and *A. magellanica* with no change in the significance status of the environmental variables (Table 4). The relationship between *A. magellanica* and *S. procumbens* (Model 2b) was negative and non-significant (Table

4). However, when both alien species were added to the model (Model 3) the relationship between *A. magellanica* and *A. stolonifera* remained positive and became significant, while the relationship between *A. magellanica* and *S. procumbens* remained negative and non-significant (Table 4).

DISCUSSION

This study quantified the fine-scale distribution of two widespread alien plant species *Agrostis stolonifera* and *Sagina procumbens* as well as the indigenous *Acaena magellanica* along rivers on Marion Island. In addition, the influence of environmental variables on the occurrence (and co-occurrence) of these species were examined. The indigenous *Acaena magellanica* was the dominant of the three species along rivers while the alien species were prevalent at coastal sites. Most alien species on the island are considered to be coprophilic (Huntley 1971; Smith 1978). Therefore, the proximity of these sites to salt-spray and manure deposits from seabirds and seals, both of which are major contributors of nutrients on the island (Huntley 1971; Smith 1978), would to some extent explain the prevalence of the alien species close to the coast. In addition, the alien species were generally recorded along flowing rivers. Apart from having high moisture content, riverbanks are rich in nutrients (Smith 2008). This can partially account for the greater occurrence of the alien species along rivers that were flowing. For this reason, the colonization, distribution and spread, especially along rivers on the north, south, and western parts of the island by both alien species, may be inhibited by the moisture status of the rivers. The main reason for this situation being that those rivers were dry when compared to rivers on the eastern side where the alien species were mostly recorded.

The eastern side of the island, where the research station is located, is the site for the majority of first documentations of the occurrence of alien species (Huntley 1971; Gremmen 1975; Gremmen & Smith 1999). Incidentally, most of the rivers that are either perennial or that flow regularly occur on this side of the island (though recognizing that much of this information on flow is inferred or anecdotal). The prevalence of the alien species on the eastern side can thus be ascribed to anthropogenic contributions to habitat disturbance (Gremmen 1975, 1982; Gremmen *et al*. 2003) and the higher percentage of flowing rivers that may be acting as dispersal vectors for propagules. How variance in climate and/or geomorphological setting may affect the distributions is not clear. Certainly it is clear that eastern parts of the island may have more variable temperature conditions and in parts reduced cloud cover by comparison with the west (Nyakatya & McGeoch 2008; McGeoch *et al*. 2008). Moreover, the west has an exceptionally steep escarpment that might also reduce total catchment area by comparison with the east (Boelhouwers *et al*. 2008). These likely influences on plant distribution require further investigation. Nonetheless, it seems likely that the eastern side is providing habitats that are better suited for the alien species. However, the prevalence of both alien species on the eastern side of the island can also be the result of this side being the initial site of colonization (Gremmen 2004). Thus, both alien species have had the opportunity to establish themselves on the eastern parts, while on other parts of the island (e.g. western), the species are probably still in the lag phase.

Environmental variables were responsible for only 17.35% of the deviance explaining occupancy of the indigenous *A. magellanica* along rivers. Additionally, the species was common and found in all habitat complexes, particularly in the slope complex. Although, the distance from the riverbank was important for the occurrence of the species, the moisture status of the rivers did not significantly influence its occurrence. The percentage deviance explained for the occurrence of *A. magellanica* was only slightly altered by the presence of the alien species to 17.60% and 17.59% when *A. stolonifera* and *S. procumbens* were respectively added to a logistic regression model, and to 17.98% when both alien species were added simultaneously. This suggested that the influence of the alien species on the occurrence of *A. magellanica* along rivers was minimal. On the other hand, the influence of environmental variables for the alien species differed. *Agrostis stolonifera* is known to flourish in sheltered and damp areas such as stream- and riverbanks (Edgar & Forde 1991; Pammenter *et al*. 1986; Frenot *et al*. 2001). This study suggested that this species can be a specialist invader with a narrow range, restricted to low altitudes, coastal areas, and moisture-rich drainage-line and slope complex habitats on Marion island. It was found that 42.95% of the deviance in the observed occupancy patterns for *A. stolonifera* was explained by environmental variables, compared to 24.82% for *S. procumbens*. Although *S. procumbens* occurrence was restricted by distance from the coast and altitude, it was not restricted by habitat, moisture status, and distance from the riverbank. Therefore, the difference in the role of environmental variables in structuring the observed occurrence of the alien species gives an indication that *A.*

stolonifera is more sensitive to the island's abiotic conditions and that *S. procumbens* may affect biodiversity at broader scales on the island.

Habitat preference and the patchiness of environmental conditions are important determinants of observed spatial aggregation patterns for species (Sakai *et al*. 2001; Labra *et al*. 2005). The alien species were more spatially aggregated than *A. magellanica*. This is expected because most alien species are still expanding their range in invaded communities, while indigenous ones have been in their native environment for much longer and most have likely had ample time to colonize suitable habitats (Brown *et al*. 1995; Sakai *et al*. 2001; Rodríguez & Delibes 2002; Wilson *et al*. 2004; Labra *et al*. 2005). While *S. procumbens* is able to colonize various habitats (Gremmen *et al*. 2001), studies on *A. stolonifera* suggest that its lack of sufficient sclerophyllous tissue may limit its distribution to sites that are sheltered from strong winds (Pammenter *et al*. 1986; Smith *et al*. 1986). Nonetheless, the spread of *S. procumbens* to other habitat complexes can be restricted by moderately suitable sites, such as the fellfield complex, a dry habitat compared to the coastal complex where the species was predominantly found. Indeed, some alien species frequently have specific environmental needs for establishment and their spread from sites of local aggregation can be restricted by the availability of suitable sites for colonization (Gould & Walker 1997). This can be the justification for the greater spatial aggregation found in this study for the alien species.

Although the alien species were more spatially aggregated than the indigenous one, all three species exhibited very similar levels and ranges of spatial aggregation. This can be a consequence of intra- and interspecific interactions between the species (Condit *et al*. 2000; Stoll & Prati 2001). The intraspecific aggregation of species is a balance between intra- and interspecific competition of species, favouring their co-occurrence (Pielou 1961). The strength of spatial aggregation may be determined by competition for resources and available ground for colonization, as well as dispersal limitation of the species concerned (Coomes *et al*. 1999; Condit *et al*. 2000). It is therefore possible that *A. magellanica* was generally less spatially aggregated at suitable habitats and became more aggregated the further it was from the riverbank or slope complex. Conversely, the alien species were probably highly aggregated in most plots they occurred in because their occurrence was more dependent on environmental variables. As highlighted by Pielou (1961), the following assumptions can be made from the inferred spatial aggregation of the species in this study. First, *A. magellanica* is better adapted to the island's abiotic and biotic conditions thereby accounting for its widespread distribution and lower percentage of spatial aggregation. This results in *A. stolonifera* and *S. procumbens* randomly colonizing remaining available space, subsequently displaying higher spatial aggregations where they occurred. Second, it is also possible that the co-occurring species have differing physiological tolerances for the same environmental variables (i.e. *A. magellanica* and *A. stolonifera*), leading to the spatial segregation of other species (i.e. *S. procumbens*) or *vice versa*. It is important to note that the influence of other plant species (that may have co-occurred in the plots) on the spatial aggregation of the species investigated here, was not accounted for in this study because they were not recorded. Therefore, the final assumption is that, the spatial aggregation of other co-occurring species also influenced the observed spatial aggregation patterns of *A. magellanica*, *A. stolonifera*, and *S. procumbens*.

There were dissimilarities in the way the alien species interacted with *A. magellanica*. Using a logistic regression model, a significantly positive relationship between *A. magellanica* and *A. stolonifera* was found. This indicates that these species have similar requirements for abiotic and biotic conditions (Daehler 2003). For example, both species had the affinity for the slope habitat complex as illustrated by the shape of their mean occupancies in the pooled data for all rivers. Furthermore, all the significant results for co-occurrence (variance ratio (VR) and C-score) indicated negative interactions between these species (i.e. competition; Gotelli & Entsminger 2001). However, there was a narrow margin between spatial association, no association, and dissociation, suggesting that the species either occurred in close proximity to each other in similar habitat conditions, as spatially segregated populations (Pielou 1961; Perry & Dixon 2002) or that their co-occurrence was structured by both negative and positive interactions (Kikvidze *et al*. 2005; Tirado & Pugnaire 2005). This was clearly demonstrated by the ordinal logistic regression for the spatial association levels, which showed that this species pair was significantly influenced by three environmental variables, i.e. altitude, habitat complex and moisture status. Because alien species are capable of undergoing changes to their life histories by adapting to abiotic and biotic conditions in the invaded habitat, these interactions may eventually force indigenous species to alter their own life history traits (Sakai *et al*. 2001). This often results in reduced indigenous species genetic diversity (Thompson 1998; Sakai *et al*. 2001; Byers 2002; Sax *et al*. 2005).

Ultimately, the interactions between alien and indigenous species with similar habitat requirements may result in lower fecundity and lower survival of one species (i.e. *A. magellanica*) while the other species (i.e. *A. stolonifera*) thrives (Schoener 1983). The results of this study support Gremmen *et al*.'s (1998) findings which showed that *A. stolonifera* often displaced *A. magellanica* along drainage lines.

While covariations between *A. magellanica* and *S. procumbens* indicated that competitive interactions were structuring their co-occurrence (Gotelli & Entsminger 2001), the spatial association index showed that their associations were either negative (dissociations) or random, with very few positive associations. The higher incidence of dissociation indicates that the species are more often segregated from one another (Perry & Dixon 2002) and that they differ in their affinities for suitable habitats (Miriti 2007). This was supported by the negative relationship (not significant) found between this species pair in the logistic regression model. In addition to this, their spatial associations were not significantly influenced by environmental variables. This was also substantiated by higher incidences of positive covariations between them. Therefore, their co-occurrences may arise because there is a balance between their occurrences along rivers and their individual environmental requirements (Miriti 2007).

Under conditions of high resource availability alien species may dominate suitable habitats, forcing indigenous species to compete for resources (e.g. space, water, nutrients, etc.) (Bertness & Callaway 1994; Daehler 2003; Tirado & Pugnaire 2005). Depending on the availability of resources, species either interact positively or negatively with each other (Daehler 2003). It has been demonstrated that in disturbed habitats, such as rivers (Hood & Naiman 2000; van Wilgen *et al*. 2001; Foxcroft *et al*. 2007; Richardson *et al*. 2007), alien species can often utilize resources more efficiently than indigenous species in invaded sites (Thebaud & Simberloff 2001; Daehler 2003; Leger & Rice 2003). This may be the case for the co-occurrence of *A. magellanica*, *A. stolonifera*, and *S. procumbens* along Marion Island's rivers. The results showed that where the three species co-occurred, positive and negative covariations were equal (with no random covariations), suggesting both negative and positive interactions. It is therefore likely that on some parts of the rivers, the conditions were suitable for all three species or the species were tolerant of the same conditions (Silvertown *et al*. 1992; Miriti 2007). The co-occurrence patterns for this species combination (*A. magellanica*-*A. stolonifera*-*S. procumbens*) could not be verified in SADIE. However, judging from the spatial association results for species pairs, I can hypothesize that competition between *A. magellanica* and *A. stolonifera*, for instance, may lead to positive associations (or interactions) between *S. procumbens* and either *A. magellanica* or *A. stolonifera* (i.e. indirect facilitation; Levine 1999; Callaway 1995). However, these findings need further corroboration through empirical investigations with regards to how these species interact with each other under different abiotic stresses.

It has been suggested that alien species are likely to be surviving close to their physiological limits on sub-Antarctic islands (Davies & Melbourne 1999). Furthermore, many alien plant species, like *A. stolonifera*, occasionally produce seeds and frequently spread by vegetative means (Gremmen 1997). It was therefore predicted that with the warming climate, these species may flourish and possibly start to produce viable seeds (Gremmen 1997). Because there is little that can be done to prevent the further spread of both the alien plant species examined in this study, and their eradication is probably impossible (Gremmen 2004), a change in the way alien species disperse may have unfavourable consequences for the general structure of the distribution of species on the island (Gremmen 1997; Bergstrom & Chown 1999).

Current climate trends suggest that warming, less variable wind conditions, with fewer calm days, but perhaps lower windspeeds than in the 1980s, and decreased precipitation can be expected for Marion Island (le Roux 2008; le Roux & McGeoch 2008b). Thus, while *A. stolonifera* may in future be able to produce viable seeds, it is likely that it will remain restricted to drainage-line and slope complex communities where it may continue to interact negatively with *A. magellanica*. The confinement of this species to these habitats may be exacerbated by the fact that *A. stolonifera* is not drought tolerant (Wu *et al*. 1975; Kik *et al*. 1990). *Sagina procumbens*, on the other hand, abundantly produces seeds that are able to lie dormant in seed banks (Grime *et al*. 1990; Gremmen *et al*. 2001). In consequence, the species may benefit from climate change. Because the moisture status of rivers was not important for *S. procumbens*, drying and a decrease in precipitation may not be enough to have detrimental effects on the further spread of the species across the island (at least at low altitudes).

In conclusion, this study investigated the occurrence and interactions of alien and indigenous plant species and has broadened current understanding of alien-indigenous species co-occurrences for Marion Island. Indirect tests (species co-occurrence, spatial aggregation and association indices) examining interspecific interactions showed that the alien plants (*Agrostis stolonifera* and *Sagina procumbens*) differed in their interactions with the indigenous *Acaena magellanica*. Environmental variables were important determinants for the occurrences and co-occurrences (associations) of these species, especially for the co-occurrence of *A. magellanica* and *A. stolonifera*. Nonetheless, the biological mechanisms shaping these inferred patterns for species interactions on Marion Island remain unknown. Therefore, future studies should investigate alien and indigenous species interactions under different environment stresses (e.g. increased resource availability or depletion) and how these interactions determine whether alien species will be successful in colonizing currently uninvaded habitats. Furthermore, in the light of climate change, factors such as physiological tolerances linked to climate related stresses (e.g. warming) should also be considered. These will be important factors when trying to predict future distributions and interactions between alien and indigenous species on Marion Island.

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TABLES

Table 1 Mean occupancies (Mean *p* with 95% confidence intervals) of *Acaena magellanica* (*Ac*), *Agrostis stolonifera* (*Ag*), and *Sagina procumbens* (*Sa*) along all and individual rivers on Marion Island. * = mean occupancies across all rivers; Max. length = maximum length of river sampled; MS = moisture status of the river; N = number of plots; ** = named according to nearest landmark; and *** = named according to nearest field hut. Only species that were present along a river are presented in this table.

River	Max. length	MS	Species	n	Mean *p* ±SE	95% C.I
All rivers*			*Ac*	616	20.06 ± 1.00	18.10; 22.02
			Ag	616	3.66 ± 0.54	2.60; 4.71
			Sa	616	2.43 ± 0.40	1.64; 3.21
Tweeling**	1500	Dry	*Ac*	42	24.24 ± 4.30	15.55; 32.93
Wild Cat Creek	1500	Dry	*Ac*	42	26.69 ± 4.00	18.62; 34.76
Storm Petrel	1500	Dry	*Ac*	42	40.33 ± 4.62	31.01; 49.66
Log Beach	1500	Dry	*Ac*	42	16.50 ± 3.70	9.03; 23.97
			Sa	42	4.93 ± 2.35	0.18; 9.68
Long Ridge**	1500	Dry	*Ac*	42	20.60 ± 3.75	13.03; 28.17
			Sa	42	4.36 ± 2.07	0.18; 8.54
van den Boogaard	1500	Flowing	*Ac*	42	21.57 ± 3.70	14.10; 29.04
			Ag	42	13.86 ± 3.60	6.60; 21.12
			Sa	42	9.48 ± 2.66	4.09; 14.86
Kapua	500	Dry	*Ac*	18	17.22 ± 4.19	8.38; 26.06
			Ag	18	14.94 ± 6.06	2.17; 27.72
			Sa	18	3.17 ± 2.55	-2.21; 8.54
Trypot Beach	1500	Flowing	*Ac*	42	12.26 ± 2.69	6.82; 17.70
			Ag	42	1.98 ± 1.48	-1.01; 4.96
			Sa	42	7.43 ± 2.94	1.49; 13.37
Macaroni Bay	500	Flowing	*Ac*	18	21.39 ± 6.69	7.27; 35.51
			Ag	18	9.72 ± 4.90	-0.62; 20.06
			Sa	18	2.11 ± 1.34	-0.72; 4.94
Hansen	1500	Flowing	*Ac*	42	12.38 ± 3.45	5.42; 19.34
			Ag	42	14.69 ± 3.66	7.30; 22.08
Soft Plume	1500	Flowing	*Ac*	42	18.71 ± 3.41	11.83; 25.60
			Ag	42	6.31 ± 2.67	0.91; 11.71
			Sa	42	0.17 ± 0.12	-0.07; 0.40
Whale Bird Point	1500	Dry	*Ac*	42	13.98 ± 2.71	8.50; 19.45
			Sa	42	2.95 ± 1.33	0.26; 5.64
Kildalkey***	1500	Flowing	*Ac*	42	21.55 ± 3.07	15.36; 27.74
			Ag	42	2.79 ± 1.67	-0.59; 6.17
			Sa	42	4.05 ± 1.77	0.47; 7.63
Watertunnel	500	Flowing	*Ac*	18	14.94 ± 6.20	1.86; 28.03
Greyheaded**	1000	Dry	*Ac*	30	10.90 ± 4.00	2.71; 19.09
Swartkop Point**	1250	Flowing	*Ac*	32	27.84 ± 5.38	16.86; 38.82
Mixed Pickle***	1500	Flowing	*Ac*	38	14.89 ± 3.97	6.84; 22.95
			Ag	38	3.79 ± 2.22	-0.70; 8.28

Table 2 Environmental variables explaining the observed association (χ) levels (i.e. association (+1), no association (0), and dissociation (-1)), obtained from SADIE, between species pairs from the cumulative ordinal logistic regression results. *AcAg* = *Acaena magellanica* and *Agrostis stolonifera*; *AcSa* = *Acaena magellanica* and *Sagina procumbens*; and *AgSa* = *Agrostis stolonifera* and *Sagina procumbens*; Moist. status = moisture status of the rivers. Note: the degrees of freedom for Coast Dist. (distance from the coast) and those for River Dist. (distance from the riverbank) are not equal for the different species pairs because SADIE only analysis species pairs that co-occur.

Species pair	Environmental predictor	Df	Wald χ^2	p-value
AcAg	Altitude (-)	1	9.1993	0.0024
	Coast Dist.	5	9.1776	0.1022
	River Dist.	2	5.231	0.0731
	Habitat	2	8.7085	0.0129
	Moist. status	1	11.1294	0.0008
AcSa	Altitude (-)	1	3.1014	0.0782
	Coast Dist.	6	8.8162	0.1842
	River Dist.	2	0.2957	0.8626
	Habitat	2	3.8817	0.1436
	Moist. status	1	0.0013	0.9718
AgSa	Altitude (-)	1	0.1525	0.6961
	Coast Dist.	5	3.8248	0.5749
	River Dist.	1	1.0159	0.3135
	Habitat	2	0.4702	0.7905
	Moist. status	1	0.0023	0.9615

Table 3 Percentages of significant instances of negative interactions (C-score and variance ratio (VR) significantly greater and smaller than expected by chance, respectively, at $p < 0.05$) across all rivers for the co-occurring species combinations. No covar. = no covariation, i.e. VR = 1). *AcAg* = *Acaena magellanica* and *Agrostis stolonifera*; *AcSa* = *Acaena magellanica* and *Sagina procumbens*; *AcAgSa* = *Acaena magellanica* and *Agrostis stolonifera* and *Sagina procumbens*, and *AgSa* = *Agrostis stolonifera* and *Sagina procumbens* species combinations.

Species combination	% C-score	% VR	% Covariation		
			Positive	Negative	No covar.
AcAg	15	15	34	40	26
AcSa	18	20	25	68	7
AgSa	13	13	50	38	12
AcAgSa	27	18	50	50	0

Table 4 Logistic regression (logit link, binomial distribution) results for the effects of environmental variables on the occurrence of indigenous *Acaena magellanica* (*Ac*) as well as aliens *Agrostis stolonifera* (*Ag*) and *Sagina procumbens* (*Sa*) (Models 1 a-c) along the rivers of Marion Island, and the effects of the two alien species on the observed occurrence patterns of *A. magellanica* (Models 2a, b, and 3).

Model (dep. var)	Indep. var.	Model goodness of fit		$\chi 2$	Df	p
		Df	% Dev. Expl.			
1a (Ac)	Dist. from coast	602	17.35	9.21	6	0.1621
	Dist. from riverbank			37.83	2	< 0.0001
	Altitude (-)			0	1	0.9757
	Habitat complex			40.17	3	< 0.0001
	Moisture status			1.44	1	0.2304
1b (Ag)	Dist. from coast	602	42.95	42.31	6	< 0.0001
	Dist. from riverbank			103.2	2	< 0.0001
	Altitude (-)			53.42	1	< 0.0001
	Habitat complex			59.05	3	< 0.0001
	Moisture status			39.55	1	< 0.0001
1c (Sa)	Dist. from coast	602	24.82	59.13	6	< 0.0001
	Dist. from riverbank			4.13	2	0.1266
	Altitude (-)			27.51	1	< 0.0001
	Habitat complex			8.12	3	0.0436
	Moisture status			2.85	1	0.0914
2a (Ac)	Log10Ag (+)	601	17.6	2.93	1	0.0869
	Dist. from coast			10.24	6	0.1149
	Dist. from riverbank			30.28	2	< 0.0001
	Altitude (-)			0.01	1	0.9352
	Habitat complex			39.31	3	< 0.0001
	Moisture status			2.57	1	0.1091
2b (Ac)	Log10Sa (-)	601	17.59	2.76	1	0.0966
	Dist. from coast			8.53	6	0.2017
	Dist. from riverbank			40.16	2	< 0.0001
	Altitude (-)			0.02	1	0.8801
	Habitat complex			44.75	3	< 0.0001
	Moisture status			0.96	1	0.3277
3 (Ac)	Log10Ag (+)	600	17.98	3.85	1	0.0497
	Log10Sa (-)			3.68	1	0.0551
	Dist. from coast			9.33	6	0.156
	Dist. from riverbank			32.35	2	< 0.0001
	Altitude (-)			0	1	0.9646
	Habitat complex			38.54	3	< 0.0001
	Moisture status			2.03	1	0.1543

FIGURES

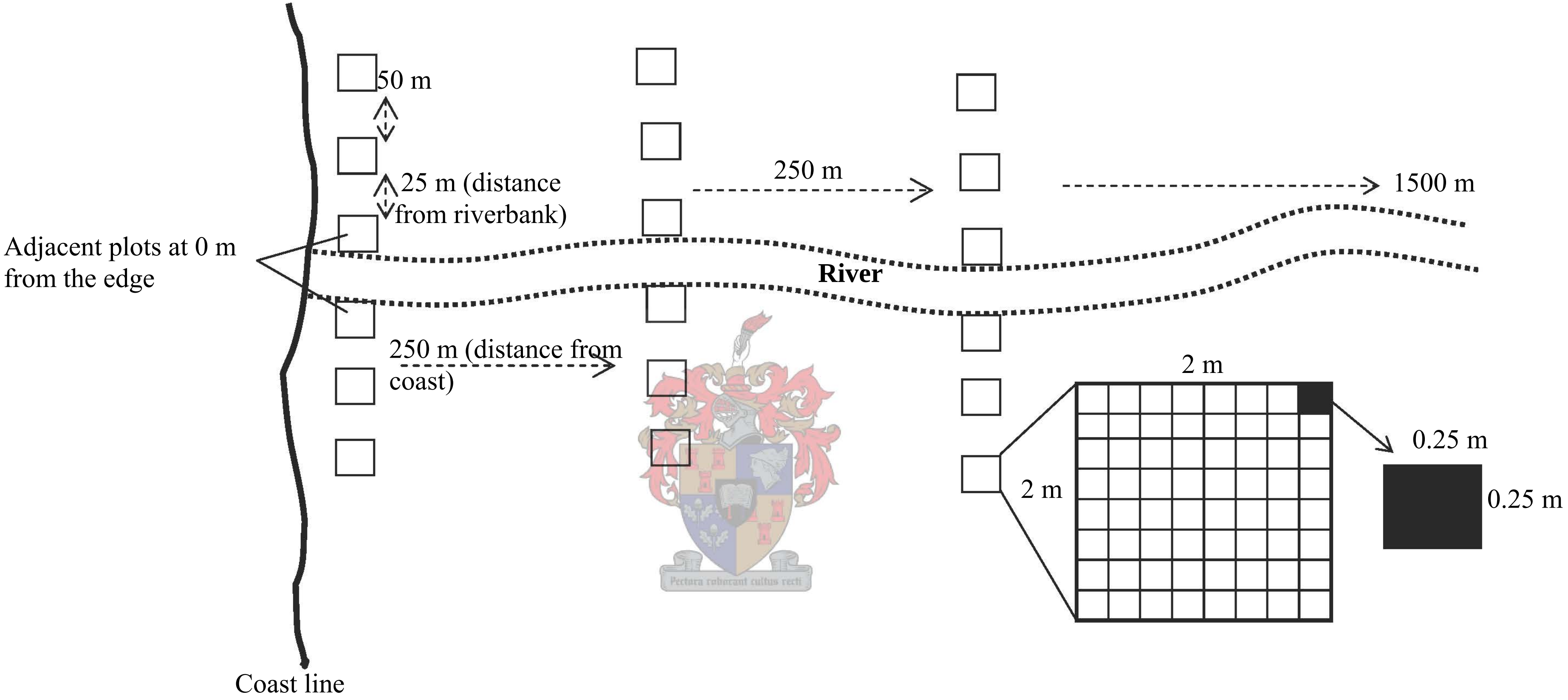

Figure 1 The sampling design for determining percentage cover for the three species along the rivers of Marion Island in 2 m x 2 m plots.

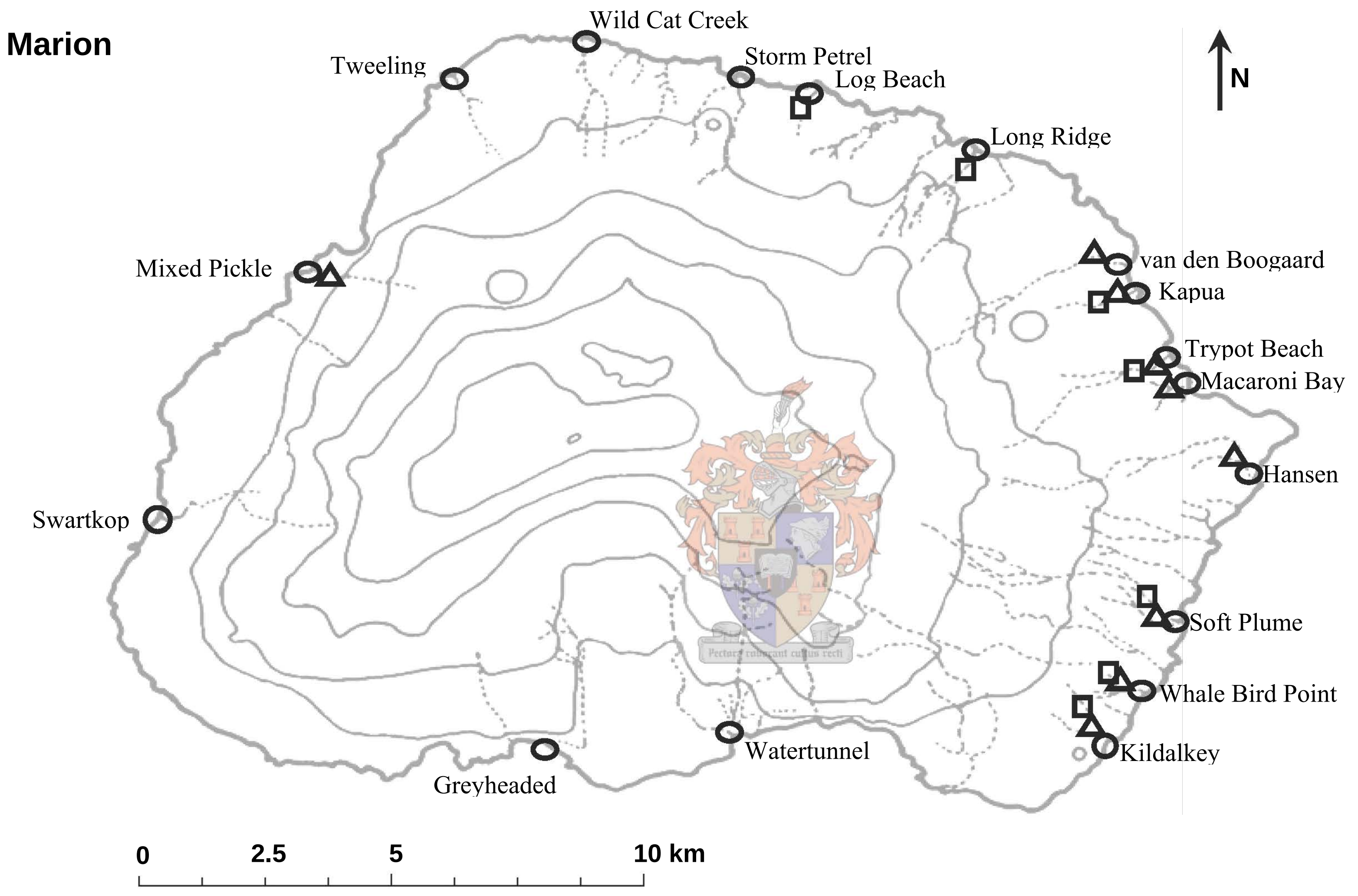

Figure 2 Sampled rivers across Marion island showing the three species recorded along each river, ○ = *Acaena magellanica*, Δ = *Agrostis stolonifera*, and □ = *Sagina procumbens*.

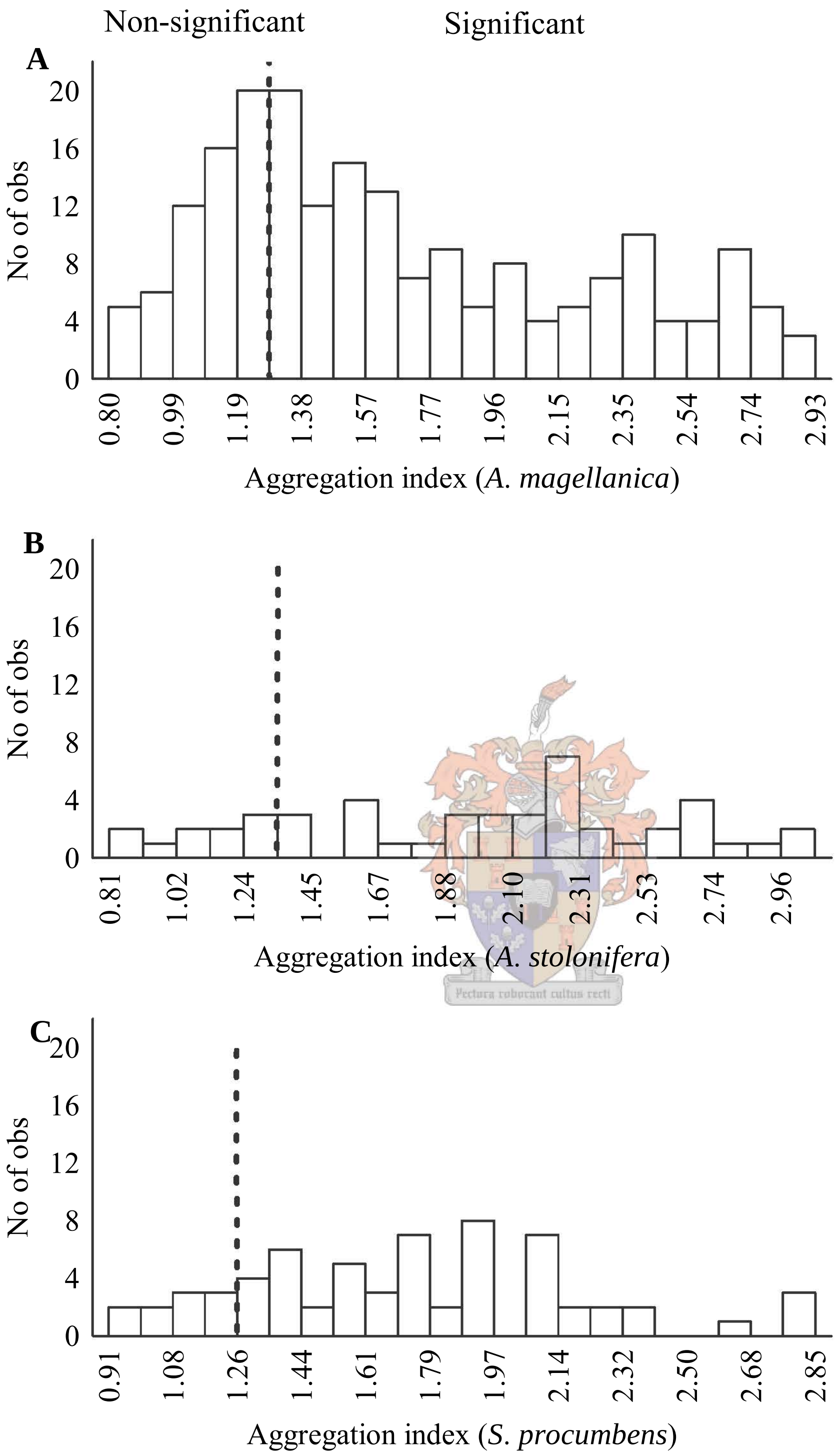

Figure 3 Frequency distributions of spatial aggregation index (I_a) values for **a** *Acaena magellanica*, **b** *Agrostis stolonifera*, and **c** *Sagina procumbens*. The dotted line divides non-significant and significant aggregations at $p < 0.05$. Note that the x-axis scale for **a**, **b**, and **c** are not the same; in this way too many gaps in the classes could be avoided

and the non-significant and significant aggregations were divided more accurately by adjusting for each species.

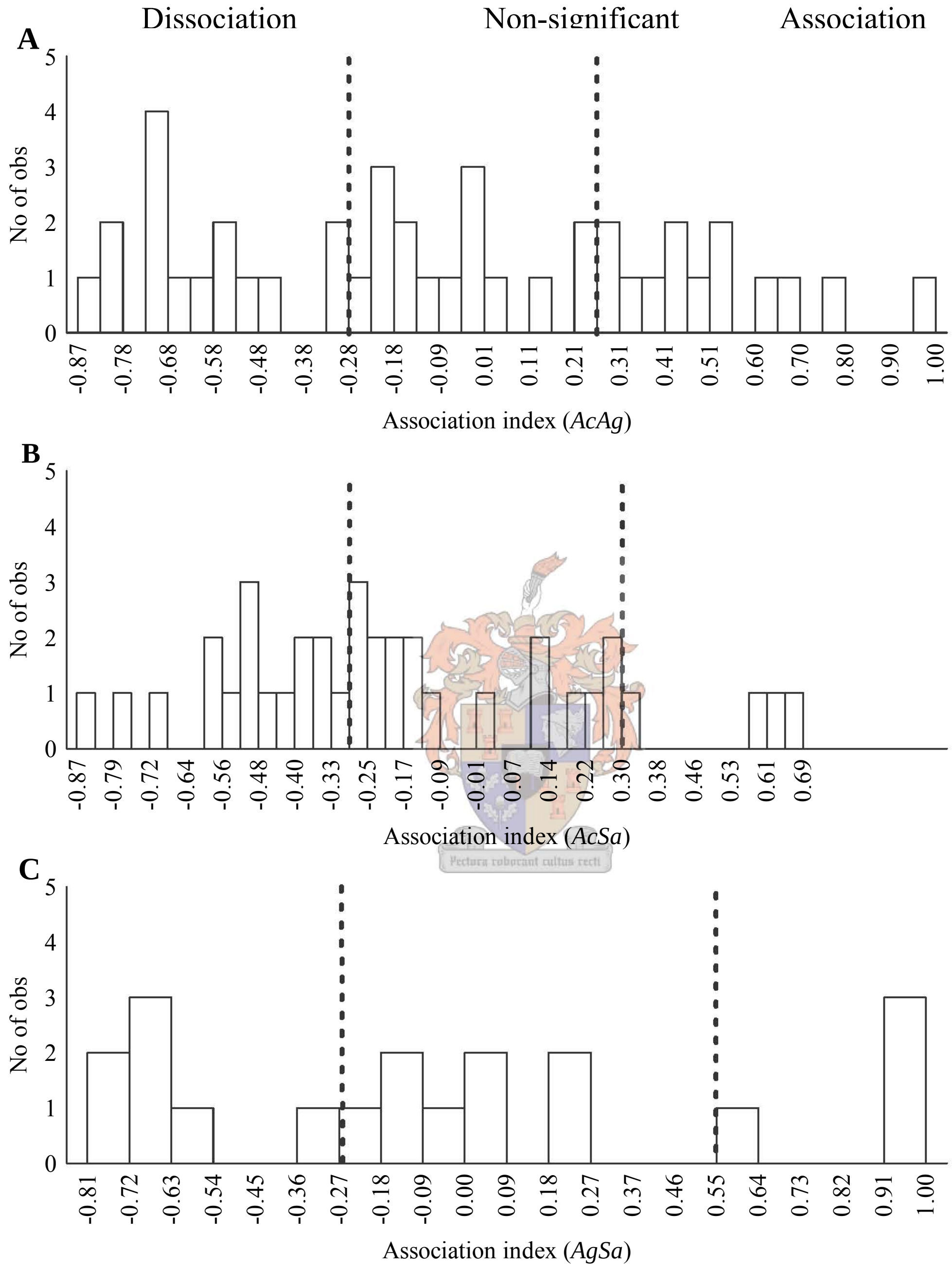

Figure 4 Frequency distributions of the spatial association index (χ) obtained from SADIE for the three species pairs (**a** *AcAg* = *Acaena magellanica* and *Agrostis stolonifera*; **b** *AcSa* = *Acaena magellanica* and *Sagina procumbens*; and **c** *AgSa* = *Agrostis stolonifera* and *Sagina procumbens*). The dotted lines separate dissociation (significant) from no association (non-significant) and association (significant). Note the x-axis scale values are not the same for reasons specified in Fig. 3.

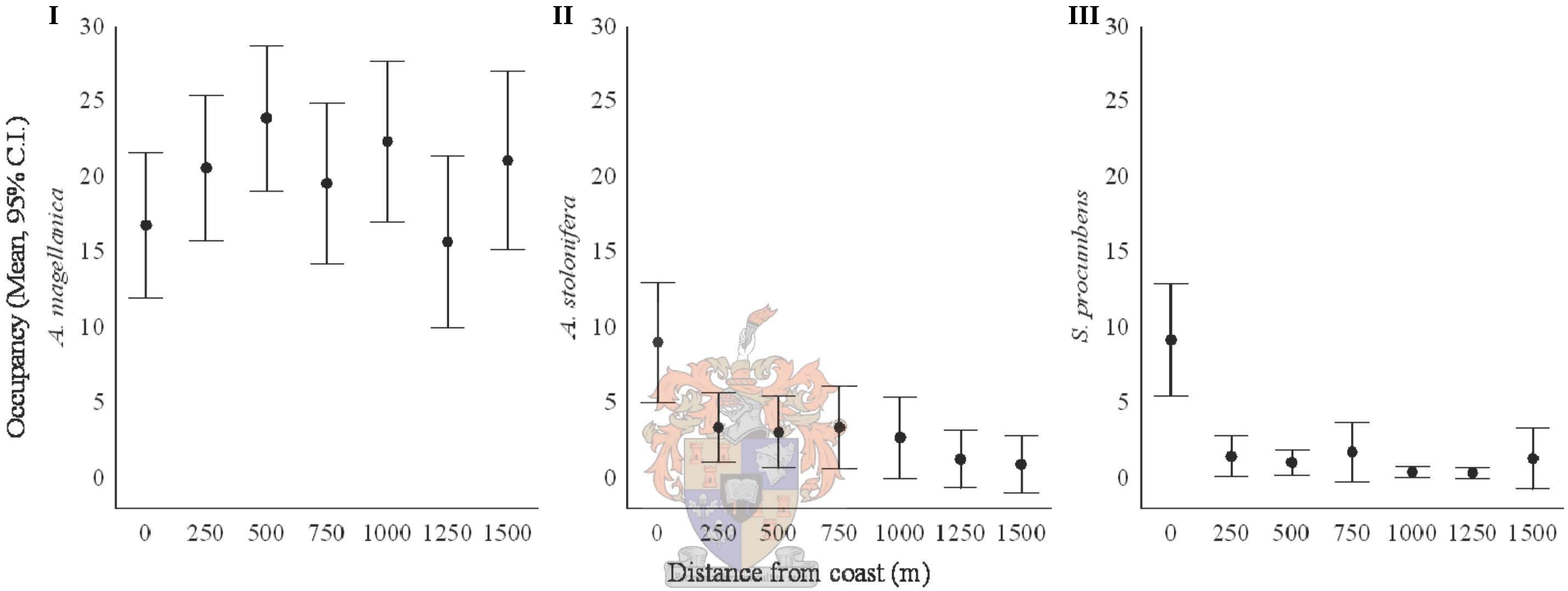

Figure 5 a The mean (± 95% C.I.) occupancy of **i** *Acaena magellanica*, **ii** *Agrostis stolonifera* and **iii** *Sagina procumbens* along rivers on Marion Island, with increasing distance from the coast.

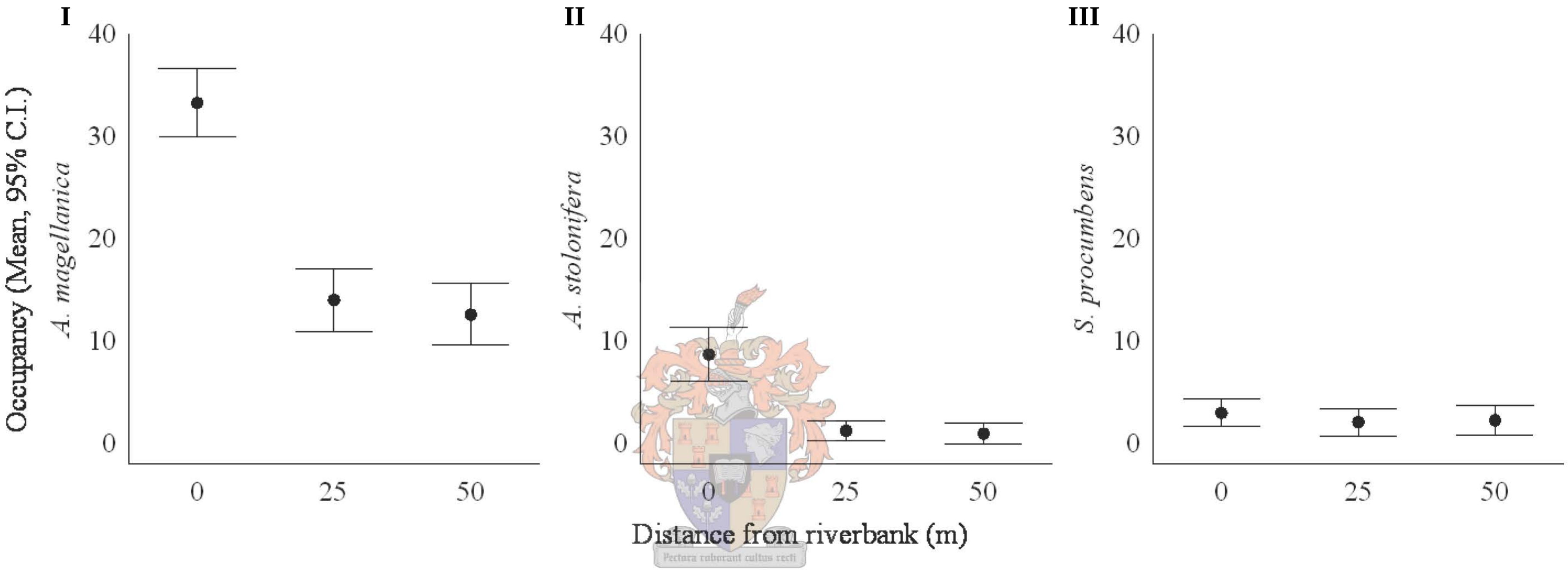

Figure 5 b The mean (± 95% C.I.) occupancy of **i** *Acaena magellanica*, **ii** *Agrostis stolonifera* and **iii** *Sagina procumbens* along rivers on Marion Island, with increasing distance from the riverbank.

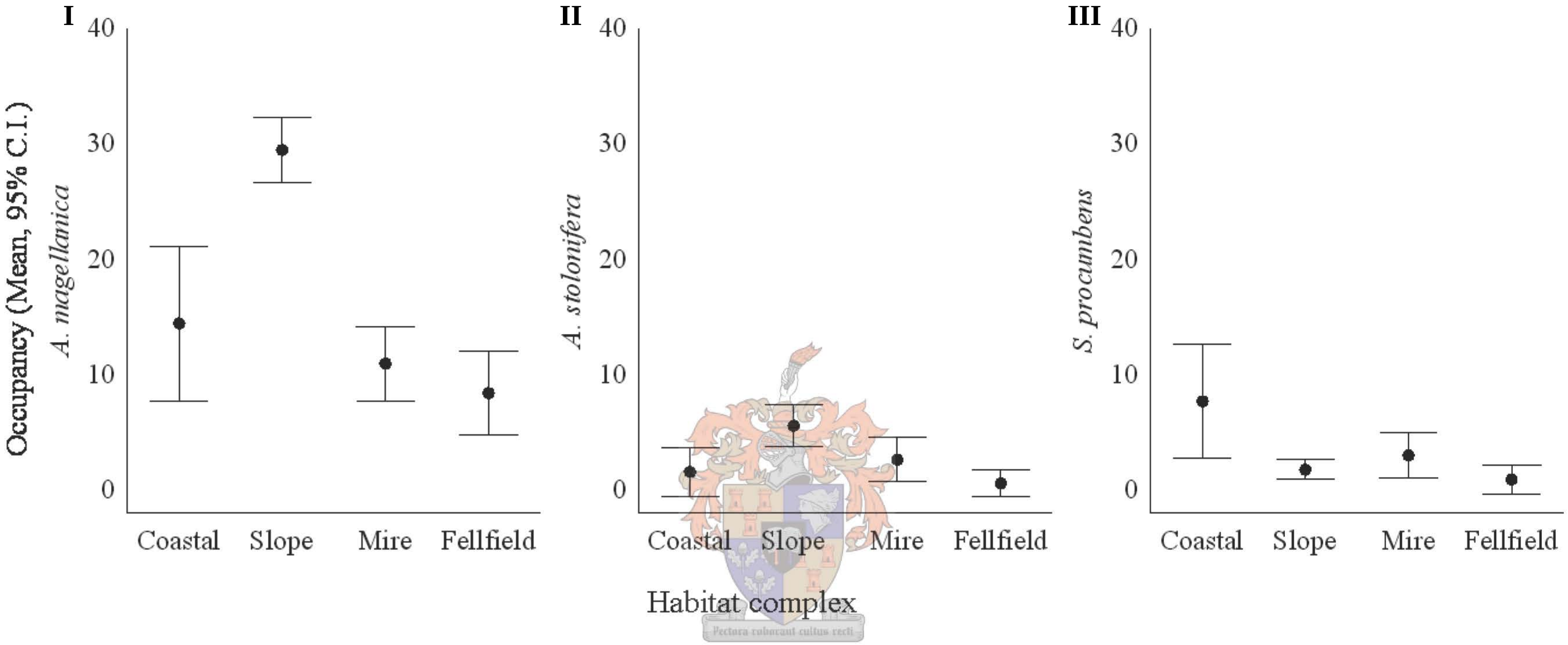

Figure 5 c The mean (± 95% C.I.) occupancy of **i** *Acaena magellanica*, **ii** *Agrostis stolonifera* and **iii** *Sagina procumbens* in different habitat complexes along rivers on Marion Island.

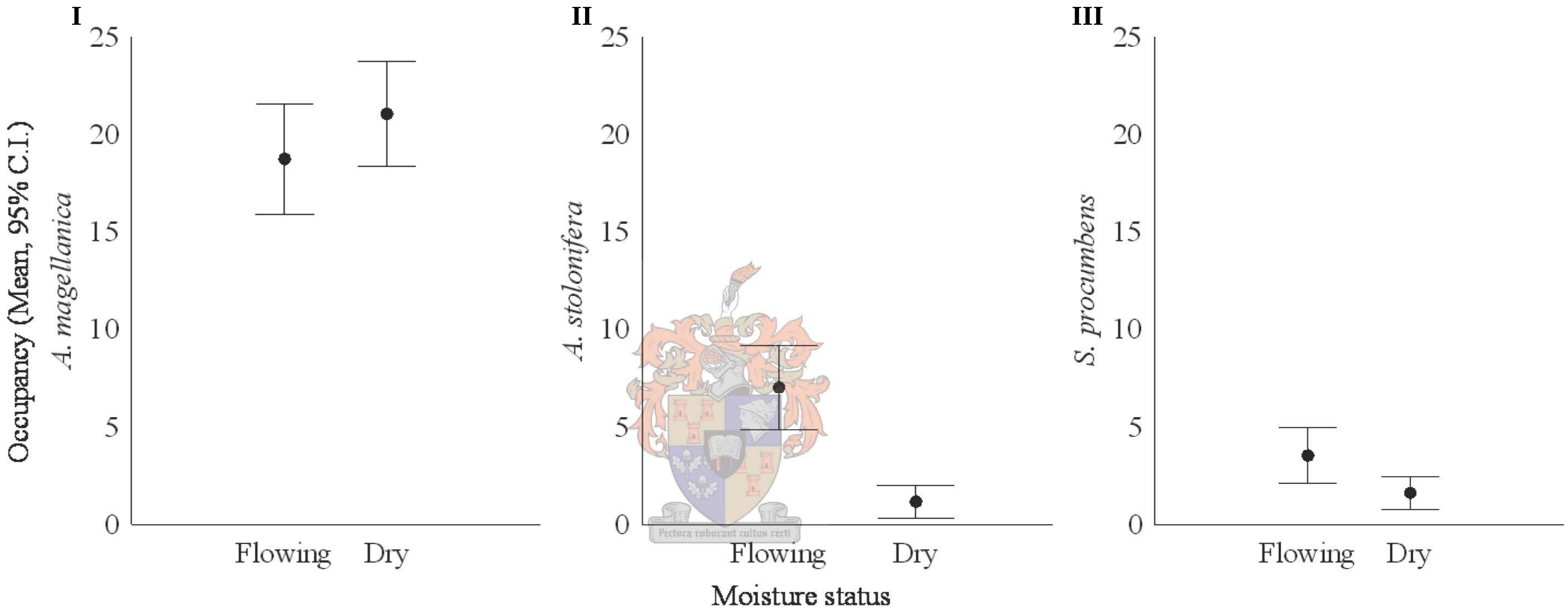

Figure 5 d The mean (± 95% C.I.) occupancy of **i** *Acaena magellanica*, **ii** *Agrostis stolonifera* and **iii** *Sagina procumbens* along rivers on Marion Island, between flowing and dry rivers (moisture status).

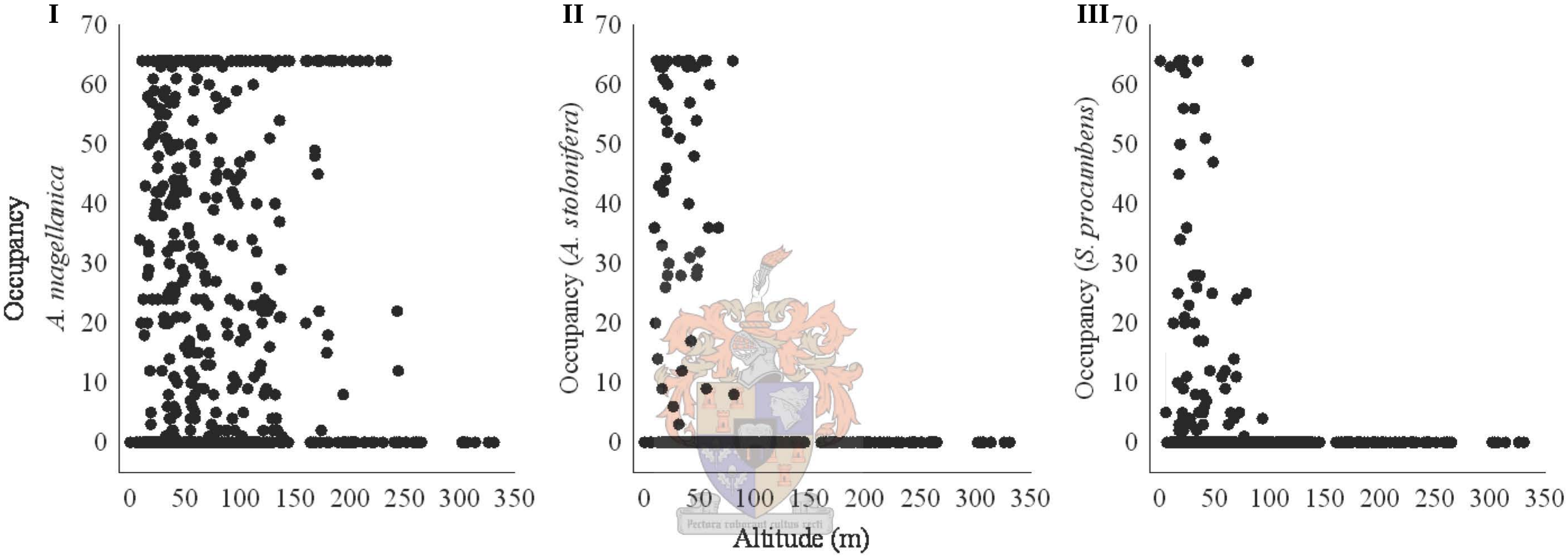

Figure 5 e The relationship between the occupancy of **i** *Acaena magellanica*, **ii** *Agrostis stolonifera* and **iii** *Sagina procumbens* and altitude along rivers on Marion Island.

Chapter 5

GENERAL CONCLUSION

The main objective of this research was to provide a descriptive account of the distribution patterns and interactions among five ecologically significant species found on sub-Antarctic Marion Island: indigenous vascular plants (*Azorella selago* and *Acaena magellanica*), naturalized alien plants *(Agrostis stolonifera* and *Sagina procumbens*) and an alien vertebrate, the house mouse (*Mus musculus domesticus*). Specifically, I examined and tested hypotheses on relationships between species occupancy, distribution, and abundance at broad (island-wide) and fine spatial scales. The interactions and impacts of terrestrial naturalized alien species on the indigenous vascular plants were also investigated.

The study found the abundance structure of the cushion-forming, keystone plant, *Azorella selago*, to be a complex patch network of high and low cushion abundances within the overall range limits of the species on the island. Furthermore, the abundance structure of the species did not support the hypothesis of an abundant centre distribution, in agreement with similar studies (e.g. Brewer & Gaston 2002, 2003; Murphy *et al*. 2005; Samis & Eckert 2007). Sharp discontinuities of *A. selago* abundance were observed at the coastal and altitudinal (667 m a.s.l.) range edges. Even over smooth environmental gradients, the abundance of a species may show an abrupt decline in distribution without any change or loss of appropriate habitat (Whittaker 1967; Brown 1984; Brown 1995; Sagarin & Gaines 2002). This was observed for *A. selago*. While the species does occur above 667 m a.s.l. (Hedding 2006), and there is adequate habitat for colonization above this altitude, its distribution is sparse. The reasons for this are unknown. However, one explanation may be the accessibility of suitable resources. Substrates found in the Polar desert habitat complex (occurring from *c*. 450 m a.s.l.) have low water-holding capacity and the soils are nutrient poor (Smith 1978; Smith *et al*. 2001). Furthermore, at high altitude sites, substrate movement is higher than at lower altitudes due to higher incidences of freeze-thaw cycles (Boelhouwers *et al*. 2003; Holness 2003). This may consequently inhibit seedling establishment (Heilbronn & Walton 1984) and colonization of the recently available habitat (as a result of climate change) (Sumner *et al*. 2004) by *A. selago*. Therefore, the observed abrupt decline in *A. selago* abundance may be attributed to associated changes in abiotic conditions, suggesting that the environmental gradients, at both the coastal and altitudinal limits, are too extreme for the survival of the species (Caughley *et al*. 1988; Sagarin & Gaines 2002).

Although it has been demonstrated that climate change will have unfavourable consequences for *A. selago* (le Roux *et al*. 2005), the impacts of alien species on the plant have until now not been investigated. As with other alien species on Marion Island, the only vertebrate alien (house mice, *Mus musculus domesticus*) is expected to have unfavourable interactions with indigenous biota and ecosystem functions (Crafford 1990; Smith & Steenkamp 1990). In this study, structural damage (in the form of burrows) caused by mice to *A. selago* was widespread across the island-wide distribution of the keystone species. Indeed, the spatial variation in the distribution of structural damage to *A. selago* indicated that mice have free access to the plant across the island. Mouse damage occurred up to 548 m a.s.l. compared to the 667 m a.s.l. altitudinal limit identified for *A. selago* in this study. With *c*. 40 % of sampled plots affected by mice, the structural damage to *A. selago* in these plots ranged from single burrows to total disintegration of the cushions of this plant. Given the slow growth rate of *A. selago* (le Roux & McGeoch 2004) and its role as a nurse plant, housing high abundances of indigenous invertebrate species (McGeoch *et al*. 2008), the detrimental effects of mice burrowing into the cushions of this plant are of grave concern. The results of this study highlight that the impact of mice may eventually alter ecosystem functions at the landscape level by directly impacting on the abundance of *A. selago*.

The degrees to which alien plants affect indigenous ones differ between the alien plants and invaded plant communities. These effects can be very slight, where only a few small alien plants enter a habitat, or extensive, resulting in the dense growth of the alien species that can completely replace indigenous vegetation (Sax & Brown 2000; Byers *et al*. 2002; Sax *et al*. 2002). This study investigated the co-occurrence of two alien plants (*Agrostis stolonifera* and *Sagina procumbens*) with the indigenous *Acaena magellanica* along rivers on Marion Island. The results demonstrated that these species respond to different environmental conditions on the island. The alien species were mostly recorded close to the coast and along rivers that were flowing, whereas *A. magellanica* was dominant along all rivers. Salt-spray and manure deposits from seabirds and seals are major contributors of nutrients on the island (Huntley 1971; Smith 1978), while fresh-water systems, such as rivers, are important for the dissemination of these nutrients (Smith 2008). The occurrence of alien species close to the coast and along flowing rivers can thus be attributed to these sites being close to nutrient sources. The fact that the alien species were more sensitive to environmental variables (i.e. distance from the coast and altitude, and additionally for *A. stolonifera*, distance from the riverbank, habitat complex, and the moisture status of rivers) highlights that habitat is important in structuring the occurrence of these species on the island. The occurrence of *A. magellanica* was only restricted by the distance from the riverbank. Spatial association patterns for the co-occurrence of *S. procumbens* with either *A. magellanica* or *A. stolonifera* suggested that these species were either spatially dissociated or randomly distributed relative to each other. These associations were not significantly influenced by environmental variables. Therefore, from this I can deduce that *S. procumbens* does not pose significant threats to *A. magellanica* along rivers and does not negatively interact with *A. stolonifera*.

Conversely, there were significant positive spatial associations in the co-occurrence of *A. magellanica* with *A. stolonifera*. The spatial association of this species pair was significantly influenced by environmental variables. However, there were narrow margins between spatial association levels (i.e. positive association, no association, and dissociation) for the co-occurrence of this species pair. This was an indication that their co-occurrences were structured by similar environmental conditions (Kikvidze *et al*. 2005; Tirado & Pugnaire 2005), occurring in competition with each other or as spatially segregated populations (Pielou 1961; Perry & Dixon 2002). Similarly, where the three species simultaneously co-occurred (i.e. *A. magellanica-A. stolonifera-S. procumbens*), there were equal signs of negative and positive covariations, suggestive of either competition (Gotelli & Entsminger 2001) or the tolerance of similar conditions (Miriti 2007). This study highlights that while both alien species pose significant threats to the island's ecosystem, their influence on indigenous vegetation is structured by different environmental conditions. *Agrostis stolonifera* is known to have negative impacts in areas it invades (Gremmen *et al*. 1998), but because environmental variables in this study were associated with its occurrence and co-occurrence with *A. magellanica*, its impact is likely to be limited to moisture-rich habitats. *Sagina procumbens*, on the other hand, seems to have a broader tolerance to environmental variables. Therefore, unlike *A. stolonifera*, it may be having broader ecosystem impacts that are yet to be quantified.

Macroecological patterns are complex (Blackburn & Gaston 1998; Blackburn & Gaston 2001; McGeoch & Gaston 2002; Storch & Gaston 2004). The complexity of these patterns is largely attributed to sampling scale (Blackburn & Gaston 1998), and in particular, to grain size and extent (McGeoch & Gaston 2002). Additionally, abiotic and biotic mechanisms such as the position of a species within its distribution range, habitat patchiness, and a species' ability to adapt to habitats, are some of the factors shaping observed macroecological patterns (McGeoch & Gaston 2002; Storch & Gaston 2004). The choice of sampling scale is therefore important when conducting ecological research in ecosystems like Marion Island where, within a kilometer, one can come across a variety of habitat types. Soil water content and lateral water movement are essential for the dissemination of nutrients (Smith 1978, 1987) and together they co-determine the occurrence of species and provide a link between habitat complexes and the distribution of vegetation across the island. Therefore, distance between sites and the patchiness of habitats were important determinants of the observed macroecological patterns in this study. Here, I examined species distributions and interactions at broad and fine spatial scales. This was useful for providing the general spatial distribution (chapter 2) and interaction of species (chapter 3) at the landscape level. Also, the fine-scale study on the interactions of plants (chapter 4) was essential for formulating predictions on how alien and indigenous plants may be interrelating at broader spatial scales. Subsequent studies can predict how current macroecological patterns of intact habitats may change as a result of alien species introductions.

It is predicted that interactions between alien and indigenous species are going to be exacerbated by climate change (Walther *et al*. 2002). Since climate change is likely to be advantageous to alien species (Walther *et al*. 2002), sub-Antarctic systems are likely to experience severe biological and ecological stresses as a result of increased intensity of interactions between alien and indigenous species (McGeoch *et al*. 2006). Nonetheless, the limited knowledge on past ecological and physiological processes driving the observed patterns is not enough to deduce links between past and current distributions of species on Marion Island. In order to make predictions for future distributions from current patterns (as quantified in this research), synergistic studies on mechanisms and processes underpinning the distribution of species need to be carried out. These should include local population dynamics, intraspecific genetic variation and physiological tolerances of both alien and indigenous species. For example, it is not known whether there is respective genetic variation within the two alien plants studied here. Furthermore, while there have been studies on the physiology of *A. stolonifera* (e.g. Pammenter *et al*. 1986), there are insufficient, if any, records on the physiology of *S. procumbens* on Marion Island. It would also be worthwhile to perform studies on the progression of alien species impacts on indigenous biota in view of climate change. In this research, I demonstrated that alien house mice affect *A. selago* at the landscape level. It is thus essential to conduct research on long term consequences of mice on the vitality of *A. selago* (and other indigenous plants), while also considering the physiological tolerances of both species and how they may react to climate change (already demonstrated for *A. selago*, le Roux *et al*. 2005). This will be useful for modelling possible changes to landscape structure.

In conclusion, this thesis provided the first comprehensive study of the abundance and distribution patterns of a plant species (*Azorella selago*) on Marion Island and in the sub-Antarctic. This study also demonstrated that alien species have significant influences on indigenous species at both broad and fine spatial scales on Marion Island. These findings for a sub-Antarctic environment provide an important basis for future studies that may explore or model mechanisms influencing the distribution of species and for understanding macroecological patterns through invasion biology in these ecosystems.

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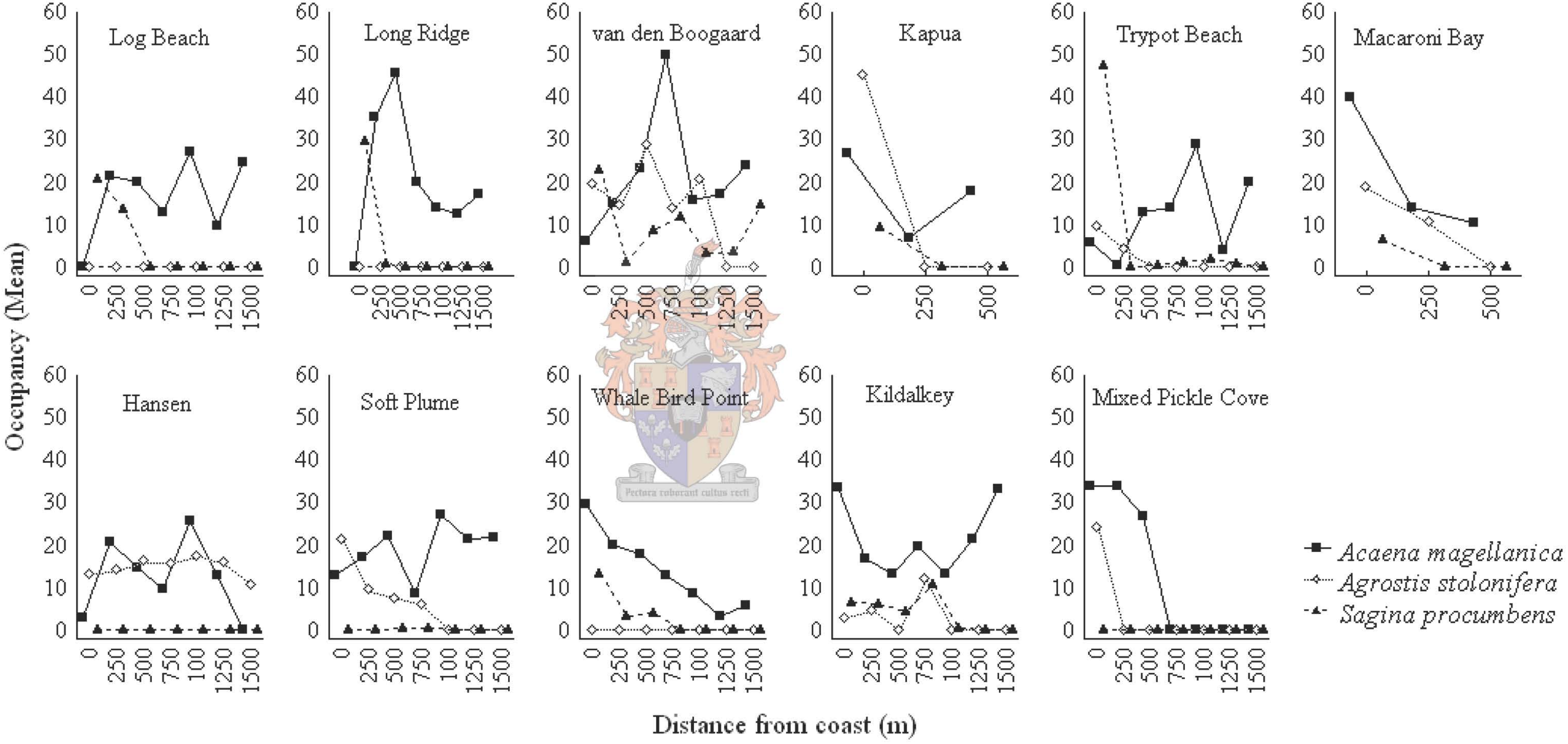
Appendix A Percentage of aggregated distributions for each species where they occurred along individual rivers on Marion Island. *Ac* = *Acaena magellanica*; *Ag* = *Agrostis stolonifera*; *Sa* = *Sagina procumbens*.

River	Species (N plots)			% significant		
	Ac	*Ag*	*Sa*	*Ac*	*Ag*	*Sa*
Hansen	12	11	0	67	72.7	0
Kapua	11	5	2	100	100	100
Kildalkey	31	4	8	65	50	75
Log Beach	16	0	7	56	0	85.7
Long Ridge	22	0	7	68	0	57.1
Macaroni Bay	8	4	4	100	100	100
Mixed Pickle Cove	8	4	0	100	50	0
Soft Plume	26	6	2	58	83.3	100
Trypot Beach	18	2	9	61	100	88.9
Van den Boogaard	21	12	18	67	83.3	83.3
Whale Bird Point	26	0	7	85	0	85.7

Appendix B Significant C-score and variance ratio values (C-score and VR significantly greater and smaller than expected by chance, respectively, at $p < 0.05$; n.s. = non-significant) for different species combinations in individual plots along individual rivers on Marion Island. *AcAg* = *Acaena magellanica* and *Agrostis stolonifera*; *AcSa* = *Acaena magellanica* and *Sagina procumbens*; *AcAgSa* = *Acaena magellanica* and *Agrostis stolonifera* and *Sagina procumbens*, and *AgSa* = *Agrostis stolonifera* and *Sagina procumbens* species combinations.

River	Species combination	C-score	p(obs>exp)	VR	p(obs<exp)
van den Boogaard	*AcAg*	667.00	<0.0001	0.38	<0.0001
	AcAg	580.00	<0.0001	0.43	<0.0001
	AcAg	136.00	0.0438	0.78	0.0392
	AcSa	612.00	<0.0001	0.36	<0.0001
	AcSa	165.00	0.0064	0.55	0.0102
	AcSa	261.00	0.0256	0.74	0.0340
	AcSa	364.00	0.0464	0.76	0.0482
	AcAgSa	426.33	<0.0001	0.61	0.0026
	AcAgSa	239.67	<0.0001	0.39	<0.0001
	AcAgSa	87.00	0.0276	0.74	0.0310
	AcAgSa	97.67	0.0348	0.92	0.3762
Kapua	*AcSa*	352.00	0.0010	0.60	0.0006
	AgSa	352.00	0.0012	0.54	0.0012
	AcAgSa	246.00	0.0032	0.79	0.1024
Trypot Beach	*AcSa*	160.00	0.0356	0.76	0.0424
	AcSa	144.00	0.0388	0.77	0.0346
	AcSa	120.00	0.0512 n.s.	0.79	0.0496
Hansen	*AcAg*	437.00	<0.0001	0.50	0.0002
	AcAg	728.00	<0.0001	0.27	<0.0001
	AcAg	186.00	0.0146	0.73	0.0146
	AcAg	170.00	0.0168	0.74	0.0174
Soft Plume	*AgSa*	144.00	0.0348	0.77	0.0318
Whale Bird Point	*AcSa*	408.00	0.0002	0.50	<0.0001
Kildalkey	*AgSa*	280.00	0.0026	0.65	0.0026
	AcAgSa	265.33	0.0006	0.54	0.0002

Appendix C The change in mean occupancies of *Acaena magellanica*, *Agrostis stolonifera*, and *Sagina procumbens* with increasing distance from the coast along individual rivers on Marion Island.



Appendix D The change in mean occupancies of *Acaena magellanica*, *Agrostis stolonifera*, and *Sagina procumbens* with increasing distance from the riverbank along individual rivers on Marion Island.