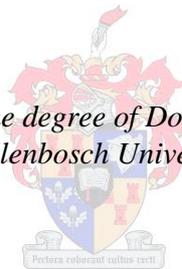


# **The biogeomorphology associated with a keystone plant species in the sub-Antarctic**

by  
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*Presented for the degree of Doctor of Science at  
Stellenbosch University*



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March 2011

## Declaration

By submitting this dissertation electronically, I declare that the entirety of the work contained therein is my own, original work, and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

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Signature

Natalie Suzette Haussmann

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Name in full

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Date

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Needle ice on Marion Island

## Abstract

There are few scientific publications that relate to biogeomorphological interactions in glacial and periglacial environments. Interactions that focus on the interface between ecology and geomorphology are very important in these environments, as a tight coupling often exists between organisms and their abiotic surroundings. In this thesis the interactions between the dominant vascular cushion plant species on sub-Antarctic Marion Island, *Azorella selago* Hook. (Apiaceae), and the surrounding geomorphological landforms, processes and measuring techniques were studied. In addition, the thesis provides suggestions to facilitate future integrated biogeomorphological research.

To understand the consequences of *A. selago* cushions for substrate movement and sorting, the grain size distribution of sediment surrounding these cushions was quantified using a combination of image analysis approaches. Through obstructing frost-related sediment transport, *A. selago* cushions are shown to affect the grain size sorting of the surrounding sediment. Particle size affects soil properties such as water-holding capacity and frost susceptibility. It is therefore important to understand the interactions between *A. selago* cushions and sediment distributions, especially in the light of recent warming and drying on the island.

Fine scale variability in soil temperature parameters was studied around cushions to improve understanding on how *A. selago* affects the surrounding soil microclimate. Despite the mild frost climate, extensive frost heave occurred in the study area, indicating that needle ice forms above the previously suggested required temperature of  $-2^{\circ}\text{C}$ . Lower and less variable winter temperatures were found on eastern than on western cushion sides, probably as a result of lower wind speeds or leeside snow accumulation on eastern cushion sides. These research findings highlight the importance of *A. selago* cushions in modifying site microclimates. Such modifications could have important potential consequences, such as providing microhabitats for soil microorganisms and seedlings.

Positive plant interactions have been suggested to dominate over negative interactions in environments with high abiotic stress. Positive associations were found between *A. selago* and both its own seedlings and those of the perennial grass, *Agrostis magellanica* Lam. (Poaceae) on Marion Island. It is suggested that both cushions and rocks trap seeds dispersed by wind, runoff and/or downslope sediment transport through frost creep. In addition, increased *A. selago* seedling numbers around cushions, but not around rocks, suggest that cushions provide a biological nurse effect to seedlings of their own kind.

Plant species' distributions have been known to vary in response to abiotic stress gradients. In light of this, determinants of *A. selago* seedling distributions and abundance, such as altitude and

substrate cover, were explored. Although there appears to be some altitudinal trend, seedling distributions and abundance patterns were largely attributed to unaccounted variation between sites.

Plants can affect the surrounding geomorphology, but also geomorphological measuring techniques. To explore the potential of cosmogenic dating techniques as geomorphological tools in fellfield habitats, accumulation rates of the cosmogenic isotope  $^{10}\text{Be}$  were assessed underneath and adjacent to an *A. selago* cushion. The results show that  $^{10}\text{Be}$  is not fully retained in the soil profile and various reasons are discussed. Furthermore, the results suggest that  $^{10}\text{Be}$  concentrations should be interpreted cautiously in fellfield habitats, as *A. selago* cushions effectively intercept the isotope in their soil-rich core.

To facilitate the integration of geomorphological and ecological principles, as was attempted in this thesis, it is important to understand the philosophies behind the different research approaches that ecologists and geomorphologists employ. Ecologists often employ a more statistics-based approach, whereas geomorphologists focus on a more descriptive approach and reasoning based on established theories. I attempt to explain why the two fields follow such different approaches, highlight some potential challenges and provide suggestions to facilitate progress in the interdisciplinary field of biogeomorphology.

## Opsomming

Min aandag is al gegee aan biogeomorfolgiese interaksies in glasiale en periglasiale omgewings. Nietemin is hierdie interaksies, wat op die skeidingsvlak tussen ekologie en geomorfologie fokus, baie belangrik in hierdie omgewings, waar organismes in noue verband met die abiotiese omgewing saamleef. In hierdie tesis bestudeer ek die interaksies tussen die vaskulêre plantspesies met die hoogste voorkoms op sub-Antarktiese Marion Eiland, *Azorella selago* Hook. (Apiaceae), en die omringende geomorfologiese landskapsvorme, –prosesse en meettegnieke. Verder verskaf die tesis voorstelle om toekomstige geïntegreerde biogeomorfolgiese navorsing te vergemaklik.

Om die gevolge van *A. selago*-plante vir sedimentbeweging en -verspreiding te verstaan, het ek die verspreiding van sedimentgroottes om hierdie plante gemeet deur middel van 'n kombinasie van fotografiese analise-metodes. Deur as sedimentbewegingsobstruksies te dien, het plante 'n waarneembare effek op die omringende sedimentverdeling. Dit is veral belangrik om hierdie interaksies tussen *A. selago* en sy omgewing te verstaan in die lig van onlangse klimaatsverandering op die eiland, omdat sedimentgrootte belangrike grondeienskappe soos waterretensiekapasiteit en vriesgevoeligheid beïnvloed.

Om die effek wat *A. selago* plante op die omringende mikroklimaat het beter te verstaan, is die kleinskaalse variabiliteit in grondtemperature om *A. selago* plante bestudeer. Groot skaalse grondligting as gevolg van fors is gemeet, ten spyte van relatief ligte forseienskappe. Dit dui daarop dat naaldys ook by temperature bo  $-2^{\circ}\text{C}$  kan vorm. Wintergrondtemperature aan die oostekant van plante was effens laer en minder veranderlik as aan die westekant van plante, waarskynlik as gevolg van laer windsnelhede en/of sneeu wat ophoop aan die oostelike, lykant van plante. Die resultate benadruk dat *A. selago* plante 'n belangrike rol speel in die verandering van mikroklimaat en dat dit belangrik is om die gevolge van sulke veranderings, soos die skep van mikrohabitate vir grondorganismes, te verstaan.

Daar word vermoed dat positiewe plantinteraksies negatiewe interaksies oorheers in omgewings met hoë abiotiese druk. Gevolglik wys ek dat daar 'n positiewe verband bestaan tussen *A. selago* plante en saailinge van beide *A. selago* self, asook van die meerjarige gras *Agrostis magellanica* Lam. (Poaceae). Ek stel voor dat beide plante en klippe sade, wat deur wind, reënval en/of afdraande sedimenttransportering as gevolg van vriesprosesse vervoer word, opvang. Verder dui verhoogde *A. selago* saailinggetalle om plante, maar nie om klippe nie, daarop dat plante een of ander biologiese voordeel aan *A. selago* saailinge bied.

Dit is bekend dat die verspreidingspatrone van plantspesies as gevolg van abiotiese stresgradiënte varieer. Met hierdie bevinding in gedagte, is moontlike faktore verantwoordelik vir

*A. selago* saailinggetalle en -verspreidingspatrone, soos hoogte bo seespieël en substraatbedekking, bestudeer. Alhoewel dit wil voorkom asof daar 'n verband tussen saailinggetalle en hoogte bo seespieël is, is saailinggetalle en verpreidings meestal afhanklik van ongemeette perseel-spesifieke eienskappe.

Plante kan die omringende geomorfologie beïnvloed, maar ook geomorfologiese meettegnieke. Om die potensiaal van kosmogeniese dateringsmetodes as geomorfologiese hulpmiddels in fellfield habitatte te verken, is die akkumulasiestempo van die kosmogeniese isotoop  $^{10}\text{Be}$  onder en langs 'n *A. selago* plant bepaal. Die resultate dui daarop dat  $^{10}\text{Be}$  nie ten volle in die grondprofiel behoue bly nie en verskeie potensiële redes word bespreek. Verder dui die resultate daarop dat  $^{10}\text{Be}$  konsentrasies in fellfield habitatte versigtig geïnterpreteer moet word, aangesien *A. selago* plante effektief  $^{10}\text{Be}$  opvang in hulle grondryke kern.

Om vordering in biogeomorfologie te vergemaklik, is dit belangrik om bewus te wees van die verskillende metodes wat geomorfoloë en ekoloë volg. Ekologiese benaderings is dikwels op strenger statistiese tegnieke gebaseer, terwyl geomorfoloë eerder fokus op 'n meer beskrywende benadering en teoretiese beredenering. Ek verduidelik hoekom die twee velde sulke uiteenlopende benaderings volg, benadruk moontlike struikelblokke en verskaf voorstelle om samewerking te vergemaklik.

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## Table of contents

<b>Declaration</b>	<b>ii</b>
<b>Abstract</b>	<b>iv</b>
<b>Opsomming</b>	<b>vi</b>
<b>Acknowledgements</b>	<b>viii</b>
<b>Table of contents</b>	<b>ix</b>
<b>Chapter 1 – General introduction</b>	<b>1</b>
<i>Biogeomorphology as a research field</i>	1
<i>Biogeomorphology in glacial and periglacial environments</i>	1
<i>Marion Island as a sub-Antarctic periglacial environment</i>	2
<i>Frost regime and periglacial processes on Marion Island</i>	3
<i>Marion Island's vegetation: The fellfield habitat complex</i>	5
<i>Cushion plants and <i>Azorella</i> selago</i>	5
<i>Thesis outline</i>	6
<i>References</i>	7
<i>Figures</i>	13
<b>Chapter 2 – Interactions between <i>Azorella selago</i> and surface sediment transport</b>	<b>15</b>
<i>Introduction</i>	15
<i>Study area and site selection</i>	18
<i>Methods</i>	19
Field procedure and image selection	19
Cushion size and shape analyses	20
Digital image analyses procedure	20
Visual estimation of particle sizes	21
<i>Results</i>	22
Cushion size and shape	22
Digital image analyses procedure	22
Visual estimation of particle sizes	23
<i>Discussion</i>	24
<i>Conclusions</i>	28
<i>References</i>	29
<i>Tables</i>	34
<i>Figures</i>	37

**Chapter 3 – Fine scale variability in soil frost dynamics surrounding *Azorella selago* cushions** **43**

<i>Introduction</i>	43
<i>Study area and site selection</i>	45
<i>Methods</i>	45
Field procedure	45
Data processing and statistical analyses	47
<i>Results</i>	48
Temperature data	48
Soil moisture data	50
Heave and erosion	50
<i>Discussion</i>	50
<i>Conclusions</i>	53
<i>References</i>	54
<i>Table</i>	58
<i>Figures</i>	59

**Chapter 4 – Contrasting nurse plants and nurse rocks: the spatial distribution of seedlings of two sub-Antarctic species** **65**

<i>Introduction</i>	65
<i>Methods</i>	67
Study area	67
Study species	67
Cushion and rock selection and seedling survey	68
<i>Results</i>	70
<i>Discussion</i>	71
<i>Conclusions</i>	74
<i>References</i>	74
<i>Table</i>	79
<i>Figures</i>	80

**Chapter 5 – Exploring the determinants of *Azorella selago* seedling densities and distributions** **85**

<i>Introduction</i>	85
<i>Methods</i>	87
Field methods	87
Data analyses	87
<i>Results</i>	88
<i>Discussion</i>	90
<i>Conclusions</i>	93
<i>References</i>	93

<i>Tables</i>	98
<i>Figures</i>	102
<b>Chapter 6 – <sup>10</sup>Be application to soil development on Marion Island</b>	<b>109</b>
<i>Introduction</i>	109
<i>Methods</i>	110
<i>Results and discussion</i>	111
<i>References</i>	113
<i>Tables</i>	114
<i>Figures</i>	116
<b>Chapter 7 – Biogeomorphology: challenges and options for integrating research approaches</b>	<b>119</b>
<i>Introduction</i>	119
<i>Methods</i>	120
<i>Results</i>	121
<i>Discussion</i>	122
A case of different natures	123
Case studies vs. generalisations	124
Historical developments	125
Modelling approaches	126
Scale-related differences: Truth or fiction?	127
The status of interdisciplinary biogeomorphological research	127
Challenges, pitfalls and suggestions	128
<i>Conclusions</i>	129
<i>References</i>	130
<i>Table</i>	132
<i>Figures</i>	133
<b>Chapter 8 – General conclusion</b>	<b>135</b>
<b>Appendix A-R</b>	<b>140</b>

# **Chapter 1 – General introduction**

## **Biogeomorphology as a research field**

In the late 1980s the term biogeomorphology emerged to describe studies focussing on the interactions between organisms and geomorphological landforms and processes (Viles, 1988). Although biogeomorphological studies were not new to science, biogeomorphology was now for the first time formally recognised as a field of research within geomorphology (Naylor, 2005). As many geomorphological studies include some form of biotic component, without explicitly discussing their findings within a biogeomorphological context, some discussion ensued on what exactly defines biogeomorphology (Naylor et al., 2002). Naylor (2005) places biogeomorphology in a broad context, as a subdiscipline of geobiology, which focuses on biosphere-geosphere interactions in general (Nealson and Ghiorse, 2001) and encompasses such divergent fields as geomicrobiology, palaeoecology and astrobiology. Other studies highlight the role of ecosystem engineers (Badano and Cavieres, 2006; Byers et al., 2006; Stallins, 2006; Badano et al., 2007), a term first used by Jones et al. (1994) to describe organisms that change the environment in such a way that they create or destroy habitats for other organisms. Although consensus has not been reached on what exactly constitutes biogeomorphology, this interface between ecology and geomorphology seems to be a common focus (Naylor et al., 2002). Since the term first emerged, an ongoing awareness in the scientific community of the importance of multidisciplinary research has led to a large number of studies exploring the ways in which biotic and abiotic systems interact.

## **Biogeomorphology in glacial and periglacial environments**

The necessity of biogeomorphological research is exemplified in areas of adverse weather conditions, where plant and animal life are affected by extreme temperatures, high wind speeds and associated landforms (see Pérez, 2002; Brancaloni et al., 2003; Cannone et al., 2004 for examples). Periglacial environments often epitomise such environments. These are the zones adjacent to ice-sheets, where landforms and landform processes are dominated by freeze-thaw action, regardless of the presence of permafrost (Whittow, 2000). Parts of the sub-Antarctic islands of the southern Indian Ocean fall into this category and as such they provide excellent biogeomorphological research opportunities. Although many of these islands do not experience extreme temperatures in a global context, their climates are viewed as extreme as a result of the large number of frost cycles that they experience, coupled with high wind speeds. Compared to aeolian, fluvial and coastal environments, little attention has been paid to biogeomorphological phenomena in periglacial

systems (Hjort and Luoto, 2009). In addition, the geographic isolation, small size, relatively low species diversity and low human population densities of sub-Antarctic islands (Bergstrom and Chown, 1999; Smith, 2002) render them ideal for studying biosphere-geosphere interactions under relatively “controlled” conditions.

A tight coupling between ecosystems and climate has been demonstrated in high latitude environments (Kennedy, 1995) with many studies of these regions and their communities highlighting their exceptional sensitivity to climate change (Kennedy, 1995; Barrett et al., 2006; Turner et al., 2007). Although sub-Antarctic Marion Island is not per definition a high latitude environment, it shares many of the characteristics of these environments, such as open, windy landscapes (Schulze, 1971) and an active soil frost environment (Boelhouwers et al., 2003; Holness, 2003). Furthermore, it has been suggested that the frost environment is exceptionally sensitive to temperature increases as a result of the island’s oceanic setting (Boelhouwers et al., 2003).

Many southern hemisphere studies rely on knowledge of periglacial processes from the northern hemisphere (Boelhouwers et al., 2003). However, despite latitudinal similarities, the Antarctic and surrounding sub-Antarctic islands differ fundamentally from their northern counterparts as far as oceanicity, geographic isolation and biodiversity are concerned (French and Smith, 1985; Chown et al., 2004) and corresponding differences in ecosystem response to perturbations, such as geomorphological disturbances, can therefore be expected. In addition, although climate change and the direct consequences thereof have been studied quite extensively on sub-Antarctic islands (e.g. Tweedie and Bergstrom, 2000; Smith, 2002; le Roux and McGeoch, 2008), many indirect consequences of climate change that can be inferred from interactions between biotic and abiotic components on these islands are not yet known or fully understood. Not only are landform and soil processes and properties (such as freeze-thaw cycles and soil stability) likely to influence the way in which the biotic environment functions in a changing environment, but plant growth forms and plant vitality are also likely to influence the way in which landscapes respond to global climate change.

### **Marion Island as a sub-Antarctic periglacial environment**

Marion Island (46° 54’ S, 37° 45’ E) and its smaller neighbour, Prince Edward Island, are located in the southern Indian Ocean and together constitute the Prince Edward Islands Group (Figure 1). Marion Island is approximately 290 km<sup>2</sup> in size and the highest peak is at 1230 m a.s.l. (de Villiers, 1976). The island is the summit of a shield volcano that arose from the Southwest Indian Ridge system (Verwoerd, 1971). Although up to eight periods of volcanism have been identified (McDougall et al., 2001), in general, distinction is made between two main periods of

volcanic activity (Verwoerd, 1971; McDougall et al., 2001). An older sequence of grey lava, of which the oldest parts have been dated at  $450\,000 \pm 10\,000$  years underlies a younger sequence of black lava (approximately 10 000 years to present) (McDougall et al., 2001). Striated, grooved and smoothed features on older grey lava provide evidence of periods of glaciation in between the two lava successions (Verwoerd, 1971).

Marion Island is located north of the Antarctic Convergence, the zone where cold Antarctic surface water sinks underneath warmer sub-Antarctic water (Deacon, 1959). Islands to the north of this boundary have a milder climate, with higher temperatures and less snowfall than those to the south (Hall, 2002). Due to the vast expanses of ocean surrounding Marion Island it experiences an exceptionally maritime climate (Schulze, 1971), with both low annual ( $3.6^{\circ}\text{C}$ ) and diurnal ( $1.9^{\circ}\text{C}$ ) temperature ranges (Smith, 2002). The average annual air temperature at 23 m a.s.l. at the South African Meteorological Station on the eastern side of the island during the 1990s was  $6.4^{\circ}\text{C}$  and annual precipitation for the same period was just over 2000 mm (le Roux and McGeoch, 2008). Furthermore, a high degree of cloudiness and predominantly northwestern gale force winds occur throughout the year (Schulze, 1971).

Recently Marion Island's climate has been characterised by large, rapid climatic changes. Between 1969 and 1999, the island experienced a total average warming of  $1.2^{\circ}\text{C}$  and a concurrent average annual precipitation drop of 25 mm/year (Smith, 2002; le Roux and McGeoch, 2008). In addition, the total annual sunshine hours have increased markedly (Smith, 2002), suggesting reduced cloud cover on the island. These climate changes have been accompanied by expected changes in landform and soil processes, such as melting ice caps and associated debris flows (Sumner et al., 2004). In addition, anticipated changes in the biota on the island, such as those involving the keystone plant species, *Azorella selago* Hook. (Apiaceae), have been and are still being examined (e.g. le Roux et al., 2005; McGeoch et al., 2006). However, studies looking at Marion Island from an explicitly biogeomorphological point of view, by examining fine scale interactions between plant or animal life and geomorphological features, are to a large extent still lacking.

### **Frost regime and periglacial processes on Marion Island**

Because of low annual temperature ranges, high rainfall and high cloud cover, frequent but short frost cycles characterise all of the sub-Antarctic islands (Boelhouwers et al., 2003; Holness, 2003), with coastal freeze-thaw days on Marion Island averaging 68 days per year at the soil surface (Holness, 2001a). At higher altitudes ( $> 1000$  m), seasonal frost cycles and sporadic permafrost have been documented on the island (Holness, 2001a,b), although this has subsequently been

refuted (Boelhouwers et al., 2008). Frost penetration is shallow, ranging from 5 to 20 cm, depending on the altitude (Boelhouwers et al., 2003). Strong wind activity and small diurnal temperature ranges distinguish sub-Antarctic frost regimes from other seasonally frozen environments and render them highly sensitive to climate change (Boelhouwers et al., 2003). In contrast to frost cycles in tropical alpine mountain regions, where large diurnal temperature ranges occur and climate change effects on frost cycles are predicted to be relatively small, a mean annual soil surface temperature increase or decrease of as little as 1–2°C has been predicted to cause a substantial change in the number of freeze-thaw cycles on Marion Island, as well as the maximum depth of frost penetration (Boelhouwers et al., 2003).

One of the periglacial processes which has been found to play a substantial geomorphological role on Marion Island is the formation of needle ice (Hall, 1979; Boelhouwers et al., 2000). This dominant form of ice segregation on Marion Island (Boelhouwers et al., 2003; Holness, 2003), is known to form on calm, clear nights and requires a temperature of at least -2°C for formation to take place (Outcalt, 1971). Ice segregation is caused by water moving upward to the freezing plane, resulting in differential water content in soil layers and capillary rise (Jumikis, 1966; see also Outcalt, 1971). Elongated ice-crystals (needles) accumulate at or near, and perpendicular to the soil surface (Washburn, 1973), with needle ice growth progressing from the surface downwards (Outcalt, 1971). As the ice needles grow, a process called frost heave is initiated with the layer of soil atop the needles pushed upward and settling back (Pérez, 1987). When the soil particles settle back, their physical structure can be quite changed (Pérez, 1987; Boelhouwers et al., 2000). Through this process of soil loosening, needle ice has been found to be the driving force behind the subsequent downslope movement of heaved and settled soil particles (Benedict, 1976; Boelhouwers et al., 2000) known as frost creep (Washburn, 1973). Adequate heat dissipation from the soil surface, as well as sufficient soil water are amongst the requirements that have to be met for needle ice initiation and growth (Outcalt, 1971).

Although, by definition, sediment sorting and resulting patterned ground features are not restricted to environments experiencing frost action (Washburn, 1956), such features are common in periglacial environments. Particle size sorting in periglacial environments has been attributed to the differences in migration between finer and coarser material at the freezing front (Corte, 1962, 1963), although the exact mechanism behind sediment sorting has been debated (Washburn, 1956). Subsequent differential frost heave, as a result of intrinsic differences in coarse and fine material, may play an important additional morphogenetic role in many frost sorting features (Washburn, 1973; Holness, 2001b).

## **Marion Island's vegetation: The fellfield habitat complex**

In 1981 Gremmen quantitatively classified the vegetation of Marion Island, relating environmental characteristics to floristic composition (Gremmen, 1981). This resulted in a classification scheme of six community complexes consisting of 41 plant communities. Later Smith and Steenkamp (2001) formulated what they called a more user-friendly classification scheme based on soil and vegetation information. This latter classification scheme consisted of 23 habitats divided over seven habitat complexes (Smith and Steenkamp, 2001). The fellfield (also termed fjaeldmark) habitat complex, which is found on exposed rocky areas (Smith, 1987) consists of two habitats (mesic and xeric) based on soil moisture, organic nutrient content and pH (Smith and Steenkamp, 2001). Fellfield soils are the most mineral soils on the island, with lower concentrations of organic and inorganic N and P, exchangeable cations (Smith and Steenkamp, 2001) and moisture contents than any of the other soils (Gremmen, 1981). The number of vascular plant species is higher at lower altitudes in fellfield complexes, where fellfield is often replaced by open fernbrake vegetation (Smith and Steenkamp, 2001). Above 300 m a.s.l. fellfield is generally the only habitat complex containing vascular plant species (Gremmen, 1981) and is dominated by the vascular cushion plant species, *Azorella selago* Hook. (Apiaceae) (Huntley, 1972).

### **Cushion plants and *Azorella selago***

Cushion plants (i.e. plants exhibiting a low-growing, prostrate, often hemispherical, compact growth form) are found world-wide, but are disproportionately common in harsh environments (Hauri and Schroeter, 1914). Cushion plants have been known to trap nutrients and buffer soil temperature and moisture, thereby creating favourable microclimates for themselves and other biota (Hedberg and Hedberg, 1979; Nuñez et al., 1999; Badano and Cavieres, 2006; Badano et al., 2007). In addition, plants in periglacial environments, including cushion plants, are known to withstand very windy environments (Bliss, 1960; Kirkpatrick et al., 2002) and provide shelter to other species on leeward cushion sides (Brancaleoni et al., 2003).

The cushion plant, *Azorella selago* (Figure 2), is widespread across the sub-Antarctic (Huntley, 1972) and the genus *Azorella* is also found at higher altitudes in the Andes (Martinez, 1993). It is found at virtually all altitudes on Marion Island (Huntley, 1972) and is the dominant species in fellfield habitat, where several species have been recorded growing epiphytically on it (Huntley, 1972; McGeoch et al., 2008). It has been suggested to play an important role in ecological succession by colonising loose and newly exposed substrates (Huntley, 1972; Frenot et al., 1998), thereby increasing slope stability and improving substrate quality (Frenot et al., 1998; Barendse and

Chown, 2001). These wind-protected “nutrient islands” create important microhabitats (Barendse and Chown, 2001) for less resilient plant species, as well as microarthropod communities (see Huntley, 1972; Hugo et al., 2004), especially in harsh climates, such as the cold, wind-subjected, low-nutrient fellfield complexes of Marion Island (Gremmen, 1981; Smith and Steenkamp, 2001). In addition, through altering sediment movement patterns, *A. selago* has been suggested to influence geomorphological processes (see Holness and Boelhouwers, 1998; Boelhouwers et al., 2000 for examples) and as such provides an excellent platform for biogeomorphological research.

Continued warming and drying under current climate change scenarios on the island have been predicted to impact negatively on *A. selago* integrity (le Roux et al., 2005). In addition, invasive plant species often seem to be favoured by climate change in cold regions (Kennedy, 1995; Chown et al., 1998; Frenot et al., 2001). *Azorella selago* has been shown to be a poor competitor, being outcompeted by more resilient species at lower altitudes (Rautenbach, 2007). Increases in the number and aerial cover of invasive plant species would therefore likely have negative impacts on cushion numbers and integrity. Lastly, introduced house mice (*Mus musculus*), which also seem to be favoured by warming and drying (see Chown and Smith, 1993; Bergstrom and Chown, 1999) have led to detrimental effects on *A. selago* vitality (Phiri et al., 2008). As a result of these complex interactions, coupled with a poor understanding of biogeomorphological interactions, the total effect of disturbances, such as climate change, on this keystone sub-Antarctic species is difficult to predict.

## **Thesis outline**

This thesis aimed to improve understanding of the interactions between *Azorella selago* and its abiotic environment, specifically geomorphological processes and properties, on Marion Island. Although all of the chapters aim to integrate ecological and geomorphological principles, chapters two, three and six, have more of a geomorphological focus, while chapters four and five are written more from an ecological perspective. The final data chapter, chapter seven, provides a synthesis on the integration of geomorphological and ecological principles in biogeomorphology. The motivation for this chapter originated from experiences gained during the PhD.

- Chapters two and three focus on the effect of *Azorella* cushions on the surrounding geomorphological processes and landforms. In chapter two sediment particle size distributions around *Azorella* cushions are investigated and the potential role of sediment distribution in *Azorella*-banked terrace formation is discussed.

- In chapter three the fine scale variability in soil microclimate surrounding *A. selago* cushions is examined. Fine scale temperature differences around *Azorella* cushions and a relatively mild frost climate, indicating that needle ice is capable of forming above previously suggested temperatures of -2°C (Outcalt, 1971), are demonstrated.
- The focus in chapters four and five changes from the effect of *Azorella* cushions on the surrounding geomorphology to the effect of the abiotic surroundings on *A.selago*, specifically seedlings. Chapter four focuses on the potential of *A. selago* cushions to act as “safe sites” for seedlings of both its own kind and those of the grass, *Agrostis magellanica*. This potential nurse effect is compared to that provided by rocks.
- In chapter five determinants of *A. selago* seedling distributions and abundance, such as altitude and substrate cover, are examined. Seedling abundance and *A. selago* size class distributions are shown to be to a large extent dependent on unaccounted site specific properties.
- In chapter six it is shown that, in addition to affecting the surrounding geomorphological processes and landforms (chapters two and three), *Azorella* cushions also affect geomorphological measuring techniques. The chapter explores the potential of the cosmogenic isotope <sup>10</sup>Be as a geomorphological tracing/dating tool in fellfield habitats. By measuring <sup>10</sup>Be concentrations underneath an *A. selago* cushion and in the surrounding soil it is shown that the cushion effectively intercepted the isotope, thereby potentially affecting interpretation of landscape evolution based on <sup>10</sup>Be concentrations.
- Chapter seven provides an assessment of the challenges that integration of geomorphological and ecological principles and approaches presented. It specifically focusses on the use of statistics and significance testing between the fields, but also provides recommendations for facilitation of future integrated biogeomorphological research.
- Finally, chapter eight provides a brief synthesis of the main conclusions of the thesis chapters.

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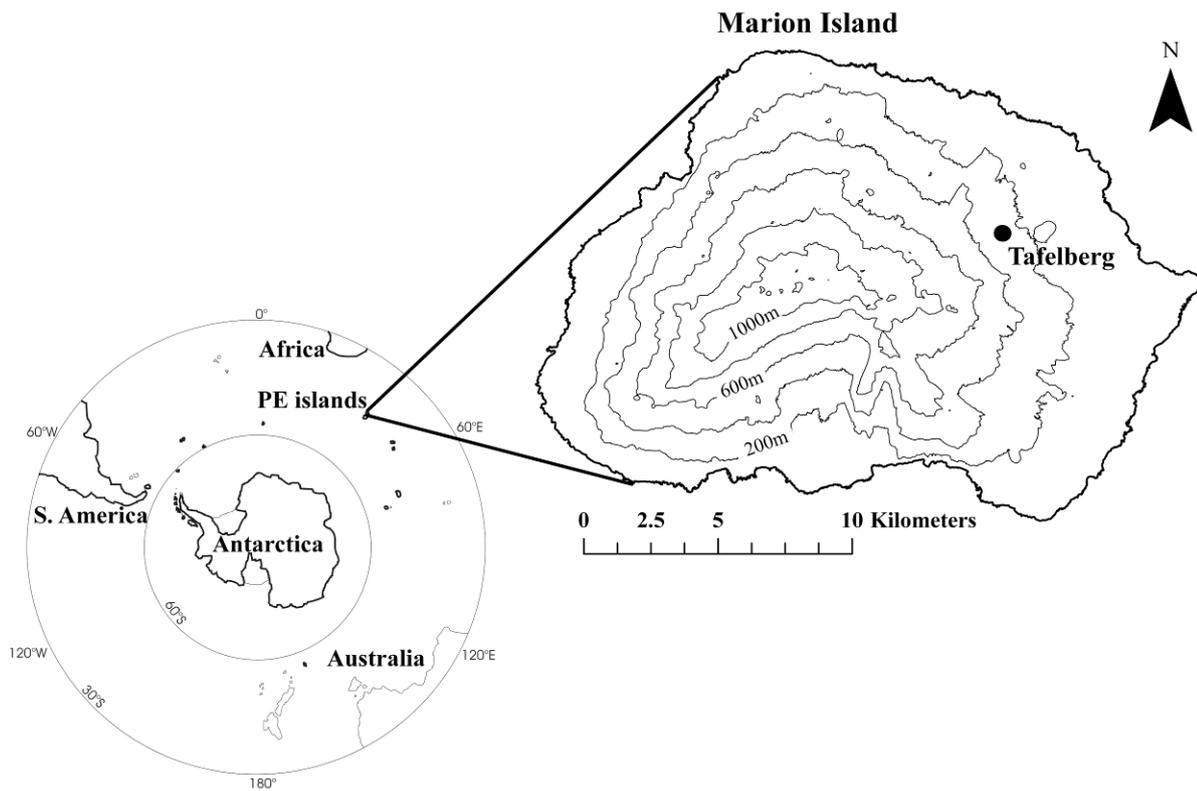


Figure 1. Location of the Prince Edward (PE) islands within the sub-Antarctic with a more detailed inset of Marion Island. Contour lines are at 200 m intervals. Field sites for chapters two, three and six were located at Tafelberg, which is indicated on the map.



Figure 2. *Azorella selago* Hook. (Apiaceae) on grey lava substrate on Marion Island. The ruler in the photograph is 15 cm long and the arrow is pointing downslope. Photograph courtesy of Jan Boelhouwers.

## Chapter 2 – Interactions between *Azorella selago* and surface sediment transport \*

### Introduction

By interacting with and changing their immediate surroundings, plants (especially pioneer species) play an important role in landscape evolution in severe environments (Heilbronn and Walton, 1984; Pérez, 1989; Chapin et al., 1994). For example, by providing protection and insulation (Pérez, 1989) and acting as physical barriers in sediment movement pathways (Pérez, 1987a), plants alter bare soil chemical and physical conditions, affecting soil frost conditions (Pérez, 1987b; 1989), slope stability (Heilbronn and Walton, 1984; Frenot et al., 1998) and ultimately sediment movement processes and patterns (Holness and Boelhouwers, 1998; Boelhouwers et al., 2000). Although plants affect their abiotic surroundings, plant spatial distributions and growth forms are also affected by the geomorphological conditions surrounding them, such as suitable, stable substrate, needed for seedling germination. In this regard, plant–landform interactions of pioneer plant species in periglacial environments are especially important, as pioneer plants colonise loose slopes and influence sediment movement and sorting (Huntley, 1972; Heilbronn and Walton, 1984; Frenot et al., 1998), thereby playing an important role in providing suitable substrates for colonisation by other plant species. The necessity of monitoring plant–landform interactions in periglacial regions has been recognised, especially in the light of global climate change (e.g. Cannone et al., 2004). Although geomorphological processes and landforms influence the way in which the biotic environment will function in a changing environment, plant growth forms will also influence the way in which landscapes respond to global climate change.

On sub-Antarctic Marion Island an important interaction exists between the geomorphology of fellfield landscapes and the dominant vascular plant species, *Azorella selago* Hook. (Apiaceae). For example, by colonising loose and exposed substrates (Huntley, 1972; Frenot et al., 1998), these cushion plants affect slope stability and improve substrate nutrient and moisture status (Huntley, 1971; Holness, 2004; Smith and Mucina, 2006). Furthermore, *Azorella* cushions are considered to influence frost creep and other sediment movement processes and play an important role in the formation of terraces and lobes (Holness and Boelhouwers, 1998; Boelhouwers et al., 2003). Marion Island is experiencing rapid and significant large-scale climate change (Smith, 2002; le Roux and McGeoch, 2008a) and a thorough understanding of these biogeomorphological

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interactions is thus especially important. A number of studies has examined the relationships between plants and the physical processes and landforms surrounding them in Arctic and temperate alpine regions (e.g. Sigafos, 1952; Anderson and Bliss, 1998; Cannone et al., 2004); areas which experience permafrost or seasonal freezing. Parallel studies have also been conducted in diurnal frost environments, but these have mainly focussed on tropical alpine mountain systems (Mark et al., 2001; Pérez, 2002; Brancaleoni et al., 2003; Cavieres et al., 2007). Although mid-latitude marine environments, such as the islands of the sub-Antarctic, also experience diurnal frost cycles, these frost environments differ markedly from those of tropical alpine mountain systems. For example, on Marion Island, small, diurnal and seasonal temperature ranges of 1.9°C and 3.6°C respectively (Smith, 2002) are conducive to rapid transitions in freeze/thaw cycle frequency and intensity under changing temperature regimes that render them especially sensitive to climate change (Boelhouwers, 2003; Boelhouwers et al., 2003).

In addition, most studies of biogeomorphological interactions in periglacial environments have looked at how geomorphological processes influence plant spatial distributions (Anderson and Bliss, 1998; Pérez, 2002), community assemblages (Kozłowska and Rączkowska, 2002; Cannone et al., 2004) or plant morphology in stressed environments (Jonasson and Callaghan, 1992). Comparatively few studies have considered the effects of plants on substrate movement and the resulting grain size sorting and distributions in diurnal frost environments. Notable exceptions are studies on vegetation-banked terrace formation on sub-Antarctic Macquarie Island (Taylor, 1955; Selkirk, 1998) as well as studies on needle ice activity in the Venezuelan Andes (Pérez, 1987a,b). These studies often found a downslope coarsening in grain size towards plants or rocks that act as physical obstructions in sediment movement pathways (Pérez, 1987a,b; Selkirk, 1998). Determining grain size and grain size distribution is important, because (1) these factors affect the inherent properties of the sediment (such as erosion and frost susceptibility), (2) they give an indication of the origin of the sediment and (3) they also determine the mechanisms by which the sediment can be transported (Goossens, 2008). Therefore, directional differences in grain size characteristics could lead to directional differences in erosion, needle ice activity and subsequent frost heave and creep, which in turn are partially responsible for driving plant growth patterns in fellfield-dominated areas (Lynch and Kirkpatrick, 1995). In addition, the particle size of substrates has been shown to affect seed entrapment (e.g. Chambers et al., 1991) and subsequent seedling establishment and survival (e.g. Jumpponen et al., 1999; Chambers, 2001; Kleier and Rundel, 2004). *Azorella selago* is widespread across the sub-Antarctic (Huntley, 1972; Frenot et al., 1993) and the genus *Azorella* is native not only to the Southern Ocean islands, but also to tropical alpine regions of South America (Martinez, 1993). As a consequence, grain size and grain size sorting around *Azorella* cushions are

potentially important determinants of landscape evolution, not only on Marion Island, but across a far broader geographic range.

On Marion Island *A. selago* cushions are found in a variety of shapes including circular, elongated and irregular. Large cushions have been found to spread out laterally and coalesce, forming almost continuous carpets in some locations (Huntley, 1972; Mortimer et al., 2008). Plant cover patterns have demonstrated that established plants facilitate the presence of other plant species by providing protection against downslope moving particles (le Roux and McGeoch, 2008b). In this regard, larger and more elongated cushions are expected to obstruct sediment particles moving downslope more than smaller or more rounded cushions. This is expected to result in larger differences in grain size characteristics between up- and downslope cushion sides for elongated cushions. Similarly, cushions growing at angles more perpendicular to the slope are expected to obstruct downslope moving particles more than cushions growing parallel to the slope. Furthermore, the shape of cushion plants in general has been shown to be related to cushion size, with small cushions being rounder and shapes becoming progressively irregular as the cushions grow (Pyšek and Liška, 1991). This relationship has also been observed for *A. selago* on Marion Island (Huntley, 1972), although it has never been formally quantified.

Traditionally, grain size is determined through sieving, sedimentation experiments and direct measurement, depending on the size range of particles (Folk, 1966). These techniques all require taking a representative sample and subsequent physical analyses of the sample, and are, as a result, both time-consuming and destructive. As an alternative, photogrammetric techniques have been applied for the quantification of grain size parameters since at least the 1970s, especially in river channel hydraulics (Adams, 1979; Ibbeken and Schleyer, 1986; Whitman et al., 2003; Graham et al., 2005a). Many previous photogrammetric studies of sediment grain sizes have involved manually outlining sediment grains on the digital image (Ibbeken and Schleyer, 1986; Ibbeken et al., 1998; Whitman et al., 2003), although, more recently, the focus of photogrammetric studies has been on automating grain detection and data generation (Butler et al., 2001; Sime and Ferguson, 2003; Graham et al., 2005a). In protected, relatively undisturbed areas, such as Marion Island (which has Special Nature Reserve conservation status) it is desirable to use techniques such as these photogrammetric methods as they minimise disturbance to the environment. Therefore, to increase the understanding of the two-way interactions of *Azorella* plants and substrate movement and sorting, the directionality in grain size distribution of sediment surrounding *Azorella* cushions of varying size and shape was quantified, using image analyses. Specific focus was on (1) relationships between cushion size and elongation on flat and sloping terrains, (2) relationships between cushion elongation and growth directionality on flat and sloping terrains, (3) differences in grain size characteristics between up-and downslope cushion sides and (4) relationships between

cushion characteristics and directional differences (up-and downslope of a cushion) in grain size characteristics. Finally, similarities and differences in plant-landform interactions between tropical alpine mountain systems and mid-latitude maritime environments, two distinct diurnal frost environments, are highlighted.

### **Study area and site selection**

Marion Island (46° 54' S, 37° 45' E), one of two islands constituting the Prince Edward Islands Group, is located in the southern Indian Ocean. The island constitutes the summit of a shield volcano and has an area of approximately 290 km<sup>2</sup> (Verwoerd, 1971; de Villiers, 1976). Two lava successions, an older sequence of grey lava underneath a younger sequence of black lava, are found on the island (Verwoerd, 1971). Striated, grooved and smoothed features on older grey lava provide evidence of a period of glaciation in between the two lava successions (Verwoerd, 1971; Hall, 2004). The island has an exceptionally maritime climate, with a mean annual air temperature of just over 6°C (Smith, 2002) and a mean annual soil temperature at the study sites of 4.7°C (5 cm depth) (Chapter 3). Both annual and diurnal temperature ranges are low (3.6 and 1.9°C respectively; Smith, 2002), giving rise to diurnal frost cycles (Holness, 2001a) and frequent needle ice formation (Boelhouwers et al., 2000, 2003; Holness, 2003). The average annual precipitation during the 1990s was just over 2000 mm (le Roux and McGeoch, 2008a), with short-lived snow cover in the study area of approximately 30 days per year (Holness, 2001a). Furthermore, a high degree of cloudiness and predominantly north-western gale force winds occur throughout the year (Schulze, 1971).

Sites for this study were selected from Tafelberg, on the eastern side of the island, at approximately 300 m a.s.l. (Chapter 1, Figure 1). The Tafelberg area is underlain by pre-glacial grey basalts. Surface material consists of a matrix-supported, unsorted glacial till and experiences approximately 60 diurnal frost cycles per year in the upper 5 cm of soil (Holness, 2001a; Boelhouwers et al., 2003). Frequent needle ice formation results in frost heave and creep of up to 20 cm/year (Boelhouwers et al., 2000; Holness, 2001a; Boelhouwers et al., 2003; Holness, 2003).

Three sites were selected within 300 m from one another, one from a relatively flat basin (4–5° slope angle) (Figure 1a) and the other two from moderately sloping terrains (7–12° slope angles for both sites), with easterly (Figure 1b) and south-easterly (Figure 1c) aspects respectively. These sites are referred to as the flat basin (FB), easterly slope (SE) and south-easterly slope (SSE). The geomorphology of the sites reflects the periglacial nature of the terrain. Relict solifluction lobes and terraces with risers of up to 0.5 m are present on sloping ground (see background slopes in Figure 1a) (Holness and Boelhouwers, 1998; Boelhouwers et al., 2008). Upfreezing of clasts from the till cover is evident by their absence down to a depth of approximately 20 cm, and reflects a phase of

deeper soil frost penetration than at present. Upfreezing and surface wash of fines explains the stony surface layer (Figure 1). Present-day soil frost action results in patterned ground in the form of miniature sorted stripes with stripe widths of 5-10 cm (Boelhouwers et al., 2003). *Azorella selago*-banked terraces are common on sloping ground (foreground of Figure 1a and whole of Figure 1b). Distinction between currently active and relict terraces cannot be based on morphology alone, but terraces on the SE and SSE sites are considered of recent origin based on current mobility of surface materials (Holness, 2001a). On the flat basin site water ponding after intensive or long-duration rainfall suggests a shallow substrate and frequent surface runoff. This is further evidenced by the localised surface deposition of well-sorted fine gravel.

## **Methods**

### Field procedure and image selection

Photographs of *A. selago* cushions of various shapes and surrounding sediment were taken at the three sites, using a digital camera (Nikon D40, 28 mm, 6.4 MP). Each photograph contained one cushion and was taken vertically as far as possible to avoid image distortion. A ruler, with an arrow pointing in the downslope direction, was placed next to the cushions as a scale bar. Images in which individual grains could not be distinguished and images where the cushion outlines were not clear were excluded from analyses. Two image analysis approaches were used, depending on the quality of the image. Images suitable for digital image analyses were analysed using the Digital Gravelometer software 1.0, LUEL (Graham et al., 2005a,b). The digital image analysis dataset consisted mostly of round cushions, as these tended to be smaller and therefore easier to photograph vertically. These images were used to infer basic directionality patterns in grain size surrounding cushions. The second approach was used for images where the angle of photography was oblique and images that were too dark to distinguish all individual grains. These images were rejected for digital image analyses, but were considered suitable for a subjective visual estimation approach. These images were mostly of elongated cushions and were used to relate cushion properties, such as elongation and growth angle, to directional differences in grain size. For digital image analyses ten images were randomly selected from the flat basin and south-easterly slope, and all eight images from the easterly slope were used. For the visual estimation approach eight photographs for the flat basin, 16 for the easterly slope and 12 for the south-easterly slope were available.

### Cushion size and shape analyses

All selected images were used to analyse cushion size and shape. Lengths of the cushion major axis (largest diameter) and minor axis (longest axis perpendicular to the major axis) and cushion area were measured using SigmaScan Pro version 5.0, SPSS. Cushion major/minor axis ratios were calculated as a measure of cushion elongation. The smallest angle between the major axis of the cushion and a line parallel to the downslope direction was measured and defined as the “growth angle” of the cushion. Analysis of Variance (ANOVA) was used to compare cushion characteristics between sites for the two datasets (digital analysis and visual estimation) separately. To determine the relationship between cushion elongation and size, Pearson correlation coefficients (for the two datasets combined) were calculated between the major/minor ratio and cushion area ( $n = 64$ ). The same was done to determine relationships between cushion elongation and growth angle, using the major/minor ratio and angle.

### Digital image analyses procedure

For each image, squares were cropped from the whole image on the upslope, downslope and remaining two opposing sides of the cushion, as close to the cushion edge as possible (Figure 2). These sides are referred to as left and right, with upslope being at the top of the image. A  $30 \times 30$  cm square was deemed suitably large to pick up differences in grain size between squares. For some images squares of this size did not fit into the photograph, as the cushion was closer than 30 cm from the image edge. In this case a  $15 \times 15$  cm square was used.

A common problem with automated identification of sediment grains is uneven lighting and shading as a result of different elevations of particles (Graham et al., 2005b). The shadow/highlight function in Adobe Photoshop CS3 was used to adjust image shadow intensities and improve grain identification by the Digital Gravelometer. Image resolution was increased artificially from 120 to 720 pixels/cm using a bicubic resampling interpolation method in Adobe Photoshop CS3 to decrease the smallest detectable particle size from 12 to 2 mm. Particles with *b*-axes smaller than 2 mm were too small to be accurately detectable. To ensure that the resampled images were true to the original, each resampled image was carefully studied and compared to the original. Despite these adjustments, grain identification by the Digital Gravelometer was not completely satisfactory due to shadow effects and differences in texture and colour within individual grains. Therefore, the resulting black and white output images of the Digital Gravelometer were manually adjusted using Photoshop (Figure 3). The manual adjustment of grain outlines and thereby the individual study of each image ensured accurate and most time-effective grain identification.

The *a*- and *b*-axes of all identified grains, and the number of particles identified, were measured using SigmaScan Pro version 5.0, SPSS. All particle sizes reported are based on the *b*-axis value. The number of particles was corrected for the two different square sizes by dividing the number of particles in the 30 × 30 cm squares by four. In addition, square size was included as a variable in the statistical analyses to assess and control for any effect thereof. To determine actual differences in grain sizes, common statistical measures were calculated for each square, including the graphical statistics of Folk and Ward (1957). To compare grain size characteristics between sites, generalised linear models (GLM) were used. Data were normally distributed after log<sub>10</sub>-transformation. One outlier was removed from the data set. ANOVA was used to identify differences in grain size characteristics between cushion sides at different sites.

### Visual estimation of particle sizes

A 15 x 15 cm square was cropped out of the upslope, downslope, and left and right sides of cushions. The percentage area covered by particles falling into each of seven different size classes was visually estimated using the following Wentworth size classes: 1) cobble (64-256 mm), 2) very coarse gravel (32-64 mm), 3) coarse gravel (16-32 mm), 4) medium gravel (8-16 mm), 5) fine gravel (4-8 mm), 6) very fine gravel (2-4 mm) and 7) < 2 mm (sand, silt and clay). Weighted mean particle sizes were calculated by multiplying the fraction of particles in each size class by the median mm value of the size class (Wentworth, 1922) and subsequently adding the values obtained for all size classes.

To determine whether particle size composition was related to cushion sides (upslope, downslope, and lateral), multivariate analysis were used on the visual estimation images (all three sites; n = 144 images). Site was included as a co-variable. Left and right cushion sides were grouped together and renamed “lateral” to simplify interpretation and because there was no a priori reason for differences in particle size composition between the two sides. The digital analysis supported this assumption. Sample heterogeneity and outliers were assessed through Detrended Correspondence Analysis (DCA) (Lepš and Šmilauer, 1999). As the DCA showed no single evident environmental gradient, a Canonical Correspondence Analysis was justified (CCA) (Lepš and Šmilauer, 1999). The CCA was used to quantify the contribution of the environmental variables (cushion sides) to overall variation in particle size distribution using CANOCO 4.5. A Monte Carlo permutation test (1000 permutations,  $p < 0.05$ , with variation inflation factors  $< 10$ ; Gross, 2003) with forward selection of environmental variables was used to determine which of the variables contributed significantly to explaining grain size composition (Lepš and Šmilauer, 1999). These CCA results were interpreted using a samples-by-environmental-variables biplot.

To determine whether differences between up- and downslope particle sizes changed with cushion elongation or growth angle, Pearson correlation coefficients were calculated using the differences between upslope and downslope particle sizes (up-down) and cushion major/minor ratio and angle ( $n = 34$ ).

## **Results**

### Cushion size and shape

Cushion major axes ranged from approximately 330 mm to 2.3 m, whereas cushion major/minor ratios ranged from just over 1 to almost 3 (Tables 1 and 2). Cushion growth angles ranged from almost parallel to the slope to almost perpendicular to the slope (Table 2). No significant differences were found in any of the cushion parameters between the three sites for the digital analysis dataset (all  $p > 0.05$ ). For the visual estimation dataset cushion major axis ( $F = 6.84$ ,  $df = 2$ ,  $p = 0.003$ ), minor axis ( $F = 8.73$ ,  $df = 2$ ,  $p < 0.001$ ) and area ( $F = 9.40$ ,  $df = 2$ ,  $p < 0.001$ ) were significantly larger at the SE site than at the FB or SSE sites. Cushion major/minor ratio and growth angle did not differ significantly between any of the three sites (all  $p > 0.05$ ).

A significant ( $p < 0.05$ ) positive correlation was found between cushion size and cushion elongation when grouping data together for all three sites, with larger cushions becoming more elongated (Figure 4). This relationship was strongest for the SE site and weakest for the FB.

A weak, but significant ( $r = 0.32$ ,  $p < 0.05$ ,  $n = 64$ ) positive correlation was found between cushion elongation and the angle that cushions were growing in relative to the slope, when grouping data together for all three sites (data not presented). However, when looking at the sites individually, this relationship was only significant for the SSE site.

### Digital image analyses procedure

#### *Between-site variation*

Mean grain size varied between fine and medium gravel (range: very fine gravel (-1 to -2  $\phi$ ) to very coarse gravel (-5 to -6  $\phi$ )) (Table 3). According to Folk and Ward's sorting index mean particle sorting was poor at all three sites (range: poorly ( $\sigma = 1$  to 2) to moderately sorted ( $\sigma = 0.5$  to 1)) (Table 3). Most distributions had a negative skew indicating a tail of coarser particles. Kurtosis values were in the range platykurtic to very platykurtic, indicating that grains were relatively better sorted in the extremes of the distribution than in the central area. Mean grain size (Wald  $X^2 = 42.32$ ,

df = 2,  $p < 0.05$ ) and variance in grain size (Wald  $X^2 = 26.58$ , df = 2,  $p < 0.05$ ) was significantly higher and the number of particles (Wald  $X^2 = 42.18$ , df = 2,  $p < 0.05$ ) was lower at the easterly slope than at the flat basin and the south-easterly slope (Table 3). Grain size distributions at the flat basin were found to be significantly more negatively skewed (Wald  $X^2 = 23.09$ , df = 2,  $p < 0.05$ ) and the grains in the extremes were less well-sorted relative to the centre (Wald  $X^2 = 24.47$ , df = 2,  $p < 0.05$ ) than at the other two sites (Table 3).

#### *Within-site variation*

At the FB mean grain size ( $F_{3, 26} = 3.48$ ,  $p = 0.03$ ) and variance in grain size ( $F_{3, 26} = 4.26$ ,  $p = 0.01$ ) was significantly greater upslope of *Azorella* cushions than downslope (Figure 5a,b). By contrast, the number of particles ( $F_{3, 26} = 4.93$ ,  $p = 0.01$ ) was greater on the downslope side of cushions than on the upslope side (Figure 5c). Grain sizes, variance and particle numbers on left and right cushion sides were intermediate to those on up- and downslope cushion sides (Figure 5a-c). In addition, no significant differences in skew and kurtosis were found between cushion sides at this site (data not presented). Grid size, i.e. whether  $15 \times 15$  cm grids or  $30 \times 30$  cm grids were used, did not have a significant effect on either mean particle size or variance in particle size at this site. At the SE site downslope grains were found to be significantly smaller than both upslope and left side grains ( $F_{3, 20} = 4.14$ ,  $p = 0.02$ ) (Figure 5a). Again the size of squares used did not have an effect on mean particle size or variance in particle size. No significant differences were found in variance in grain size, particle numbers, skew or kurtosis between cushion sides at this site. No significant differences in mean grain sizes, variance, numbers of particles, skew or kurtosis were observed between cushion sides at the SSE site (Figure 5a-c).

#### Visual estimation of particle sizes

A clear difference in particle size composition between the variables downslope and the other directions (upslope and lateral) was apparent from their clear separation on the first axis of the CCA diagram (Figure 6). After accounting for the effects of site, downslope was found to contribute significantly ( $F = 5.21$ ,  $p = 0.002$ ) towards explaining grain size composition, being associated with the two smallest particle sizes ( $< 2$ mm and very fine gravel). However, upslope and lateral were not found to contribute significantly towards explaining particle size composition, i.e. particle size composition downslope of cushions differed significantly from those upslope and on lateral cushion sides, but upslope and lateral did not differ significantly from one another.

No significant correlations were found between directional differences (upslope and downslope) in grain size and the cushion major/minor ratio ( $r = -0.05$ ,  $n = 34$ ,  $p = 0.78$ ) or cushion angle ( $r = -0.04$ ,  $n = 34$ ,  $p = 0.82$ ) when grouping data for the three sites together. No significant correlations were found for individual sites either.

## Discussion

The shape of cushion plant species has been related to cushion size, with small cushions being rounder and shapes becoming progressively irregular as the cushions grow (Pyšek and Liška, 1991). Although this relationship has also been observed for *A. selago* (Huntley, 1972), it has not yet been quantified. The results from this study on cushion size and shape suggest that as cushions become larger, they become more elongated, confirming general field observations. During a previous field survey, it was very hard to find either large, round cushions or small, elongated cushions. Rounder, smaller cushions are found growing at all angles to the slope. As cushions become larger and more elongated, growth is orientated mainly perpendicular to the slope. For example, all of the cushions with major/minor ratios larger than 2 ( $\log_{10}$ -transformed value = 0.3) were found at slope angles of  $\geq 30^\circ$ . Except for one cushion, with a major/minor ratio of 2.74, cushions at the FB site did not grow quite as elongate as cushions from the two slope sites, i.e. slope conditions apparently facilitate the growth of elongated cushions. An important distinction between the FB site and the slope sites is the poor drainage and high water table at the FB. The ground water table reached the ground surface repeatedly during the fieldwork period and water was often found to dam up behind *Azorella* cushions. In contrast, the sloping and micro-stepped topography at the two slope sites provides better local drainage, possibly facilitating directional cushion growth at these sites. This is particularly the case at terraces where coarser material has accumulated on upslope cushion sides. Wind exposure or directionality could also explain differences in cushion growth patterns between sites. Taylor (1955) emphasised the importance of wind in terrace formation on Macquarie Island. He found terraces to be orientated in such a way that vegetation always received least wind. Although the effect of wind on cushion growth was not formally assessed in this study, it can certainly not be excluded as a contributing factor to growth directionality patterns.

For all three sites particles on downslope cushion sides were smaller than those of upslope cushion sides (although this was only significant for the FB and SE site). This is also supported by the visual estimation dataset, where downslope is associated with smaller particle size classes than upslope or lateral cushion sides. Similarly, although not always significant, there were consistently more particles and better sorted particles on downslope cushion sides. Reports on the banking up of

downslope moving particles on upslope sides of larger boulders as well as vegetation, which act as sediment obstructions, are numerous for periglacial environments (Pérez, 1987a; Holness and Boelhouwers, 1998; Selkirk, 1998; Mark et al., 2001; Holness, 2004). Movement of these particles is often ascribed to needle ice heaving, which lifts isolated stones from a matrix of finer particles, and subsequent downslope transportation of heaved particles by frost creep (Pérez, 1987a,b; Lawler, 1993; Holness, 2004). Needle ice is characteristic of brief, but frequent freeze-thaw cycles (Troll, 1958) and is favoured by soils with high silt content (Meentemeyer and Zippin, 1981), such as the gravely loams of fellfield habitats (Smith, 1977; Gremmen, 1981). Needle ice has also been identified as an important geomorphological agent on Marion Island (Hall, 1979; Boelhouwers et al., 2003; Holness, 2003) and probably also plays a dominant role in facilitating downslope particle transportation through frost heave and creep in the study area. The vertical tilting of platy stones in the study area, often showing imbrication patterns, is a direct indicator of the role of frost heave and creep (Benedict, 1970; Washburn, 1979; Holness and Boelhouwers, 1998). Preferential downslope movement of coarser sediment through frost creep (Benedict, 1976; Holness, 2001a; Holness, 2004) results in these clasts accumulating against *Azorella* cushions. This accumulation of coarser particles upslope of cushions results in a depletion of coarser clasts on downslope sides of cushions.

The decrease in particle sorting towards upslope cushion sides is a likely consequence of a negative feedback. As downslope transport slows down due to obstruction and material becomes coarser and thus better drained, frost penetration is no longer sufficient to sustain upheaving and subsequent frost creep, resulting in less sorted material. Contrary to frost creep-dominant movement, where the stones move faster than the surrounding soil matrix, solifluction, where the soil matrix moves and carries stones with it, results in less sorted particles (Benedict, 1970). This may in part explain the less sorted material at the SE site, compared to the other two sites. It is possible that slope movement at this site is presently, or was in the past, dominated by solifluction rather than needle ice creep. Solifluction requires frost penetration beyond the level for needle ice growth (deeper than approximately 5 cm at the altitude of the study sites) and thus tends to displace a deeper layer of soil (Boelhouwers et al., 2003). This process results in larger steps than those formed through needle ice alone. These larger steps then create larger, protected microhabitats which allow the growth of larger *Azorella* cushions (as seen at the SE site) and their lateral spreading along a pre-existing riser. A preferential occurrence of solifluction at the SE site is not readily explained under current climate conditions, but the terraces may be inactive forms, with secondary needle ice activity maintaining/modifying forms under the present climate, as observed elsewhere on the island at similar altitude (Holness and Boelhouwers, 1998).

Terrace formation is often found commencing across slopes in diurnal frost environments, such as the sub-Antarctic islands (Taylor, 1955; Holness and Boelhouwers, 1998; Holness, 2001b)

and tropical alpine mountain systems (Pérez, 1992; Mark et al., 2001), often in association with vegetation (Holness and Boelhouwers, 1998; Selkirk, 1998). The exact mechanisms of terrace formation are still debated (Taylor, 1955; Löffler, 1983; Selkirk, 1998) and it is still unclear whether *Azorella* cushions exploit an already existing stable terrace riser or whether the riser develops in interaction with the laterally spreading *Azorella* cushion. In all likelihood, both scenarios are possible and may operate synergistically. Initial downslope changes in soil conditions, caused by grain size sorting through frost creep, or any other frost-protected location, may result in locally stable habitats for *Azorella* seedling establishment and lateral cushion growth on slopes. As the cushion grows, its role as a local obstacle to sediment displacement increases and an upslope–downslope soil textural differentiation develops. With time the cushions spread laterally along the terrace riser and coalesce with neighbouring cushions (Mortimer et al., 2008). Selkirk (1998) describes gravel chutes as areas in between terraces or cushions where stone transport is faster. Where the vegetation is able to grow faster than the stone encroachment, stable terraces are able to form. Similarly, Pérez (1987a) reports a higher rate of particle movement on the sides of large boulders, compared to up- or downslope sides of boulders. This accelerated particle movement on lateral cushion sides could possibly contribute towards cushion damage and turf exfoliation caused by needle ice (Pérez, 1992). These zones of instability and increased particle movement rates initially limit the lateral extent of terrace development. However, over time coarse material at the base of a chute starts blocking material, which imbricates against the larger less mobile material, creating a stable coarse slope segment.

Mechanisms of sediment sorting probably differ somewhat between the two slope sites and the FB. At the FB, a very uniform fine gravel deposit was often seen on downslope cushion sides, with upslope cushion sides containing larger, less uniform particles. Furthermore, although particle sorting was higher on downslope cushion sides than upslope cushion sides at all three sites, the FB was the only site where this difference was significant. Pérez (1987a, 1993) describes fine earth flags below rock dams in the Venezuelan Andes as “elongated downwards-tapering areas where coarse clasts are missing” and presents the phenomena as evidence of needle ice activity. Holness (2004) also reported this feature from cinder cones on Marion Island, again in an area dominated by needle ice activity. It is interesting to note that both authors report these features exclusively from slopes, whereas it was seen exclusively on the FB in this study. A likely explanation is that sorting to the extent seen around these cushions at the FB is not the result of needle ice activity and frost creep alone. Frost creep by needle ice probably plays a dominant role in slowly moving frost heaved surface clasts across the low-angled local surface. However, the cushion (or large immobile block) barrier restricts clast movement and results in clast depletion downslope of the barrier. Surface wash across the exposed bare soil will then result in the washing-in of small, well-sorted

gravel. Selkirk (1998) emphasises the importance of water for gravel movement and sorting around terraces on Macquarie Island. The importance of water transport on Marion Island, which receives more than double the amount of rainfall as Macquarie, should certainly not be overlooked. It is possible that on slopes the flow velocity is too high for the washed-in gravel particles to settle and therefore this feature is not found there. The poor drainage conditions and high water table at the FB compared to the slope sites further supports the notion that surface wash plays an important role in particle settling and grain size sorting at this site.

The correlation analyses did not pick up any relationships between cushion growth angle or shape and differences between up- and downslope particle sizes, as expected. The effect of cushion growth angle on differences between upslope and downslope particle sizes could not be distinguished from cushion shape and therefore size, as there were no elongated cushions growing parallel to the slope. Rounder, smaller cushions, growing parallel to slopes are apparently equally effective at trapping particles and causing grain size sorting as their larger, more elongated counterparts, which grow at angles more perpendicular to the slope.

The fact that downslope particles were consistently smaller than upslope particles has important implications for microenvironmental conditions, such as drainage, frost susceptibility and needle ice growth as well as cushion growth and die-back patterns. As stones get stacked they alter the microclimate, so that frost cannot penetrate through the coarse layer to the more fine, frost susceptible soil beneath, as a result of the superficial frost penetration of 5 to 10 cm at this altitude (Boelhouwers et al., 2003). Upslope particles will therefore be more stable and their heave rates smaller, whereas the potential for needle ice creep and surface disturbance will be larger on downslope cushion sides, creating a positive feedback to terrace development. Downslope cushion sides probably also develop a higher water retention capacity, as water can easily run through upslope blocks. This means that downslope sides have more potential for ice crystal growth as there is more water, increasing the potential for needle ice creep and surface disturbance on these sides. This in turn would facilitate terrace exfoliation on downslope cushion sides, as is often observed in the field. Rising temperatures and decreasing rainfall on Marion Island (Smith, 2002; le Roux and McGeoch, 2008a) could lead to decreasing occurrences of needle ice and related sorting around cushions. On the other hand, predicted decreasing cloud cover (Smith and Steenkamp, 1990) and snow insulation could result in an increase in the number of freeze-thaw days and the spatial variability thereof (Boelhouwers et al., 2007) and increasing importance of needle ice related sorting patterns. Therefore, the future implications of climate change for directional grain size sorting patterns and consequent sediment properties are not yet fully understood. To be able to predict landscape evolution and the future of grain size sorting patterns, sediment properties and

terrace development in the light of a changing climate, continuing studies furthering our understanding of plant–landform interactions are essential.

## Conclusions

This study aimed to assess the relationships between *A. selago* cushion size, shape and the angle that cushions grow at, relative to the slope. As expected, *A. selago* cushions become more elongated and tend to grow more perpendicular to the slope as they become larger. In addition, this study aimed to explore sediment particle size distributions around *A. selago* cushions. In this regard, the research findings demonstrate a distinction between particle size classes on upslope and downslope cushion sides. As cushion growth commences, interactions with the surrounding sediment may lead to sediment partitioning and terrace formation, a consequence of a combination of frost-related sediment transport and *Azorella* cushions acting as sediment obstructions. These results support the hypothesis that *Azorella*-banked terrace development is a self-organising system where interactions between *Azorella* cushions and sediment movement provide important feedbacks resulting in spatially organised landscape patterns. Furthermore, results of this study regarding the role of vegetation in sediment redistribution across diurnal soil frost environments are consistent with those from other maritime mid-latitude islands and high-altitude tropical mountains.

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Table 1. Cushion parameters across the three sites for the digital analyses dataset. Values are means  $\pm$  S.E. Values in brackets indicate ranges. FB = flat basin, SE = easterly slope, SSE = south-easterly slope. No significant differences were found for these parameters between sites (ANOVA,  $p < 0.05$ ).

	Site		
	FB	SE	SSE
Slope angle (°)	4-5	7-12	7-12
Aspect	n/a	east	south-east
Number of cushions	10	8	10
Major axis (mm)	662 $\pm$ 57 (444 – 970)	570 $\pm$ 61 (328 – 906)	610 $\pm$ 46 (437 – 868)
Minor axis (mm)	550 $\pm$ 52 (360 – 857)	494 $\pm$ 60 (231 – 753)	500 $\pm$ 28 (336 – 629)
Major/minor ratio	1.21 $\pm$ 0.04 (1.09 – 1.47)	1.18 $\pm$ 0.05 (1.03 – 1.42)	1.21 $\pm$ 0.03 (1.03 – 1.38)
Area (mm <sup>2</sup> $\times$ 10 <sup>5</sup> )	2.7 $\pm$ 0.5 (1.1 – 5.8)	2.1 $\pm$ 0.5 (0.6 – 4.9)	2.2 $\pm$ 0.3 (1.1 – 3.7)
Growth angle (°)	42.5 $\pm$ 6.7 (14.8 – 80.1)	47.9 $\pm$ 8.2 (11.6 – 85.1)	51.1 $\pm$ 7.0 (21.5 – 82.4)

Table 2. Cushion parameters across the three sites for the visual estimation dataset. Values are means  $\pm$  S.E. Values in brackets indicate ranges. FB = flat basin, SE = easterly slope, SSE = south-easterly slope. Different superscripts indicate significant differences between sites (ANOVA,  $p < 0.05$ ).

	Site		
	FB	SE	SSE
Number of cushions	8	16	12
Major axis (mm)	956 $\pm$ 160 <sup>a</sup> (519 – 1924)	1476 $\pm$ 120 <sup>b</sup> (868 – 2298)	992 $\pm$ 60 <sup>a</sup> (532 – 1315)
Minor axis (mm)	555 $\pm$ 56 <sup>a</sup> (327 – 816)	712 $\pm$ 42 <sup>b</sup> (456 – 1032)	489 $\pm$ 27 <sup>a</sup> (329 – 630)
Major/minor ratio	1.69 $\pm$ 0.17 (1.28 – 2.74)	2.06 $\pm$ 0.11 (1.55 – 2.83)	2.03 $\pm$ 0.08 (1.62 – 2.44)
Area (mm <sup>2</sup> $\times$ 10 <sup>5</sup> )	3.8 $\pm$ 0.9 <sup>a</sup> (1.3 – 9.5)	7.3 $\pm$ 0.9 <sup>b</sup> (3.3 – 14.6)	3.5 $\pm$ 0.4 <sup>a</sup> (1.4 – 5.9)
Growth angle (°)	53.5 $\pm$ 9.9 (11.0 – 89.7)	53.4 $\pm$ 5.2 (5.2 – 88.0)	67.4 $\pm$ 6.7 (7.7 – 89.8)

Table 3. Grain size statistics across the three sites. Values reported are across sampling unit (cropped squares) means  $\pm$  S.E. F & W = Folk and Ward. FB = flat basin, SE = easterly slope, SSE = south-easterly slope. Different superscripts indicate significant differences between sites (GLM, all  $p < 0.05$ ).

		Site		
		FB	SE	SSE
Number of cushions		10	7	10
Number of particles		163.54 $\pm$ 27.61 <sup>a</sup>	43.24 $\pm$ 8.26 <sup>b</sup>	155.84 $\pm$ 18.13 <sup>a</sup>
Grain size	<i>b</i> -axis (mm)	12.07 $\pm$ 1.81 <sup>a</sup>	22.05 $\pm$ 2.16 <sup>b</sup>	9.44 $\pm$ 0.60 <sup>a</sup>
	<i>b</i> -axis (F&W)	-2.69 $\pm$ 0.16	-3.71 $\pm$ 0.84	-2.72 $\pm$ 0.07
	F&W category	fine gravel	medium gravel	fine gravel
Sorting index	S.D. (mm)	14.93 $\pm$ 2.16 <sup>a</sup>	22.66 $\pm$ 2.55 <sup>b</sup>	9.93 $\pm$ 0.86 <sup>a</sup>
	S.D. (F&W)	1.11 $\pm$ 0.05	1.35 $\pm$ 0.16	1.13 $\pm$ 0.03
	F&W category	poorly sorted	poorly sorted	poorly sorted
Skew	Skew (mm )	6.59 $\pm$ 0.83 <sup>a</sup>	3.21 $\pm$ 0.51 <sup>b</sup>	3.52 $\pm$ 0.32 <sup>b</sup>
	Skew (F&W )	-0.31 $\pm$ 0.04	-0.06 $\pm$ 0.03	-0.21 $\pm$ 0.02
	F&W category	very negative	nearly symmetrical	negative
Kurtosis	Kurtosis (mm)	86.19 $\pm$ 20.18 <sup>a</sup>	22.59 $\pm$ 9.66 <sup>b</sup>	20.70 $\pm$ 4.62 <sup>b</sup>
	Kurtosis (F&W)	0.68 $\pm$ 0.02	0.62 $\pm$ 0.01	0.63 $\pm$ 0.01
	F&W category	platykurtic	very platykurtic	very platykurtic



Figure 1. Three sampling sites (a) the flat basin (FB), (b) the slope with easterly aspect (SE) and (c) the slope with south-easterly aspect (SSE).

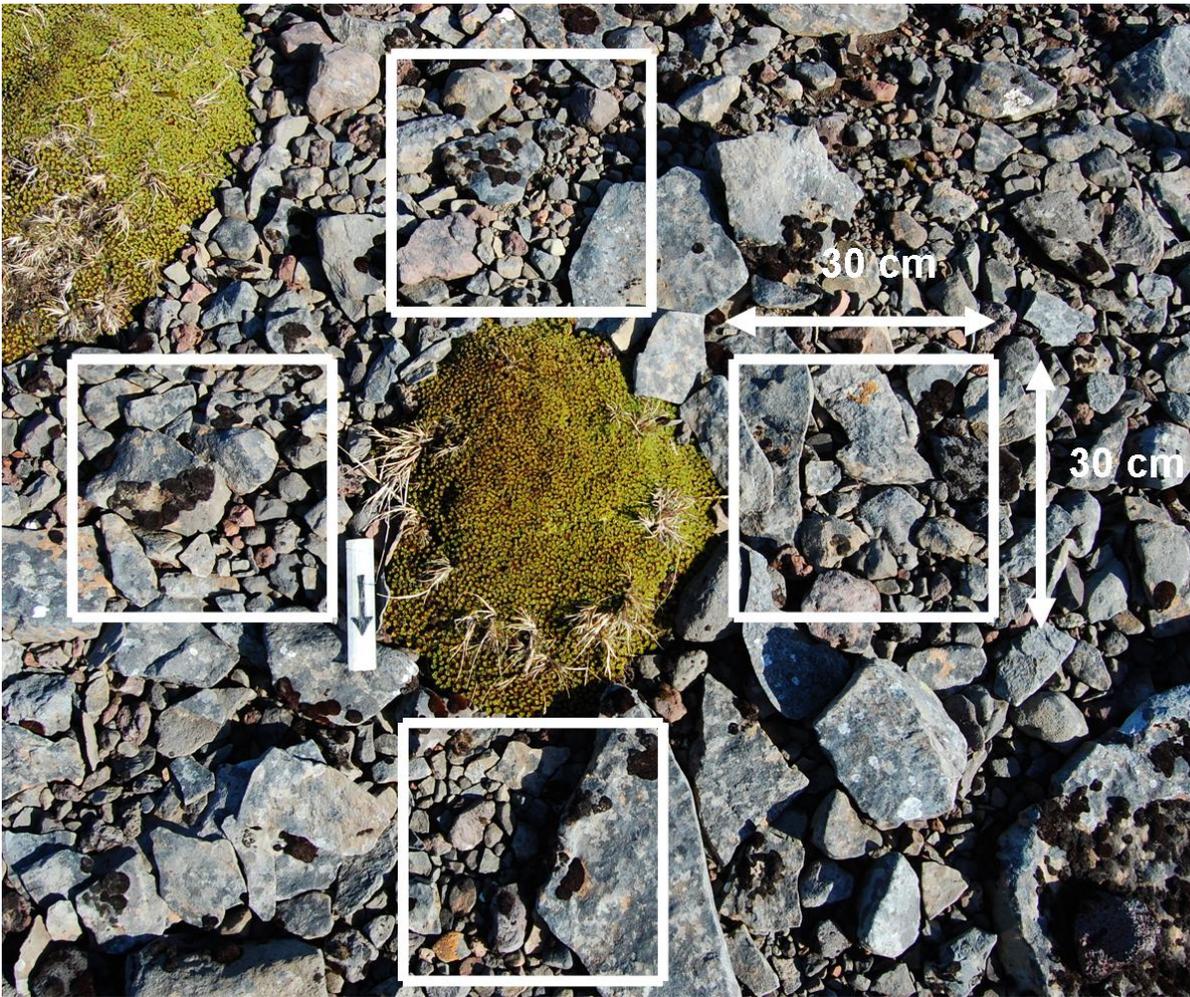


Figure 2. Photograph of one of the *Azorella* cushions showing the cropped out squares on upslope, downslope, and left and right sides. The ruler in the photograph is 15 cm long and the arrow is pointing in the downslope direction.

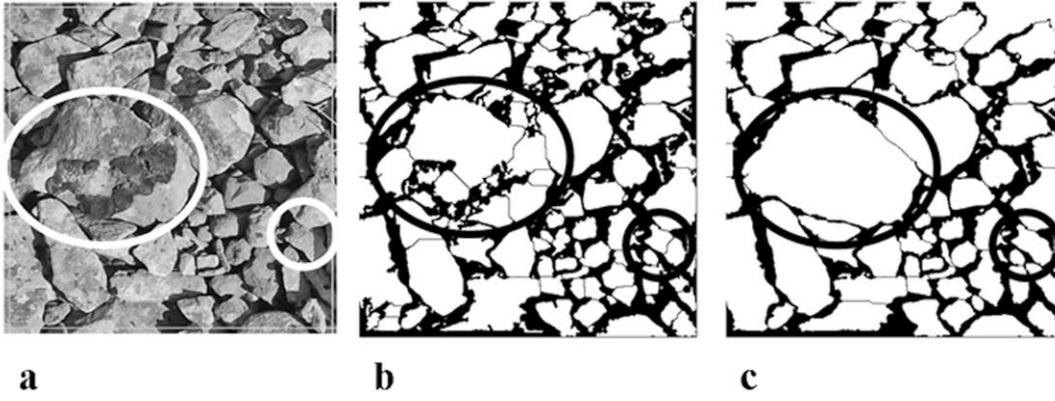


Figure 3. Steps of the image analysis procedure, showing (a) the original image, (b) the results from the digital gravelometer and (c) the results after some manual corrections.

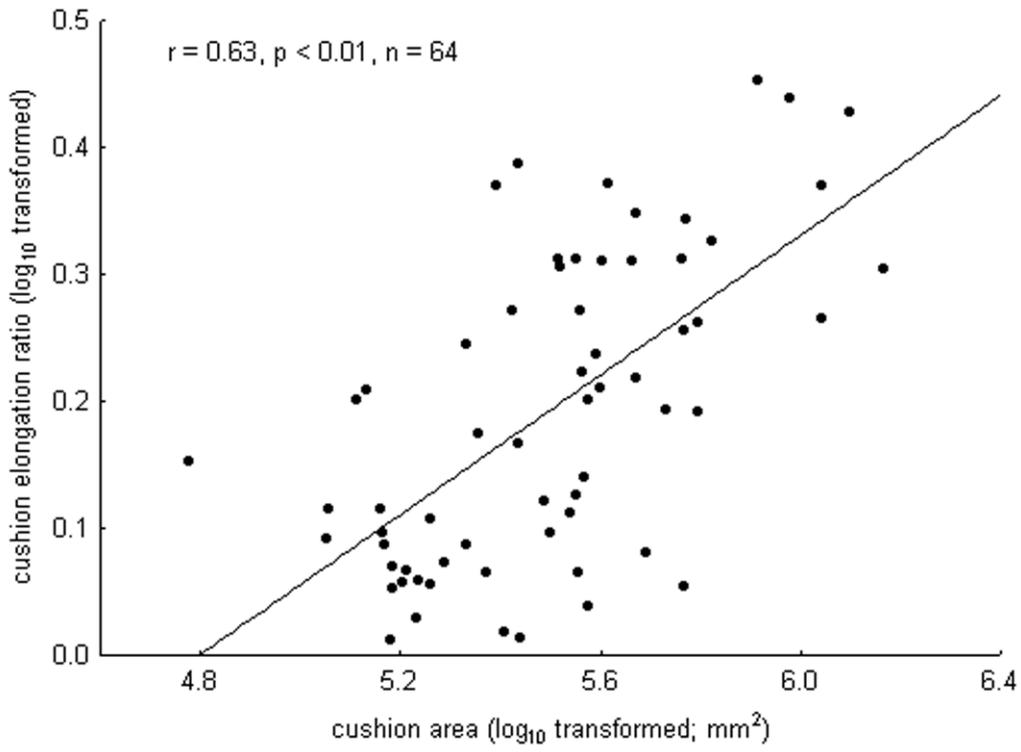


Figure 4. Relationship between cushion area and the cushion elongation ratio for all cushions.

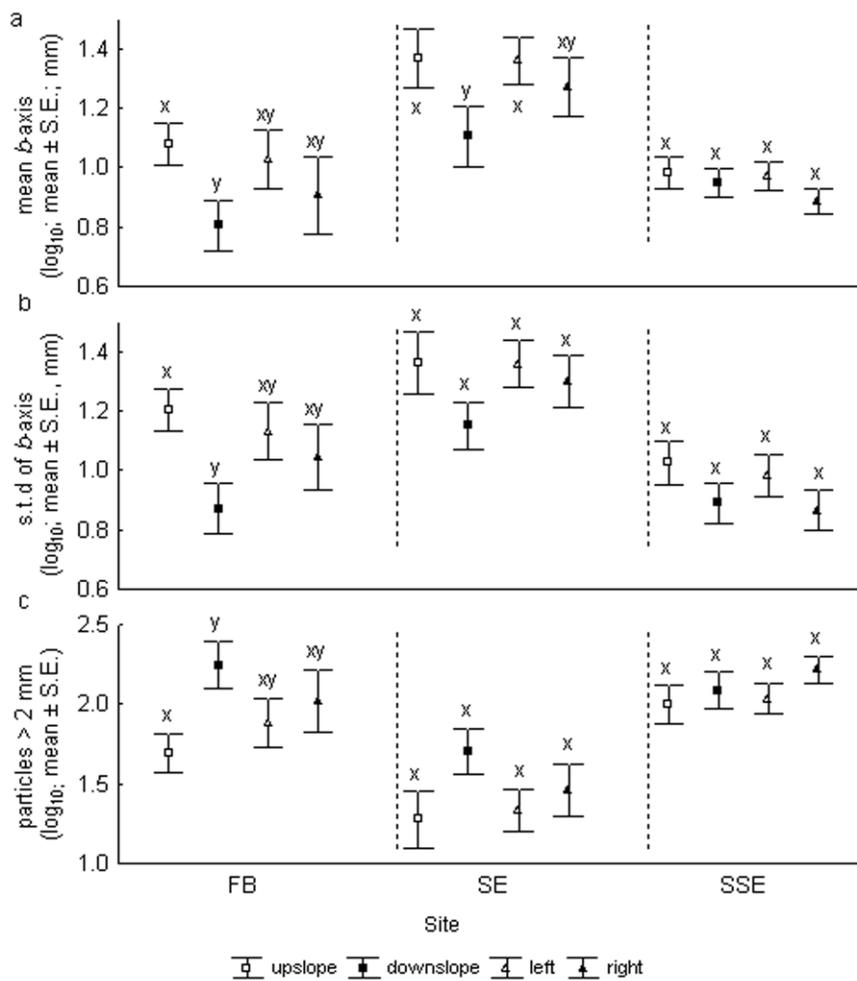


Figure 5. Results of particle size analyses. (a) Mean *b*-axis of particles, (b) standard deviation of *b*-axis and (c) number of particles > 2 mm. Graphs of skew and kurtosis are not shown. FB = flat basin, SE = easterly slope, SSE = south-easterly slope. Different lower case letters denote significant differences between cushion sides at respective sites ( $p < 0.05$ ).

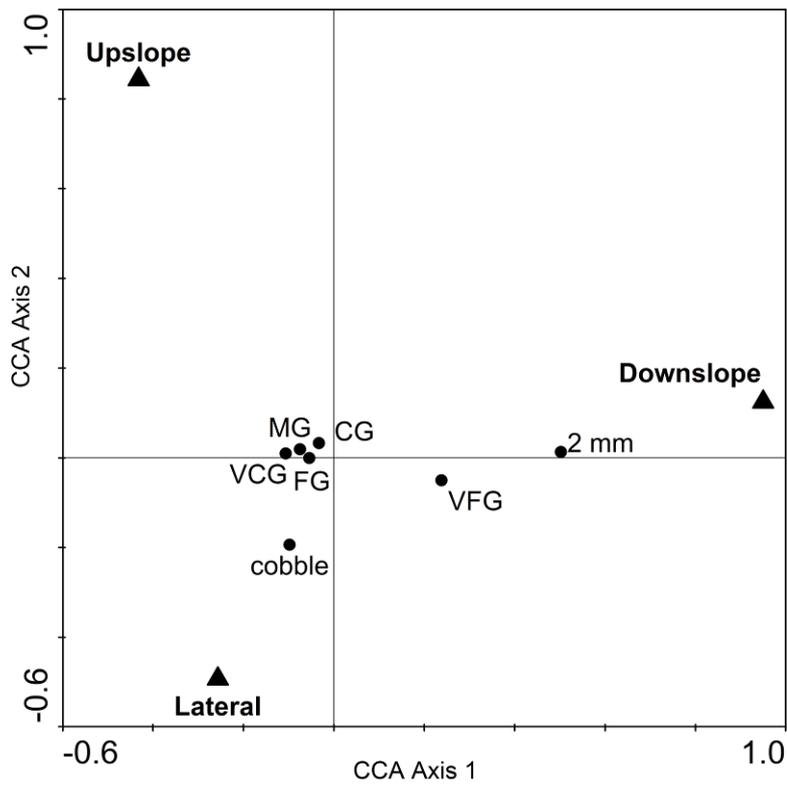


Figure 6. Species-environment biplot from the CCA summarising the effects of cushion sides on particle size distribution after removing the effect of sites. VCG = very coarse gravel, CG = coarse gravel, MG = medium gravel, FG = fine gravel, VFG = very fine gravel, 2 mm = 2 mm and smaller.

## Chapter 3 – Fine scale variability in soil frost dynamics surrounding *Azorella selago* cushions\*

### Introduction

The effects that plants have on the biotic and/or abiotic properties of soils have been well-studied, especially in the context of plant-soil feedbacks (see Kulmatiski et al., 2008 for a recent review). Specific attention has been paid to the effects plants have on microbial communities (Kardol et al., 2007), soil pathogens (Mills and Bever, 1998) and soil chemical properties (Bezemer et al., 2006). However, through changing soil thermal regimes (Ng and Miller, 1977; Pérez, 1987; Arroyo et al., 2003), soil moisture status (Badano et al., 2006; Cavieres et al., 2007) and affecting weathering and erosion processes (see Gabet et al., 2003 for a recent review), plants have an equally important effect on the physical properties and structure of soils. Such changes in soil physical properties could in turn facilitate the establishment or survival of other plant (Arroyo et al., 2003; Cavieres et al., 2007) and animal species (Hugo et al., 2004). As such these physical pathways often provide excellent examples, not only of plant-soil feedbacks (Kulmatiski et al., 2008), but of ecosystem engineering (Jones et al., 1994) in general.

Interactions between the vegetation and physical soil properties are particularly relevant in climatically extreme environments, such as the islands of the sub-Antarctic (Ng and Miller, 1977; Frenot et al., 1998). These areas are often subjected to severe weather conditions, leading to recurrent soil frost cycles and soil instability, which both affect (Tierney et al., 2001; Pérez, 2002), and are affected by vegetation (Ng and Miller, 1977; Matthews et al., 1998). On sub-Antarctic Marion Island the dominant vascular cushion plant, *Azorella selago* Hook. (Apiaceae), is said to play an important role in landscape evolution by interacting with frost creep and other sediment movement processes (Chapter 2; Holness and Boelhouwers, 1998; Boelhouwers et al., 2003). As prevailing warming and drying on the island is likely to affect their nature and extent, understanding these biogeomorphological interactions is especially important for predicting the consequences of climate change for landscape evolution. Vegetation-banked terraces for example have been seen as synergistic, self-regulating systems, where cushion growth facilitates terrace formation, and terraces in turn provide favourable conditions for further latitudinal cushion growth (Chapter 2). However, relatively little is known about the mechanisms (such as through temperature and moisture

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amelioration) by which terrace formation and related cushion establishment provide favourable conditions for cushion growth.

A number of studies have focussed on the relationship between vegetation cover and soil frost cycles (Ng and Miller, 1977; Walker et al., 2003). These studies often relate frost cycle dynamics to canopy cover, organic horizon thickness or plant biomass. However, cushion plants have a compact, prostrate growth-form and as such do not provide a canopy or litter cover to the surrounding soil. Nevertheless, the role of cushion plants in modifying frost cycle dynamics (see for example Pérez, 1987) should not be overlooked. On Marion Island for example, temperature and moisture levels inside *Azorella* cushions have been shown to differ markedly from surrounding ground temperatures (Huntley, 1971; Nyakatyá and McGeoch, 2008). Furthermore, by colonising exposed slopes (Huntley, 1972) and because of their extensive root system (Frenot et al., 1998), *Azorella* cushions are likely to stabilise slopes and play an important role in biogeomorphological succession, i.e. succession facilitated by plant-landform interactions (Corenblit et al., 2008). In large areas of Marion Island these cushions are the dominant form of vegetation cover and very often one of only a few vascular plant species, particularly at high altitudes (Huntley, 1971) and as such play a dominant role in maintaining ecosystem structure and function on the island.

Although temperature and moisture levels have been measured inside *Azorella* cushions and compared to those next to the cushion (Huntley, 1971; Nyakatyá and McGeoch, 2008), no detailed fine-scale measurements of soil thermal conditions and frost heave around cushions have previously been taken. As these are the sites where seedlings are likely to establish and cushion growth is likely to commence (as opposed to inside the plant), determining the spatial variability of frost dynamics around cushions is also important. Furthermore, as frost cycle characteristics such as frost durations, frequency of cycles and amplitudes of temperature variations have been shown to affect soil nutrient budgets and micro-organisms (see Henry, 2007 for a recent review), variability in frost cycle dynamics is biologically relevant.

Here it is hypothesised that soil thermal and moisture patterns show spatial variation around *Azorella* cushions that will affect soil frost frequency, intensity and duration on different aspects of the cushion. This may take the form of shading affecting the micro-scale radiation balance (Oke, 1987, p. 232), leeward snow accumulation (snow fence effect) providing thermal insulation and altering ground frost regimes (Hinkel and Hurd, 2006), or windward sides of cushions showing drying and cooling effects due to enhanced evaporation.

Spatial variation in thermal and moisture regimes are subsequently expected to translate into differential frost heave and erosion around cushions. For example, cushion decay has previously been ascribed to leeward needle ice formation and heave-related turf exfoliation, resulting in crescent

cushions advancing into the wind (Boelhouwers et al., 2003). It is therefore further hypothesised that frost heave will be more severe on leeward cushion sides than on windward cushion sides.

## **Study area and site selection**

Marion Island (46° 54' S, 37° 45' E), which forms part of the Prince Edward Islands Group, is located in the southern Indian Ocean. The soil frost regime on the island is characterised by diurnal frost cycles and frequent needle ice formation (Boelhouwers et al., 2003) as a result of the island's maritime climate with both low annual (3.6°C) and diurnal (1.9°C) temperature ranges (Smith, 2002) and high rainfall of just over 2000 mm/year (le Roux and McGeoch, 2008). Fellfield vegetation, consisting of open plant communities, is restricted to rocky, windswept ridges at lower altitudes, but is the dominant vegetation type above 200 m a.s.l. (Huntley, 1971).

The specific site for this study was the Tafelberg area, an area situated on the eastern side of the island at approximately 300 m a.s.l. (Chapter 1, Figure 1). The vegetation at this site is classified as fellfield (Gremmen, 1981) and is dominated by cushions of *Azorella selago*. Surface material consists of a matrix-supported, unsorted glacial till that is subject to superficial frost heave and creep. A 4-7 cm depth of sorting has been found at similar altitudes on grey lava on the island (Holness and Boelhouwers, 1998). Boelhouwers et al. (2003) found a freeze-thaw frequency of 72 cycles per year at 200 m a.s.l. and 1 cm depth on the island, while Smith and French (1988) estimated the number of frost free days at 5 cm depth in fellfield below 300 m a.s.l. to be 273. Frost creep is considered the dominant form of sediment movement in this terrain (Holness, 2001).

## **Methods**

### Field procedure

Sample size was restricted by cost and time constraints to three *Azorella selago* cushions (Figure 1), which were selected from the Tafelberg area. Although this sample size is small, I aimed at representing general cushion conditions on Tafelberg by choosing cushions of two commonly occurring shapes (round and crescent-shaped) and from two slope angles (flat and moderately sloping). Two cushions, one round and the other considered crescent-shaped, were selected from a relatively flat terrain (4-5° slope angle with northerly aspect). These are hereafter referred to as RF (Figure 1a) and CF (Figure 1b) respectively. The CF cushion showed signs of decay on the southern cushion side and was therefore seemingly advancing in a northerly direction. The third cushion also had a round shape and was selected from a moderately sloping terrain (7-12° slope angle) with

south-east orientation, i.e. the upslope cushion side faced north-west and the downslope cushion side south-east. This cushion is referred to as RS (Figure 1c). Apart from aforementioned shape and slope criteria, cushion selection was based on cushion size (maximum cushion diameter of at least 50 cm) and nearest neighbour criteria (no neighbouring cushion within 1 m distance from study cushion).

Data loggers (Model MCS 130M1, MC Systems, South Africa) with soil temperature (Model MCS154, MC Systems, South Africa) and moisture probes (Decagon, Model EC-20, Decagon Devices) were used for soil temperature and moisture monitoring on eastern and western cushion sides, deemed the windward and leeward sides of cushions for this site. Automated weather station (AWS) measurements taken at hourly intervals from April 2007 to April 2008, as well as the presence of scattered heaved-out dowels on eastern cushion sides in April 2008 supported this initial hypothesis of a dominant westerly wind direction. Soil temperature and moisture probes were set to record instantaneous values every hour. The accuracy of the soil temperature probes is reported to be 0.2°C and that of the moisture probes 4% (volume/volume) (Decagon, Model EC-20, Decagon Devices, [www.decagon.com](http://www.decagon.com)). The temperature probes were inserted at 50 mm distance from the cushion and 20, 50 and 100 mm depth and soil moisture probes at 50 mm distance and 50 mm depth (Figure 2). As a result of cost constraints, temperature and moisture measurements were performed at only one distance from the cushion. Less expensive i-button temperature loggers (DS 1922L/T ThermoChron i-buttons, Dallas Semiconductor Corporation, USA) were initially used to measure temperatures at other distances and directions from the cushion. However, as differences between distances and directions were mostly smaller than the accuracy of the i-buttons (0.5°C), these data were not analysed.

All three microstations became inoperative early in November 2007. Therefore only six months of data were available from the measurements. However, a full year soil temperature record from the i-button temperature loggers around the cushions showed that the period from the beginning of May 2007 to the beginning of October 2007 contained more than 90 % of the frost cycles. Thus, data analysis, based on the May-October record, captured the main frost season. As a result of the microstation malfunctioning, soil moisture data were also only available for the first six months and only for the CF cushion (both sides) and the RF western cushion side.

Wooden dowels of 10 mm diameter and 100 mm length were used to measure frost heave around the cushions. The dowels were inserted completely (or as far as possible) into the soil in April 2007 (see Pérez, 1987; Holness, 2004 for more on this method). The difference in exposed length between April 2007 and April 2008 was used as an indication of total annual frost heave. Soil erosion was measured using steel pins of 4 mm diameter and 300 mm length. The steel pins were inserted into the soil up to a depth of at least 200 mm, i.e. well below the depth of expected

frost creep of 5 cm (Holness, 2004). The difference in exposed pin length between April 2007 and April 2008 was used as an indication of erosion. Dowels and pins were alternated in a grid extending approximately 0.5 m from the cushion edge (Figure 2). The distance in between the grid nodes was between approximately 100 and 200 mm, depending on the presence of rocks. Dowels and erosion pins were measured in the field to 0.1 mm accuracy using a calliper.

#### Data processing and statistical analyses

All data were analysed using the three cushions as replicates. Cushions were deemed suitable replicates despite differing in shape and slope angle, as there was no reason to suspect that east-west temperature patterns between the three cushions would not be similar. Indeed, a visual comparison of temperature parameters for the three cushions separately confirmed that east-west temperature patterns were consistent.

#### *Temperature and moisture data*

Two sets of temperature parameters were calculated, namely frost indices and actual temperature parameters. As frost indices, numbers of frost cycles, durations of the frost events and their intensities were calculated. A frost cycle was identified as a drop in temperature below 0°C followed by a rise above 0°C. The duration of a frost event was defined as the length of time spent below 0°C and the intensity of the event as the absolute minimum temperature reached during the cycle. Mean frost event duration and intensity were calculated per month. In addition, total frost duration (the total length of time that the soil was frozen) was calculated per month. Actual temperature parameters consisted of means, maxima, minima and standard deviations as a measure of variability and were calculated per month. The same parameters were calculated for soil moisture.

All depths were used to compare the numbers of frost cycles between eastern and western cushion sides statistically, as, in this context, zero (indicating no frost cycles) is a meaningful value. However, only the 2 cm depth data were used for comparison of durations and intensities, as the other two depths did not have substantial numbers of frost cycles. In this case a value of zero would incorrectly imply frost cycles with no durations or intensities.

Numbers of frost cycles were compared between cushion sides (east/west) using Generalised Estimating Equations (GEE). A GEE provides a model for analysing observations that are not temporally independent. In addition, it is capable of analysing non-normally distributed variables (Liang and Zeger, 1986). Direction (east/west) was used as the main independent factor of

interest. The effects of depth and month were also tested, but interactive effects could not be tested using GEE. A negative binomial distribution was used for modeling the distribution of the independent variable.

Repeated measures analysis of variance (ANOVA) was used to test for differences in frost durations and intensities between cushion sides using direction (east/west) as independent factor. Month was included as a co-variable and interactive effects between month and direction were also tested. Repeated measures ANOVA was also used to test for differences in mean temperatures, maxima, minima and standard deviations, using direction (east/west) as independent factor. Depth and month were included as co-variables and interactions between co-variables were also tested. Data were approximately normally distributed. Soil moisture data were not analysed as differences between cushion sides were smaller than instrument accuracy.

### *Heave and erosion data*

Field photographs were used to measure the shortest distance from each dowel/ pin to the outer edge of the cushion and the compass direction from the centre of the cushion. Heave and erosion were compared between cushion sides (north-south and east-west) using non-parametric (Kruskal Wallis analysis of variance (ANOVA)) tests. To determine the relationship between heave and erosion and distance from cushion Spearman rank correlation coefficients were calculated.

## **Results**

### Temperature data

#### *Frost index analyses*

The frost season was typically characterised by low intensity, shallow frost cycles, with many frost cycles being the result of fine-scale fluctuations around 0°C (Figure 3). The inlay in Figure 3 clearly shows the large number of fluctuations around 0°C on a smaller time scale of one week for the CF cushion, as well as the soil moisture trends on eastern and western cushion sides. Over all three depths, eastern cushion sides were found to have significantly fewer frost cycles than western cushion sides ( $Z = -2.06$ ,  $n = 54$ ,  $p < 0.05$ ).

Frost cycles lasted between 1 hour and more than 100 hours (Figure 4a), although the majority of frost cycles had durations of less than 20 hours. No interactive effects were found between month and direction (east/west) for mean frost durations or total frost durations. Direction

and month separately had no significant effect on mean frost durations. Only month had a significant effect on total frost durations, with August having the longest total frost duration and September and October having significantly shorter total frost durations than any of the other months.

Frost cycles in general were not very intense, with mean frost intensities above  $-1^{\circ}\text{C}$  (Figure 4b). No interactive effects were found for month and direction for average frost intensity. Furthermore average frost intensities did not differ significantly between months or directions.

#### *Means, maxima, minima and standard deviations*

No significant third order interaction was found between direction (east/west), month (May-October) and depth (2, 5 or 10 cm) for mean temperatures ( $p = 0.05$ ), but there were significant second order interactions. Depth and direction did not interact. However, there was a significant interaction between month and direction ( $F_{5, 10} = 5.96$ ,  $p < 0.01$ ). Mean temperatures on eastern cushion sides were lower in the colder months (June, July and August) than on western cushion sides, whereas there were no differences between eastern and western cushion sides in the warmer months (Figure 5a). This trend was strongest at 2 cm depth. Furthermore, a significant interaction between month and depth was found for mean temperature ( $F_{10, 20} = 33.51$ ,  $p < 0.01$ ). Temperatures of the 2 cm depth were lower than the other two depths in the colder months, with no differences in the warmer months.

For maximum temperatures, the third order interaction (month/depth/direction) was found to be significant ( $F_{10, 20} = 3.59$ ,  $p < 0.01$ ). For all three depths maximum temperatures on eastern cushion sides were lower than those on western cushion sides in colder months, but these directional differences were found to diminish in warmer months (Figure 5b). Furthermore, the increase in maximum temperature towards summer declined with depth. Although maximum temperatures declined with depth during all months; this decline was stronger in the warmer months than in the colder months.

No third order or second order interactions were found to be significant for minimum temperatures (Figure 5c). No significant differences were found in minimum temperatures between eastern and western cushion sides. However, minimum temperatures increased significantly with depth ( $F_{2, 4} = 12.84$ ,  $p < 0.05$ ) and July was found to have significantly higher minimum temperatures ( $F_{5, 10} = 5.52$ ,  $p < 0.01$ ) than all the other months, except for October (results not shown).

Variability in temperature showed a significant third order (month/depth/direction) interaction ( $F_{10, 20} = 4.34$ ,  $p < 0.01$ , Figure 5d). Variability in temperature dropped with depth and

evened out over the months with depth, so that at 10 cm, May and October had very similar variabilities, but at 2 cm variability in October was much higher than in May. Eastern cushion sides were less variable in the colder months than western cushion sides, with the trend reversing in the warmer months for the 2 cm depth (Figure 5d). This was especially clear at the RS cushion (Figure 3c). At the other two depths this trend had merely weakened (Figure 5d).

#### Soil moisture data

Soil moisture differences between the eastern and western cushion side of the CF cushion were in the order of 2%. As the accuracy of the soil moisture probes is reported to typically be in the order of 4% (Decagon, Model EC-20, Decagon Devices, U.S.A.), these differences were not significant. However, soil moisture was above the values needed for needle ice growth, even for very coarse-grained soils and therefore posed no limit on needle ice growth potential (Meentemeyer and Zippin, 1981).

#### Heave and erosion

Mean heave was approximately 85 mm, with a large number of dowels (75.4%) completely heaved out (Table 1). No significant differences in heave were found between cushion sides (north/south and east/west,  $p = 0.05$ ). A weak, but significant positive correlation ( $r = 0.20$ ,  $n = 198$ ,  $p < 0.05$ ) was found between heave and distance from cushion (Figure 6a). However, dowels that were heaved out completely were found at any distance from the cushions.

Maximum erosion was high at all three cushions, with one value (for the RF cushion) as high as 160 mm (Table 1). This value was seen as an outlier and excluded from analyses, as it was far larger than the mean erosion value (Table 1).

No significant differences were found for erosion between cushion sides (north/south and east/west). A weak, but significant positive correlation ( $r = 0.14$ ,  $n = 256$ ,  $p < 0.05$ ) was found between erosion and distance from cushion (Figure 6b).

### **Discussion**

This discussion is based on the six month period for which data were recorded. No conclusions can be drawn for the remaining six months. However, as the i-button measurements pointed out, the measured period captured more than 90% of the frost cycles and was therefore seen as representative of the 2007 frost season on Tafelberg. Soil thermal and moisture patterns do

indeed show spatial variation as hypothesised. The results indicate a thermally more uniform, but slightly cooler winter climate, on eastern cushion sides as opposed to western cushion sides. Fewer frost cycles were found on eastern cushion sides. On Marion Island, insolation differences between eastern and western sides of an object have been shown to typically result in a shift in the timing, but not in the magnitude, of temperatures (Boelhouwers et al., 2007). In addition, at higher altitudes, soil temperature variations by aspect have been shown to be influenced by factors other than radiation, such as snowcover (Boelhouwers et al., 2007). The sustained period of temperatures at, but mostly just below 0°C at the surface layer on the eastern leeward cushion side in Figure 3 (inlay) suggests snow accumulation on this cushion side to be present up to the warm front passage on 5 August 2007. Snow accumulation on eastern cushion sides in winter explains the smaller variability in temperature, compared to western cushion sides. Larger temperature fluctuations on the western cushion side, compared to the eastern cushion side in Figure 3 (inlay) indicate that snow has not accumulated here, possibly as a result of high westerly wind speeds. As soil mean temperatures are positive, snow accumulation, and its subsequent melt, also has a cooling effect, which is consistent with lower mean values on the eastern side of cushions. In addition, the soil moisture data suggest that drying effects in the soil are more rapid and larger on western cushion sides (Figure 3, inlay), whereas the eastern cushion side shows more stable soil moisture conditions, providing further support for the initial hypothesis that high wind conditions enhance evaporation on wind-exposed cushion sides.

Despite temperatures, numbers of frost cycles and soil moisture differing between eastern and western cushion sides, no directional differences in either frost heave or erosion were found between eastern and western cushion sides. Either these differences were too small to translate into aspect-differentiated heave, or there were actually differences in heave, but because the dowels were almost all heaved out, these differences could not be measured. Longer dowels (> 100 mm) or more frequent field measurements could be used to determine such differences.

Both heave and erosion values showed a slight tendency to increase with distance from the cushion edge. Furthermore, although some sediment removal against the cushion edges occurred, the erosion values right against the cushion edge were all under 2 cm and a number of values indicated burial of pins against the cushion edge. This accumulation of coarse material specifically on upslope cushion sides (Chapter 2) will change the frost susceptibility of the material and may be a possible factor contributing towards the heave-distance trend. However, soil strength provided by the cushion rooting structure, which is probably denser around the cushion edges, should also be considered.

The large number of heaved-out dowels clearly show that the study area was subjected to effective and extensive frost heave. Based on the shallow frost penetration of mostly less than 10

cm and numerous field observation reports (Hall, 1979; Boelhouwers et al., 2003), needle ice growth is considered responsible for frost heave in the area. Despite such extensive frost heave, minimum temperatures hardly reached  $-2^{\circ}\text{C}$ , the suggested required temperature for needle ice nucleation (Outcalt, 1971). The results strongly indicate that needle ice nucleation also occurs at temperatures above  $-2^{\circ}\text{C}$ . Furthermore, the results suggest that frost heave took place by a frost pull mechanism and not frost push, as frost penetration in general did not reach 10 cm (the depth that most dowels were inserted). This frost pull of the dowels can be viewed as a model for plant root damage, especially for very vulnerable individuals, such as seedlings with a single tap root. The results therefore demonstrate the potential effect of needle ice growth on seedling mortality, as suggested by McGeoch et al. (2008).

The erosion data indicate the combined action of frost heave and surface runoff to be an important component of surface denudation. Runoff evidence is available from visual signs of particle size sorting, rill development and concentrated overlandflow on the grey lava slopes and the cushion sites particularly. Ferrick and Gatto (2005) demonstrated that freeze-thaw cycles contribute towards soil erosion in cold climates and on Marion Island Boelhouwers et al. (2000) describe how frost heave by needle ice lifts cohesive soil and creates a friable surface layer of soil that is rapidly removed by surface flow. Overlandflow develops from saturation of the thin grey lava till cover, especially at the base of *Azorella* terraces and other convex breaks of (micro) slope. Channelisation in the form of rills is clearest where runoff is concentrated between cushions, stones or terraces or at the base of cushions. The unexpected high erosion values around the cushions suggest this mechanism may be more widespread on the more compact and shallow grey lava soils on the island and needs further investigation. Furthermore, although care was taken to minimise initial site disturbance during sensor and marker installation this must also be considered a factor in the high erosion rates obtained. Marker installation necessarily involved some degree of soil disturbance, thus affecting soil cohesion and structure, and removing surface gravel that protects the underlying fines. Newly exposed soil can be expected to be at erosion risk of direct raindrop impact through splash erosion as well as runoff in response to the 860 mm of precipitation over the monitoring period.

Boelhouwers et al. (2003) ascribe *Azorella* cushion decay on Marion Island to turf exfoliation as a result of needle ice growth on leeward cushion sides. As a result, cushions at their study site were found to advance into the wind. In this study, however, the crescent-flat cushion was not found to advance into the wind, but rather in a northerly direction. Clearly cushion orientation is site specific and other factors, such as potentially solar radiation, also play a role. In addition, no directional differences in either frost heave or erosion were found around cushions. Again, as most

dowels were completely heaved out it was difficult to determine whether there were not in actual fact directional differences in needle ice growth and frost heave rates.

Microarthropod communities have been shown to vary directionally inside *Azorella selago* cushions, with higher abundances on cooler, less wind-blown sides than on warmer, windy sides (Hugo et al., 2004). In addition, the grass, *Agrostis magellanica*, which grows epiphytically on *A. selago* cushions, has been found to be unequally distributed between plant sides (le Roux et al., 2005). These studies illustrate the significance of microclimates created inside *Azorella* cushions (see also Nyakatia and McGeoch, 2008). The results from this study emphasise that these subtle microclimatic differences exist not only inside *Azorella* cushions, but also in the surrounding soil, with potential consequences for biota. For example, it may be suggested that higher thermal variability in winter on wind-exposed, western cushion sides is likely to disfavour seedling establishment and microarthropod numbers, while snow accumulation sites on eastern cushion sides may provide more favourable microhabitats. Clearly further work is needed to understand the complex microclimate, soil frost and vegetation interactions in this diurnal frost environment better.

The potential effects of climate change on freeze-thaw cycle characteristics are not yet fully understood (Henry, 2008). Warming and drying trends, such as those experienced on Marion Island (le Roux and McGeoch, 2008), have been predicted to increase cycle frequency as a result of decreased insulation by snow cover (Isard and Schaetzl, 1998). This could therefore potentially have a larger impact on eastern cushion sides, where snow accumulates in winter. Furthermore, freeze-thaw cycles have been shown to affect soil properties ranging from physical soil properties to microbial biomass, microbial community composition and nutrient dynamics (see Henry, 2007 for a recent review). Climate change could thus have potentially far-reaching consequences on the island's biota, not only through direct effects, but also indirectly through changing frost cycle dynamics and microclimate structure and functioning.

## **Conclusions**

Winter soil temperatures were found to be lower and less variable and soil moisture more stable on eastern, leeward sides of *Azorella selago* cushions than on western cushion sides. This variability is probably the combined result of (1) snow accumulation on leeward cushion sides, inducing insulation and cooling, and (2) drying on windward cushion sides. The very effective frost heave, often induced at temperatures above  $-2^{\circ}\text{C}$ , predominantly resulted in complete dowel heave. As a result, no expected directional differences in frost heave could be demonstrated around cushions and therefore no evidence was found to suggest that frost heave is responsible for directional turf exfoliation and crescent cushion formation. Similarly, erosion rates showed no

directionality around cushions. Further attention must be given to the consequences of the demonstrated microclimatic variations in assessing the role of *Azorella selago* as an ecosystem engineer in sub-Antarctic fellfield habitats. While more measurements on abiotic processes around cushions are clearly needed, directionality in microbiological activity and seedling establishment around cushions should also be included in future studies.

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Table 1. Mean, maximum and minimum heave and erosion. Maximum measurable heave was 100 mm.

	N	Mean $\pm$ S.D.	Max	Min	% Completely heaved
Heave (mm)	198	84.8 $\pm$ 30.9	100.0	3.9	75.4
Erosion (mm)	256	9.1 $\pm$ 16.6	160.8	-47.4	



Figure 1. The three monitored cushions (a) the round-flat (RF) cushion, (b) the crescent-flat (CF) cushion and (c) the round-slope (RS) cushion. Arrows in the bottom left-hand corner point north.



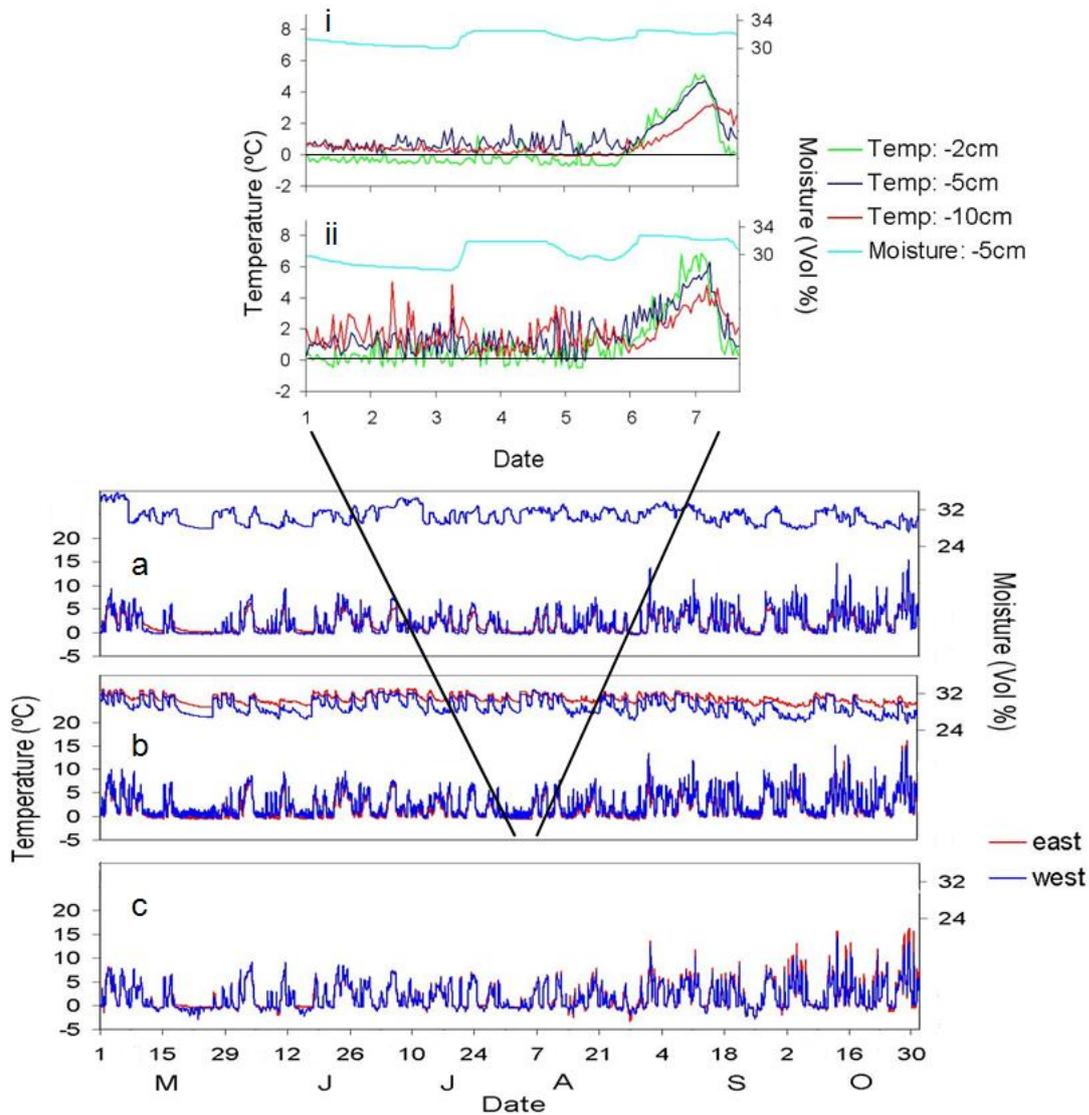


Figure 3. Temperature and moisture time series for the six month measuring period at -2 cm for (a) the round-flat (RF) cushion, (b) the crescent-flat (CF) cushion and (c) the round-slope (RS) cushion. The large number of fluctuations around 0°C is characteristic of the frost season. High, near-saturated soil moisture values are evident throughout the series. The inlay shows a one week period for the CF cushion on (i) eastern and (ii) western cushion sides. The sustained period of temperatures at or below 0°C up to the warm front passage on 5 August on the eastern cushion side is indicative of snow accumulation. Larger fluctuations on the western cushion side show that no snow has accumulated here.

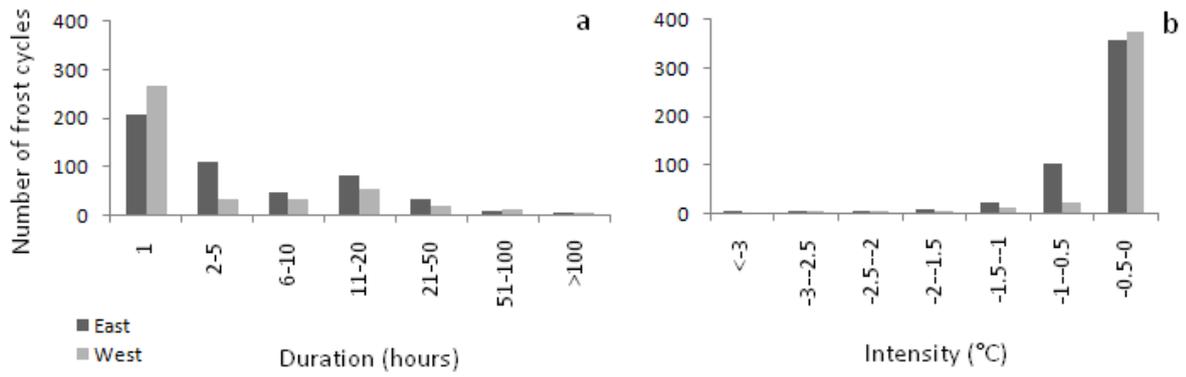


Figure 4. Frequency distribution of (a) frost durations and (b) frost intensities at -2 cm. A large proportion of the frost cycles have very short durations. Despite the substantial heave recorded frost cycle minima are predominantly above -2°C.

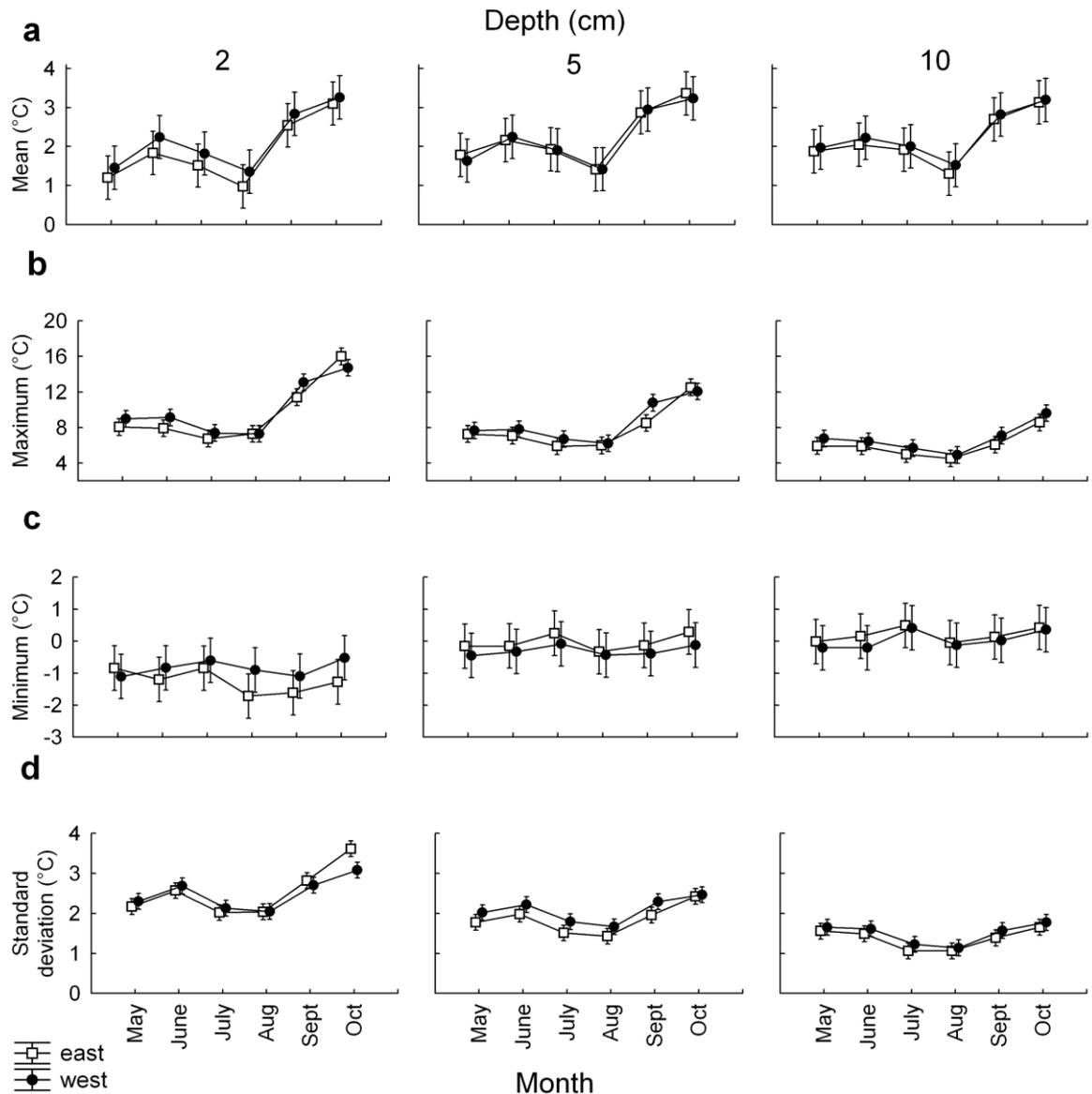


Figure 5. Mean temperatures (a), maximum temperatures (b) and standard deviations of temperatures (d) were found to be slightly lower on eastern cushion sides than on western cushion sides in colder months, whereas no differences were found for minimum temperatures (c). Vertical bars denote 95% confidence levels.

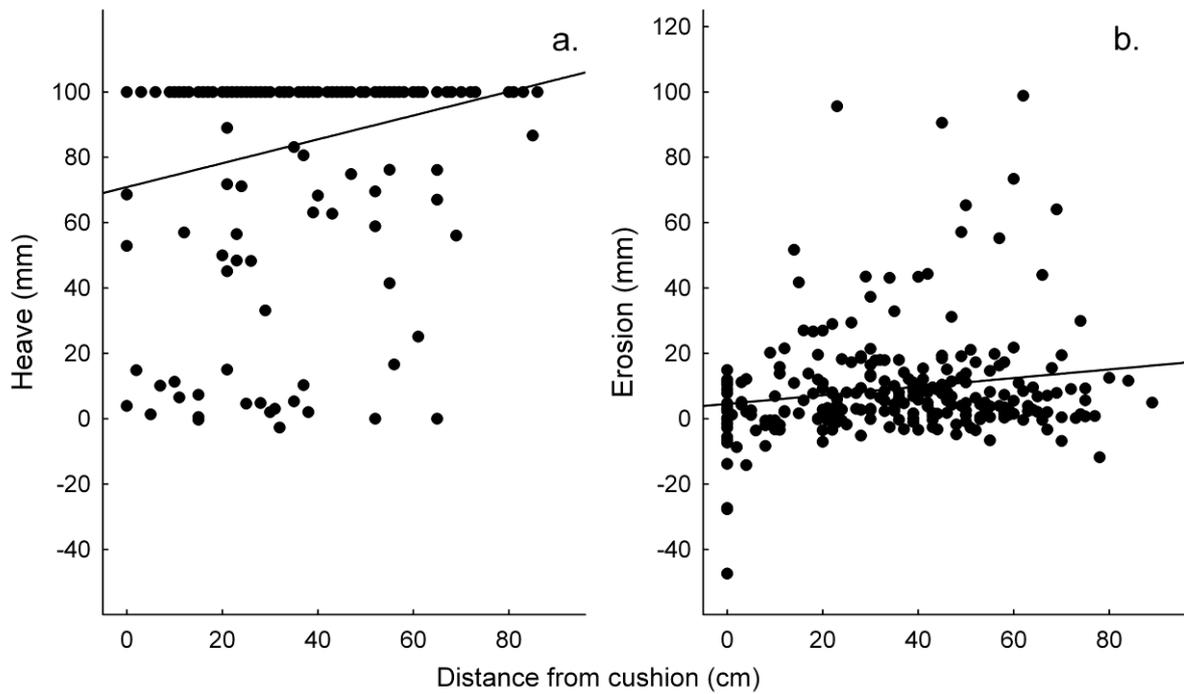


Figure 6. Relationship between distance from cushion and (a) heave ( $r = 0.20$ ,  $n = 198$ ,  $p < 0.05$ ) and (b) erosion ( $r = 0.14$ ,  $n = 256$ ,  $p < 0.05$ ). Maximum measurable heave was 100 mm. Data for all three cushions are pooled.

## Chapter 4 – Contrasting nurse plants and nurse rocks: the spatial distribution of seedlings of two sub-Antarctic species \*

### Introduction

There has been an increasing interest in facilitation amongst plant communities in recent years (see Brooker et al., 2008; Brooker and Callaway, 2009 for recent reviews). Certain plant species have been found to act as nurse plants through their facilitative effects on other plants, including seedlings (Ryser, 1993; Arroyo et al., 2003; Gómez-Aparicio et al., 2005; Cavieres et al., 2008). Such positive plant associations are especially important in climatically severe environments (Schlag and Erschbamer, 2000; Klanderud and Totland, 2004; Badano et al., 2006; Cavieres et al., 2007), where facilitation has been proposed to be the dominant plant-plant interaction (Kleier and Lambrinos, 2005). Competition has been suggested to overrule facilitative effects mainly in more productive habitats (Bertness and Callaway, 1994; Brooker and Callaghan, 1998). However, some disagreement on this point exists (Grime, 2001, pg. 35-37), with some studies finding impeded seed germination and seedling growth in the presence of other vegetation in climatically severe environments (Moen, 1993; Olofsson et al., 1999).

One specific group of plants that has been shown to act as nurse plants in climatically severe environments is plants with a compact, prostrate growth-form, known as cushion plants (Arroyo et al., 2003; Badano et al., 2006; Cavieres et al., 2007; Cavieres et al., 2008). Cushion plants have been known to ameliorate soil temperatures (Chown and Crafford, 1992; Nyakatia and McGeoch, 2008) and increase soil moisture (Badano et al., 2006; Cavieres et al., 2007), provide shelter against moving substrate and wind stress (Brancaleoni et al., 2003; le Roux and McGeoch, 2008b) and improve soil nutrient status (Nuñez et al., 1999). Through mitigating such abiotic stresses, cushion plants have been known to facilitate seedling establishment and plant survival of some species (Cavieres et al., 2008).

The majority of studies investigating the nurse effect of cushion plants in climatically severe environments have focussed on the cushion plant itself as a nurse substrate, as other plants are often found growing epiphytically on this life form (Arroyo et al., 2003; Cavieres et al., 2008). On sub-Antarctic Marion Island for example, cushions of the dominant vascular plant species, *Azorella selago* Hook (Apiaceae), are known to form nutrient-rich habitats (Huntley, 1971), facilitating the establishment of a number of species that grow epiphytically on them (Huntley, 1972; McGeoch et al., 2008), as well as microfauna communities living inside them (Barendse and Chown, 2001;

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Hugo et al., 2004). However, by acting as wind shelters (Huntley, 1971) and affecting sediment movement patterns (Chapter 2; Holness and Boelhouwers, 1998; Boelhouwers et al., 2000), these cushions could also potentially provide “safe sites” for plant establishment adjacent to cushions. Particle sizes on upslope cushion sides, for example, have been shown to be larger than those on downslope cushion sides (Chapter 2) potentially facilitating seed entrapment (Chambers et al., 1991, Combrinck et al., unpublished) and seedling establishment and survival (Jumpponen et al., 1999) on upslope cushion sides. Alternatively, sediment damming on upslope cushion sides (Pérez, 1987) could have a negative effect on seedling establishment and prevent establishment on upslope cushion sides. This would result in higher seedling establishment on sheltered, downslope cushion sides (le Roux and McGeoch, 2008b). Furthermore, soils on eastern cushion sides have been shown to have slightly lower and less variable winter temperatures than those on western cushion sides, possibly as a result of snow accumulation on eastern, leeward cushion sides, again potentially affecting seedling establishment (Chapter 3).

Alternatively, cushions could have a potentially negative effect on seedling establishment, especially in the immediate vicinity of the cushion, as a result of competition for resources in the nutrient-poor fellfield soils where these cushion plants are predominantly found on Marion Island (Smith and Steenkamp, 2001). This would lead to fewer seedlings closer to the cushion edge and increasing seedling abundance with distance from the cushion. Furthermore, the same plant species can act as both a nurse plant and competitor, depending on the environmental conditions. Klanderud and Totland (2004) found, for example, a shift from a nurse effect to a more competitive effect as the percentage cover of the so-called nurse plant increased. This effect was, however, not observed in climatically very extreme sites (Klanderud and Totland, 2004).

By comparing the effects of nurse organisms to those of inanimate nurse objects, such as rocks, biological and mechanical nurse effects can be distinguished (see for example approach by Kawai and Tokeshi, 2006). The rationale behind these comparisons is that a nurse object (such as a rock) will only provide a physical/mechanical (such as sediment obstruction, shading or wind sheltering) nurse effect, while a nurse organism, in this case a plant, could provide both mechanical and biological (such as improving soil nutrient status, providing mycorrhizae, see van der Heijden and Horton, 2009 for a recent review) nurse effects, and potentially also negative impacts through competition for resources (Olofsson et al., 1999), attracting herbivores (Rousset and Lepart, 2000) or hosting pathogens (Mills and Bever, 1998).

In light of the above, the main aim of this chapter was to determine the spatial variability in *Azorella selago* and *Agrostis magellanica* Lam. (Poaceae) seedling distribution and abundance around *Azorella selago* cushions and rocks. Specific research questions were: 1) Are seedlings non-randomly distributed with respect to cushions and rocks? 2) Do seedling numbers differ with

direction (N, S, E or W) from cushions/rocks? 3) Do seedling numbers differ between cushion/rock sides (upslope, downslope, left or right)? 4) What is the relationship between seedling abundance and distance from cushion/rock?

## Methods

### Study area

Marion Island (46° 54' S, 37° 45' E) and its nearby, smaller neighbour, Prince Edward Island, constitute the Prince Edward Islands Group. Marion Island has a maritime climate with both low seasonal (3.6°C) and diurnal (1.9°C) temperature ranges and a mean annual air temperature of approximately 6°C (Smith, 2002). Mean annual precipitation has declined steadily since the 1960s with just over 2000 mm reported for the 1990s (Smith, 2002; le Roux and McGeoch, 2008a). Apart from scattered scoria cones, two substrate types are found on the island, older, pre-glacial grey lava and younger post-glacial black lava (Verwoerd, 1971). Above 200 m a.s.l. fellfield vegetation dominates. This vegetation type is characterised by nutrient-poor soils (Smith and Steenkamp, 2001) and low plant cover of less than 25% (Huntley, 1971). Because of these nutrient poor soils, gale-force wind speeds (Schulze, 1971; le Roux, 2008) and shallow, but numerous frost cycles (Boelhouwers et al., 2003), fellfield habitats were considered harsh environments for seedling establishment and survival.

### Study species

*Azorella selago* has a low-growing, compact cushion growth-form. It is widespread across the sub-Antarctic (Huntley, 1972) and the genus *Azorella* is also found at higher altitudes in the Andes (Martinez, 1993). It is the most widespread vascular plant species on Marion Island, where it is found growing at virtually all altitudes (Huntley, 1972). In addition, it is the dominant species on fellfield vegetation, where a number of species, including *Agrostis magellanica* has been recorded growing epiphytically on it (Huntley, 1971). Fruits of *A. selago* weigh on average 0.87 mg (S.E. = 0.05, n = 20, author's own measurements) and are elliptical in shape. Each fruit contains two seeds. Seed numbers differ considerably between cushions (mean  $\pm$  S.E. =  $39.57 \pm 11.55$ , n = 65, Frenot and Gloaguen, 1994). Furthermore, no relationship between seed number and cushion size has been observed (Frenot and Gloaguen, 1994).

The perennial grass, *Agrostis magellanica*, is the second-most widespread vascular plant on the island (Huntley, 1971). It is found growing both in the soil and rooted epiphytically into

*Azorella selago* cushions (Huntley, 1972). *Agrostis magellanica* seeds are transported within spikelets, which contain several caryopses (grass fruit). These caryopses have a mean weight of 0.29 mg (S.E. = 0.09, n = 150) and are irregular in shape with jagged edges (Combrinck et al., in prep.). Frenot and Gloaguen (1994) found an average of approximately 38 spikelets per inflorescence (mean  $\pm$  S.E. =  $37.87 \pm 1.24$ , n = 100) and approximately 3 inflorescences per plant (mean  $\pm$  S.E. =  $2.66 \pm 0.08$ , n = 100).

### Cushion and rock selection and seedling survey

A study site was selected on a gentle south-facing slope (< 5 degrees) at approximately 220 m a.s.l. on grey lava soil in fellfield vegetation on the eastern side of the island (see Figure 1). Twelve cushions, separated by approximately 20 m, were selected based on relative isolation (a minimum number of other cushions and rocks within a 0.5 m radius) and size (maximum diameter of at least 30 cm) within an area of 60 x 40 m. Large cushions were selected, as these were considered more likely to affect their surroundings and act as nurse plants or objects, both in terms of abiotic and biotic effects, than smaller cushions.

For each cushion, a rock of similar height was selected that was relatively isolated from other rocks (and cushions) of the same (or larger) size. For a given height, rocks generally had a smaller diameter than cushions. Therefore, whereas rocks and cushions were both found across the height spectrum, maximum diameters of selected rocks were smaller than those of selected cushions (but all rocks had a maximum diameter of at least 30 cm).

In addition, for each cushion, an adjacent plot with only open soil, i.e. containing no plants or rocks higher than approximately 5 cm, was chosen within the study plot, forming cushion/rock/open soil triplets. The same isolation criteria that were followed for the rocks and cushions (i.e. relative isolation from other cushions and rocks) were followed for the open soil plots. As these areas were hard to find, selection of the open soil plots was based on those that best matched all the criteria.

The maximum diameter, perpendicular maximum diameter and height of all study cushions and rocks were measured. In addition, the height of all rocks and cushions higher than 5 cm within a 0.5 m radius from the study rock/cushion/open soil triplet were documented and the direction and distance from the study rock/cushion/open soil triplet were noted. A circular area surrounding and 15 cm wider than the cushion/rock/open soil plot was searched for *A. selago* and *A. magellanica* seedlings. For this study, an *A. selago* seedling was defined as a small plant with up to three leaves in addition to the cotyledons and an *A. magellanica* seedling was defined as an individual with up to ten leaves and a maximum height and basal diameter of 25 and 2 mm respectively. To ensure that

the same area was searched for the open soil plots as for the cushion and rock, a rope that was shaped around the circumference of the cushion was placed in the open soil area and the area inside the rope excluded from the search effort (see Figure 2 for clarification).

The cushion/rock side (upslope, downslope, left or right) when viewed from the downslope side and cardinal compass direction (N, S, E or W) of every seedling found with respect to the centre of the cushion/rock was documented. In addition, the shortest distance from the seedling to the edge of the cushion/rock was measured. Digital photographs (Pentax Optio W60, 5-25 mm, 10 MP) of all the selected cushions, rocks and open soil plots were taken in the field. Photographs were taken at the highest resolution (10 megapixel) and highest quality JPEG compression. Photographs were taken from an approximate height of 1.5 m and vertically as far as possible to avoid image distortion. The size difference between cushions and rocks introduced a potential bias in the total area searched around them respectively. The areas of the 15 cm-wide circular areas searched around cushions and rocks were therefore calculated from the photographs using image analysis software (SigmaScan Pro version 5, SPSS). The search area around cushions was approximately 1.2 times larger than the search area around rocks. Seedling densities were therefore used instead of seedling numbers.

Seedling densities were compared between rocks, cushions and open soil areas using a generalised linear model (GLM) with Poisson distribution and log link function (Quinn and Keough, 2002). The same statistical approach was used to compare seedling densities between different directions (N, S, E or W) and sides (upslope, downslope, left or right) of cushions and rocks, and to test for interactions between direction and cushion/rock, and side and cushion/rock. *Azorella selago* and *Agrostis magellanica* data were analysed separately and direction (N/S/E/W) effects were also analysed separately from side (upslope/downslope/left/right) effects. Where necessary Poisson models were corrected for overdispersion and model significance subsequently determined using Type III likelihood-ratio tests.

The distances of seedlings from cushion and rock edges were plotted as histograms. Under an assumption of an even distribution of seedlings, the expected abundance of seedlings in each distance category was estimated as proportional to the surface area covered by that distance category. While the relative sizes of the different distance categories depends on the size of the cushion/rock being examined, these areas were calculated based on the mean cushion and rock diameter (approximately 60 and 40 cm respectively), assuming a round cushion/rock shape. Expected seedling numbers, based on an even distribution, were then calculated for the various distance categories according to the following equation:

$$E = T / (a/A) \dots \dots \dots \text{equation 1}$$

where  $E$  = the expected number of seedlings in a specific distance category,  $T$  = the total number of seedlings found for cushions and rocks respectively,  $a$  = the area of the distance category and  $A$  = the total area searched.

## Results

A total of 111 seedlings was found, 83 of which were *A. magellanica* and 28 *A. selago* seedlings. In total 58 seedlings were found around cushions, 40 around rocks and 13 around the open soil areas (Table 1).

*Azorella selago* seedling densities were significantly higher around cushions than around rocks and open soil ( $X^2 = 23.5$ ,  $df = 2$ ,  $p < 0.0001$ , Figure 3a). However, no differences were found in *A. selago* seedling densities between rocks and open soil areas. Because only three *A. selago* seedlings were found around rocks, direction and side effects could not be tested for *A. selago* seedlings around rocks. No significant differences were found in *A. selago* seedling densities between either cushion directions ( $X^2 = 6.2$ ,  $df = 3$ ,  $p = 0.10$ , Figure 3b) or cushion slope sides ( $X^2 = 3.3$ ,  $df = 3$ ,  $p = 0.35$ , Figure 3c).

*A. magellanica* seedling densities were significantly higher around cushions and rocks than around open soil areas ( $X^2 = 7.1$ ,  $df = 2$ ,  $p = 0.03$ , Figure 4a), but no difference was found between cushions and rocks. Neither the two-way interaction between direction and cushion/rock ( $X^2 = 5.6$ ,  $df = 3$ ,  $p = 0.14$ ), nor direction alone ( $X^2 = 4.4$ ,  $df = 3$ ,  $p = 0.22$ ) had a significant effect on *A. magellanica* seedling densities (Figure 4b). The two-way interaction was also not found to be significant for side and cushion/rock ( $X^2 = 5.8$ ,  $df = 3$ ,  $p = 0.12$ ). However, when data were grouped for cushions and rocks, significantly higher *A. magellanica* seedling densities were found on upslope sides than downslope or on either side ( $X^2 = 9.5$ ,  $df = 3$ ,  $p = 0.02$ , Figure 4c).

There were substantially more *A. selago* seedlings than expected based on searched area between 3 and 10.5 cm from cushion edges, but fewer than expected in the categories above and below this range (Figure 5). *A. magellanica* seedlings around cushions followed a similar pattern, with most seedlings at or above the expected values in the range 3 to 13.5 cm from cushion edges (Figure 5). Seedling numbers above and below this range were lower than expected. The pattern of *A. magellanica* seedlings around rocks differed from that of *A. selago* and *A. magellanica* seedlings around cushions in that far more *A. magellanica* seedlings than expected were found against the rock edges (Figure 5).

## Discussion

The clearest pattern emerging from the data is the association of seedlings of both species with *A. selago* cushions. In addition, *A. magellanica* seedlings are also associated with rocks. Three possibilities are considered for explaining these observed patterns.

First, it is possible that *A. selago* seedlings found around cushions were from seeds of the study cushions themselves and that observed patterns are therefore indicative of very localised seed dispersal rather than nurse effects of the cushion. Short primary dispersal distances (<50 cm) have been suggested to be dominant in alpine species (Spence, 1990; Marchand and Roach, 1980). At the same time, however, seedlings of some pioneer alpine species, including low-growing cushion forms, have been found exclusively at distances of over 2 m from potential parent plants (Marchand and Roach, 1980), indicating that longer-range transport is also possible. Chapuis et al. (2004) attribute the slow recovery of *A. selago* on denuded areas of Kerguelen to the low dispersal capacity of their seeds and their late sexual maturity. Indeed, *A. selago* seeds occur very cryptically, almost hidden in the leaf rosettes on the cushion surface. Melcher et al. (2000) conclude on the basis of seed morphology that seeds from the genus *Azorella* are adapted to water dispersal and Chapuis et al. (2004) limit seed dispersal by wind to 30 – 100 m. However, although cushions were chosen that were not in immediate proximity to rocks or other cushions (minimum distance of 50 cm), there were many rocks and other cushions in the study area, at a distance much closer than 30 m. Seeds therefore do not have to be dispersed across very large distances to end up around rocks or cushions other than their parent cushions. Nevertheless, it cannot be ruled out that some of the *A. selago* seedlings were from the study cushions themselves. The sampling scheme for this study was not designed to distinguish between seedling sources. Genetic analyses will be useful to conclusively exclude (or alternatively confirm) seedling sources for *A. selago* seedlings found around cushions. The association of *A. magellanica* seedlings with both cushions and rocks, however, provides support that, at least for *A. magellanica*, something other than local dispersal effects is responsible for the observed patterns.

Second, the possibility is considered that cushions and rocks act as traps for dispersed seeds. Kleier and Lambrinos (2005) suggest that plants can act as seed traps in barren windy landscapes (see also Bullock and Moy, 2004) and Pérez (2009) discusses how the presence of rocks affects sediment movement and plant distributions. A trapping mechanism could certainly be the case for *A. magellanica*, where significantly more seedlings were found around both cushions and rocks, compared to open soil plots. *A. magellanica* seeds are transported within their spikelets, which are jagged, potentially enhancing adherence to surfaces (Combrinck et al., unpublished results). In contrast to Pérez (2003), who concluded that seedlings of the “giant” rosette,

*Argyroxiphium sandwicense*, establish more readily downslope of large clasts that provide protection from downslope moving sediment, significantly more *A. magellanica* seedlings were found on upslope cushion and rock sides in this study. It is possible, however, that the larger particle sizes found upslope of obstructions such as cushions and rocks (Chapter 2; Pérez, 2003), facilitate effective seed entrapment (Chambers et al., 1991; Jumpponen et al., 1999). Transport of trapped *A. magellanica* seeds is probably through wind dispersal, especially as *A. magellanica* seeds are presented on culms that extend 15 cm or higher into the air, thereby facilitating wind dispersal. Alternatively, downslope sediment transport through frost creep could disperse seeds of both species. Needle ice, which is known to form on calm, clear nights (Outcalt, 1971), is the dominant form of segregation ice on the island (Boelhouwers et al., 2003; Holness, 2003). As the needle ice crystals grow, they push a layer of soil particles upwards, which is subsequently transported downslope as the soil settles back upon thawing, a process known as frost creep (Washburn, 1973). It is likely that seeds are transported along with these soil particles (see for example Castor and Arroyo, 1997; Arroyo et al., 1999) and subsequently trapped on upslope cushion sides. Another potential seed transport mechanism on slopes that would lead to seeds being trapped and concentrated around objects such as rocks and cushions is overlandflow. According to Melcher et al. (2000) both the genera *Azorella* and *Agrostis* possess adaptations to water dispersal. .

A trapping mechanism is also considered possible for *A. selago* seeds. In this case, either trapped seeds do not germinate or seedlings do not survive around rocks, or, alternatively, cushions are more effective at trapping *A. selago* seeds than rocks. However, rocks appear to be quite effective seed traps for *A. magellanica* seeds. As there is no apparent reason that rocks would act as differential seed traps, trapping seeds of one species, but not of the other, this latter possibility is considered unlikely. It is therefore considered more likely that *A. selago* seeds are trapped by both cushions and rocks, but that cushions provide some form of nurse benefit, e.g. increased nutrient concentrations, mycorrhizal associations (see review by van der Heijden and Horton, 2009) that rocks do not provide, which favour *A. selago* seed germination or seedling survival. No differences were observed in *A. selago* seedling numbers between different cushion directions or sides, providing further support that the nature of the nurse effect is biological, rather than mechanical (e.g. protection from directional wind or moving sediment).

The third possibility is that seeds are dispersed randomly and not trapped by cushions or rocks, i.e. that they also reach the open soil plots. At lower altitudes, open soil areas in fellfield habitats are littered with *A. magellanica* seedlings in the coleoptile stage in late summer and autumn, suggesting that *A. magellanica* seeds are, at least in some instances, capable of reaching open areas. Seedlings probably do not establish in these areas due to scouring by wind-blown gravel. If seeds do indeed reach open soil plots, the results imply a biological nurse effect of *A.*

*selago* cushions for *A. selago* seedlings, as more seedlings were found around cushions than around rocks or open soil plots. No significant difference in *A. magellanica* seedling numbers were found around cushions and rocks, indicating that, in addition to benefiting from the nurse effects of cushions, the requirements of *A. magellanica* seedlings are such that they are also able to benefit from the physical nurse effects provided by rocks (see Pérez, 2009 for a recent review of such nurse effects). Buffered soil temperatures and higher soil moisture levels have, for example, been found next to large boulders compared to open soil areas in the Chilean Andes (Kleier and Rundel, 2009). Furthermore, upslope cushion/rock sides mostly coincided with northern cushion sides, where increased seedling abundance (albeit not significant) was observed. Increased *A. magellanica* seedling numbers on upslope (northern) cushion and rock sides could therefore be a result of increased solar radiation, leading to higher soil and cushion temperatures (see Hugo et al., 2004) on northern sides.

For both species, more seedlings than expected were found in the centre of the 15 cm range from the cushion edges, with fewer seedlings than expected closer to and further away from the cushion. This could indicate increased competition, possibly for nutrients, closer to the cushion edges, especially as far more *A. magellanica* seedlings than expected were found against rock edges. It is also possible that seeds of both species are dispersed from the *A. selago* cushions through water (either from rain or snowmelt) running off the cushion, resulting in a different distribution of seedlings with distance from cushions (which host seeds) and rock edges. Lastly, other potential factors affecting seedling numbers are seed shed, which is probably much greater for *A. magellanica* than *A. selago* at the study site, and post-dispersal seed predation, which possibly varies between the two species (see Muñoz and Cavieres, 2006). Although these factors could explain differences in the numbers of seedlings found, they do not explain the specific seedling distribution patterns adequately.

Although cushion plants have also been known to propagate asexually through a process of fragmentation (Armesto et al., 1980; Mortimer et al., 2008), in general sexual reproduction seems to dominate (Frenot and Gloaguen, 1994; Bergstrom et al., 1997; Fajardo et al., 2008). However, little is known about the reproductive capacity of either *A. selago* or *A. magellanica* (Frenot and Gloaguen, 1994), as germination experiments with seeds of both species have proven unsuccessful (Frenot and Gloaguen, 1994). In addition, *A. selago* and *A. magellanica* are the most widespread and second most widespread vascular plants respectively on the island (Huntley, 1972) and there is evidence to suggest that the interaction between the two species affects larger scale community composition patterns (le Roux and McGeoch, 2008b). It is therefore advocated that, to further our understanding of spatial distributions and interactions of these two species, an increased knowledge of seed and seedling requirements, distribution patterns and microhabitats is necessary.

## Conclusions

*Azorella selago* cushions positively affect the distribution of both intra-specific seedlings and those of the perennial grass, *Agrostis magellanica*. It is unlikely that this is the result of very localised seed dispersal. However, whether these distribution patterns are the result of cushions acting as seed traps or alternatively, providing some form of mechanical and/or biological nurse effect or a combination of both mechanisms cannot be shown conclusively. Genetic analyses are needed to determine the origin of *A. selago* seedlings found around cushions. Furthermore, seed dispersal studies are needed to gain insights into dispersal patterns and trapping mechanisms of both species.

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Table 1. Overview of *Azorella selago* and *Agrostis magellanica* seedling numbers around cushions, rocks and open soil plots. N = 12 in all three cases.

	<i>Azorella selago</i>		<i>Agrostis magellanica</i>	
	Mean ± S.D.	Total	Mean ± S.D.	Total
Cushion	2.00 ± 2.09	24	2.83 ± 2.08	34
Rock	0.25 ± 0.45	3	3.08 ± 3.65	37
Open soil	0.08 ± 0.29	1	1 ± 0.95	12
Total		28		83



Figure 1. The study site. Notice the high percentage of rock cover characteristic of fellfield vegetation, interspersed with cushions of *Azorella selago*. The site ( $46^{\circ} 52.6' S$ ,  $37^{\circ} 39.1' E$ ) was located on grey lava substrate at an altitude of  $220 \pm 5$  m a.s.l.



Figure 2. Example of a.) a cushion, b.) a rock and c.) an open soil area used for the seedling inventory. The ruler in the photos is 15.5 cm long and the arrow points north.

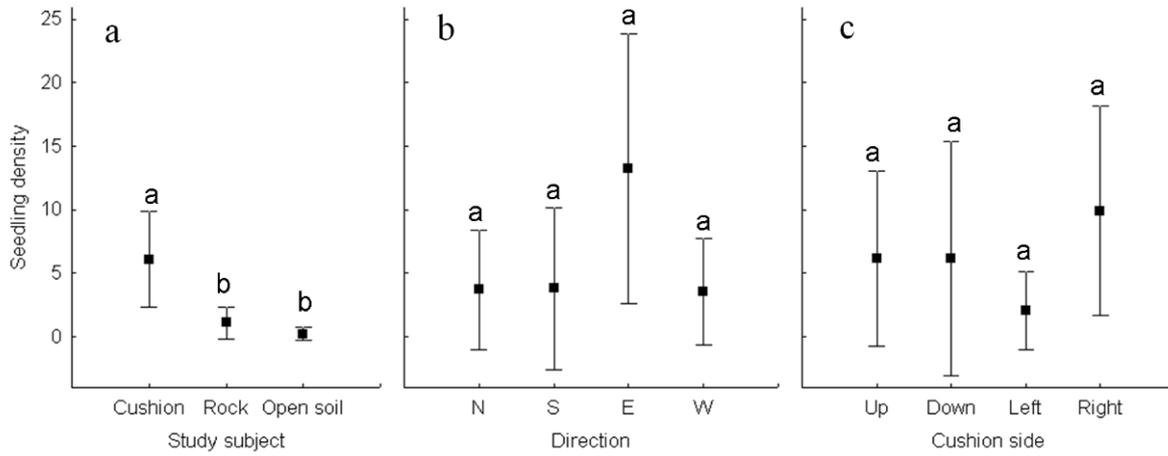


Figure 3. *Azorella selago* seedling densities (seedlings per m<sup>2</sup>) a.) around *A. selago* cushions, rocks and open soil, b.) on different directions from *A. selago* cushions and c.) on different sides of *A. selago* cushions. Values are means  $\pm$  95% confidence intervals. N = 12 in all cases. Lower case letters denote differences at the 95% significance level.

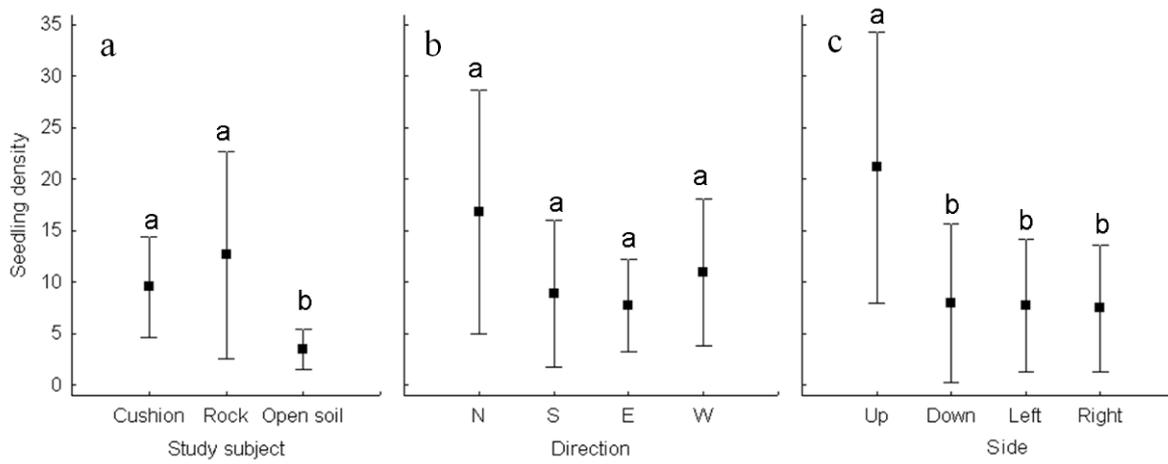


Figure 4. *Agrostis magellanica* seedling densities (seedlings per m<sup>2</sup>) a.) around *Azorella selago* cushions, rocks and open soil, b.) on different directions from cushions and rocks and c.) on different sides of cushions and rocks. For graphs b and c cushions and rocks were grouped together as the interactive effects were not significant. Values are means  $\pm$  95% confidence intervals. N = 12 for graph a and 24 for graphs b and c. Lower case letters denote differences at the 95% significance level.

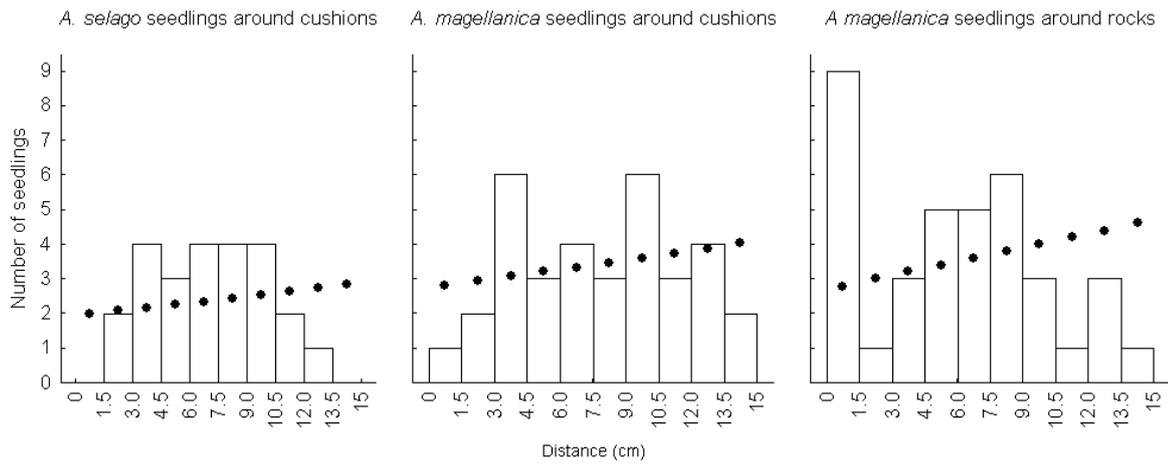


Figure 5. Histograms of distance of seedlings from cushion/rock edges. From left to right is *Azorella selago* seedlings around cushions (total number of seedlings = 24), *Agrostis magellanica* seedlings around cushions (total number of seedlings = 34) and *Agrostis magellanica* seedlings around rocks (total number of seedlings = 37). *Azorella selago* seedlings around rocks are not shown, as only three seedlings were found in this instance. The black dots give expected seedling numbers, based on an even distribution. The expected seedling numbers increase with distance from cushion/rock, as the search areas increase.

## Chapter 5 – Exploring the determinants of *Azorella selago* seedling densities and distributions

### Introduction

Plant species' distributions have been known to vary in response to abiotic stress gradients, such as temperature and moisture levels or wind stress (Huntley, 1970; Klanderud and Birks, 2003; Daehler, 2005). For example, on sub-Antarctic Marion Island (46° 54' S, 37° 45' E) vascular plant species' altitudinal limits have mainly been attributed to the effects of temperature and wind chill (Huntley, 1970), which can be severe, especially at higher altitudes (Schulze, 1971; le Roux and McGeoch, 2008c). These altitudinal limits have recently been shown to have shifted upslope (le Roux and McGeoch, 2008b) in response to warming on the island (Smith, 2002; le Roux and McGeoch, 2008a), demonstrating the tight coupling between ecosystems and climate in severe environments (Klanderud and Birks, 2003). It is thus necessary to understand the interactions between plant species' distributions and climatic severity in such environments, especially in very young individuals, which are particularly vulnerable to climatic variability (Fenner, 1987). In this respect, altitudinal gradients provide excellent opportunities for studying plant species' (including seedling) responses to climatic variability (Paiaro et al., 2007), especially in the context of climate change (Klanderud and Birks, 2003; le Roux and McGeoch, 2008b).

A number of studies have used altitudinal gradients to study variation in seedling recruitments and seed dynamics globally (Funes et al., 2003; Akasaka and Tsuyuzaki, 2005), often in the context of invasive species research. These studies often demonstrate the ability of invasive species to establish at higher altitudes (Akasaka and Tsuyuzaki, 2005; Paiaro et al., 2007), thereby emphasising the vulnerability of native species at higher altitudes and the need for increasing our understanding of native seedling distributions. Although the altitudinal limits of the complete vascular flora on Marion Island have been determined (Huntley, 1970; le Roux and McGeoch, 2008b), relatively little is known about the distribution of seedlings. For example, Phiri (2008) demonstrated that, despite the gradual altitudinal decline in temperatures and corresponding increase in soil frost features (Boelhouwers et al., 2003), the abundance of the keystone, dominant vascular cushion plant species on the island, *Azorella selago*, does not decline gradually, but instead shows an abrupt, stepped altitudinal decline at approximately 670 m a.s.l. (with the maximum recorded *Azorella* individual found at 840 m a.s.l. (Huntley, 1971; le Roux and McGeoch, 2008b)). However, Phiri (2008) focussed on adult cushions and did not specifically include seedlings in her study. Such adult *Azorella* cushions have been reported to have quite extensive root systems, providing anchorage and support against recurrent soil frost cycles (Frenot et al., 1998). Seedlings

in general, however, have been known to be particularly vulnerable to environmental stresses (Fenner, 1987). Seedling mortality as a result of needle ice and frost heave, for example, has been well documented (Haasis, 1923; Schramm, 1958; Mack and Pyke, 1984; Goulet, 1995).

In addition to increased abiotic stresses associated with altitudinal increases, plant species (including seedlings) are also affected by the surrounding sediment substrate. Effective seed entrapment has, for example, been shown to be related to particle size, with bigger size classes trapping seeds more effectively (Chambers et al., 1991). In addition, sediment particle size has also been shown to affect subsequent seedling establishment and survival (e.g. Jumpponen et al., 1999; Chambers, 2001; Kleier and Rundel, 2004). Furthermore, seedlings in climatically severe environments have often been shown to be associated with rocks and other objects providing “safe sites” for establishment and growth (Chapter 4; Ralph, 1978; Pérez, 1987; Jumpponen et al., 1999; Schlag and Erschbamer, 2000; Kleier and Rundel, 2004), suggesting that seedling distributions could potentially be co-determined by the surrounding substrate.

Spatial analysis of ecological data has received considerable attention in ecological research lately (see for example Liebhold and Gurevitch, 2002). Determining species’ spatial aggregations could potentially provide information regarding competition, facilitation, resource availability and dispersal patterns. Decreasing spatial aggregation with age has, for example, been found for certain tree species, with aggregated seedling distributions and more random distributions at later life stages (Haase et al., 1996; Deckers et al., 2005). This has subsequently been ascribed to density dependent mortality as a result of intraspecific competition (see also Nyakatya, 2006 for this hypothesis concerning *A. selago*).

Lastly, because of high frost and wind stress, it was hypothesised that only a small percentage of *A. selago* seedlings survive, despite *A. selago* recruitment being high, so that the number of small cushions is very low (see le Roux and McGeoch, 2004; Mortimer et al., 2008). Once seedlings have an established root system, however, it is easier for them to survive and it was therefore hypothesised that the numbers of larger cushions therefore increases again (also see Fajardo et al., 2008).

In light of the above, the aim of this study was to explore the determinants of *A. selago* seedling densities and distributions. This was done by firstly describing the seedling environment in terms of the surrounding substrate, then describing *A. selago* seedling distributions in terms of spatial aggregation and lastly exploring relationships between *A. selago* size class distributions, seedling abundance, altitude and substrate.

## Methods

### Field methods

Nine study sites were selected on the eastern side of Marion Island to represent three altitudinal categories: 100-200 m a.s.l., 200-300 m a.s.l. and 300-400 m a.s.l. (Figure 1). The study sites were selected from three grey lava ridges (and outcrops located inland of these ridges), namely Stoney Ridge, Skua Ridge and Longridge. These grey lava ridges and related outcrops traverse the eastern side of the island from the coast towards the interior, comprising long stretches of relatively flat terrain. As such they presented ideal locations for studying altitudinal variation in seedling numbers on fellfield vegetation, while controlling for slope angle. For each of the three altitudinal categories, three study sites (hereafter referred to as Stoney (low, mid, high), Skua (low, mid, high) and Longridge (low, mid, high)) with slope angles of no more than 5 degrees were selected (Table 1).

At each site twenty 1 x 1 m quadrats were sampled systematically for seedlings. The quadrats were arranged in a rectangle of 5 x 4 rows (Figure 2). The distance between quadrats was between approximately 10 and 20 m, depending on the size over which the area met all three criteria (fellfield vegetation, grey lava substrate and relatively low slope angles) and was determined by walking 10-20 steps between quadrats. Photographs (Pentax Optio W60, 5-25 mm, 10 MP) of each quadrat were taken vertically at the highest resolution (10 megapixel) and highest quality JPEG compression (Appendix A-I). Each 1 x 1 m quadrat was searched for *A. selago* seedlings and cushions smaller than 15 cm. For this study a seedling was defined as a small plant with up to three leaves in addition to the cotyledons, as these were identified by Fenner (1987) as commonly used criteria for defining a seedling in ecological studies. Furthermore, the substrate in which the seedling was found to be rooted was described.

For plants larger than seedlings, but smaller than 15 cm diameter, the maximum diameter, maximum diameter perpendicular to the maximum diameter and height were recorded. Such a plant was considered inside the quadrat when the approximate centre of the plant was located inside the quadrat. In addition, cushions larger than 15 cm diameter were recorded from a larger quadrat (20 x 20 m), extending from and including the first 1 x 1 m quadrat at each site (Figure 2).

### Data analyses

Substrates were described in terms of the area of each quadrat covered by each of the following sediment size classes (see Wentworth, 1922): boulder (> 256 mm), cobble (64-256 mm),

very coarse gravel (32-64 mm), coarse gravel (16-32 mm), medium gravel (8-16 mm), fine gravel (2-8 mm) and sand (< 2mm). These values were estimated from the photographs of the 1 x 1 m quadrats. Furthermore, the area of each quadrat covered by *Azorella selago* cushions, moss, grass (*Agrostis magellanica*) and other vegetation was also estimated from the photographs. Principle Component Analysis (PCA) was used to assess relationships between cover class (substrate and vegetation classes), site and altitude. Variables were square root transformed prior to analysis and results were subsequently visualised using a species-by-samples biplot.

For each of the nine sites, SADIE (Spatial Analyses for Distance Indices) was used to assess seedling distributions in terms of spatially explicit aggregation (Perry, 1995; Perry and Dixon, 2002). The dimensionless index  $v_i$  was calculated as a measure of clustering using red-blue techniques (Perry et al., 1999) and the software package SADIEShell (SADIEShell, version 1.22, 2001, Kelvin F. Conrad and Rothamsted Research). Because the data were not normally distributed, the non-parametric option was selected for the analyses (Perry and Dixon, 2002). Values of  $v_i > 1.5$  indicate patchiness, whereas  $v_i < -1.5$  indicates membership of a gap. Values approaching one indicate a random distribution (Perry et al., 1999).

Seedling numbers were compared between sites using a generalised linear model (GLM) with Poisson distribution and log link function (Quinn and Keough, 2002). Seedling numbers were corrected for overdispersion and model significance subsequently determined using Type III likelihood-ratio tests. Total numbers of seedlings were calculated per site, as well as the total contribution (in m<sup>2</sup>) of each of the various substrate and vegetation classes to the total area (20 m<sup>2</sup>) assessed. Each of the explanatory variables (absolute altitude, number of adult cushions, substrate cover) were subsequently plotted against seedling numbers and Spearman rank correlation coefficients were used to test for linear relationships across sites. Spearman rank correlations were also used to test for linear relationships between seedling numbers and substrate cover (sediment or vegetation) within each of the nine sites. As “other vegetation” did not occur at 6 of the nine sites and had very low cover values at the sites where it did occur (between 0.1 and 1 %), this variable was excluded from the correlation analyses.

Lastly, *A. selago* size class distributions were calculated and described per site for the whole range of size classes by extrapolating the numbers of seedlings and small cushions (< 15 cm) from a 20 m<sup>2</sup> area to a 400 m<sup>2</sup> area (the size of the area used to measure larger cushions).

## Results

A total of 276 seedlings were found across all nine sites, with the number of seedlings per 1 x 1 m quadrat varying between 0 and 13 (Table 2, Figure 3, Appendix J-R). Almost half (80) of the

180 quadrats searched across all nine sites were found to host no seedlings (Figure 3). Seedlings were found to occur in various different substrates, ranging from the rich dark humus material left behind when pieces of an adult *Azorella* cushion breaks off to medium-sized gravel of approximately 10-15 mm diameter (Figure 4 and 5). Approximately one third (32.6%) of all seedlings were found to occur in a mixture of humus, moss and gravel of ranging size.

The first two PCA axes (PC1 and PC2) were found to explain 46 % of the total variation in substrate distribution. Variables for which more than 50 % of the variation was accounted for by these two axes were fine gravel, medium gravel, coarse gravel and cobble. Variables for which less than 50 % of the variation was accounted for were not included in the species-by-samples biplot (Figure 6). Some of the sites formed clear clusters and were clearly related to one or more substrate classes, e.g. Stoney Mid was clearly related to higher values of MG (Figure 6). The majority of sites, however, did not show any clear relationships with any substrate classes. Furthermore, altitude categories were also not clearly related to any of the substrates (Figure 6, white, black and grey markers).

The spatially explicit aggregation index  $v_i$  indicated that none of the sites showed spatial distributions differing significantly from random (Table 3). Total seedling numbers varied greatly, especially at higher altitudes, and differed significantly between sites ( $X^2 = 47.02$ ,  $df = 8$ ,  $p < 0.001$ , see also Table 2). The only variable that was significantly correlated with seedling numbers when averaging the data per site was area covered by grass ( $\rho = 0.78$ ,  $p < 0.05$ , see also Table 4). However, when looking at each site individually, only one site showed a significant correlation between the area covered by grass and seedling numbers (Longridge High,  $\rho = 0.65$ ,  $p < 0.05$ ). Although the highest seedling abundance was consistently recorded at the lowest altitude (100-200 m), overall seedling abundance was not significantly correlated with altitude and no consistent patterns were observed for seedling abundance between the remaining two altitude categories (200-300 and 300-400 m, see also Table 2).

The total number of cushions (excluding seedlings) recorded from the 400 m<sup>2</sup> area varied between sites, from 98 to 488, resulting in mean cushion densities ranging between 0.25 cushions/m<sup>2</sup> and 1.22 cushions/m<sup>2</sup>. Both the smallest and largest cushion numbers were recorded from sites in the highest altitude category (Table 2). In addition, no significant correlation was found between the number of adult cushions and altitude ( $\rho = -0.06$ ,  $p > 0.05$ ). Mean cushion diameter ranged from 10.1 cm to 125.3 cm and great variation was recorded within each site (Table 2). Again, both the smallest and largest mean diameters were recorded from sites in the highest altitude category (Table 2) and no significant correlation was found between cushion diameter and altitude ( $\rho = -0.14$ ,  $p > 0.05$ ).

In general no consistent patterns were observed in *A. selago* size class distributions and, although several sites had lacking size classes, no consistent gaps were noted in the size class distributions across all sites. Seedlings were, however, the most frequently occurring size class at all nine sites. In addition, the proportion of individuals that were seedlings were higher at the low-altitude sites than at the mid- and high-altitude sites (Figure 7).

## Discussion

The mean annual air temperature on Marion Island shows a clear altitudinal decrease from 4.8 °C at 200 m a.s.l. to 1.5 °C at 750 m a.s.l. to 0.8 °C at 1000 m a.s.l. (measurements at 10 cm height, Boelhouwers et al., 2003; see also Deere et al., 2006 for soil temperature data). Concordant variations in percentage plant cover (Gremmen, 1981), community composition (Gremmen, 1981; Smith and Steenkamp, 2001), and interactions between species (le Roux and McGeoch, 2008c) with altitude have been documented on the island. Despite these altitudinal patterns, no clear links between altitude and either substrate distributions or seedling abundance were found in this study. Although needle ice and related frost heave occur at all altitudes (Boelhouwers et al., 2003), an altitudinal increase in the number of freeze-thaw days and depth of soil freezing has been documented as well as altitudinal patterns in patterned ground morphology (Boelhouwers et al., 2003; Holness, 2003), demonstrating an increase in frost severity with altitude. An altitudinal increase in frost related periglacial weathering processes could therefore be hypothesised, leading to altitudinal variation in substrate size and morphology. However, altitudinal differences in this study were likely too small to detect such variation. Nevertheless, the aggregation of some sites (e.g. Stoney Mid) into clusters and the related association with specific size classes on the species-by-samples biplot indicates that variation in some unaccounted properties between sites (such as lithology or local climatic variables) plays a role to some extent in determining substrate size class distributions.

Results of the SADIE analyses show that seedlings were randomly distributed at this spatial scale at all nine study sites, i.e. quadrats of higher seedling densities were randomly distributed amongst quadrats of lower seedling densities. This absence of a consistent spatial pattern to seedling distribution could indicate that microsites occur on very small spatial scales and are randomly distributed at the study sites, i.e. there are no clear spatial gradients from favourable microclimates to less favourable microclimates at this spatial scale. However, it is important to note that spatial aggregation is scale-dependent. It is therefore possible that spatial aggregation is present at lower spatial scales, for example if quadrats were arranged closer together. At very low spatial scales (within the 1 x 1 m quadrats) seedlings were occasionally clumped together in small clusters

(with the highest number of seedlings recorded from a single 10 x 10 cm cell being four). However, seedling densities were mostly too low (the highest number of seedlings from a 1 x 1 m quadrat was only 13) for clustering patterns at this very low spatial scale to be ecologically meaningful.

Although seedling distributions did not differ significantly from random, there were some localised areas of higher seedling densities within the study sites (i.e. seedling densities were not evenly distributed). Results could therefore be indicative of dispersal patterns, with seedlings possibly distributed in small pockets and some of the quadrats having more favourable microsite conditions for seed germination. Alternatively, seed distribution could be even and seed numbers quite high and favourable microsite conditions variable, resulting in high seedling densities in areas of more favourable conditions and lower seedling densities in areas where seeds were not able to germinate.

Although seedling abundance in the study did not differ significantly between altitudes, the highest number of seedlings was consistently recorded at the lowest (100-200 m a.s.l.) altitudes. Furthermore, the percentage of all individuals that were seedlings was consistently highest at the lowest altitude sites, suggesting that either recruitment is higher in less severe environments or seedlings are better able to survive under reduced environmental stress. However, cushion (non-seedling) numbers did not always follow seedling distributions, i.e. sites with the highest seedling abundance did not necessarily have the highest number of adult cushions, suggesting that recruitment is largely dependent on site specific properties. Topographically related variations in snow cover and wind exposure as well as microclimatic differences in soil nutrients and moisture have been suggested to be important factors for plant performance in climatically severe environments (Frenot et al., 1993; Callaghan and Carlsson, 1997; Jumpponen et al., 1999). These factors probably also affect growth and reproduction dynamics on Marion Island.

For two of the three ridges, both seedling and adult cushion abundance were higher at the high-altitude (300-400 m) sites than at the mid-altitude (200-300 m) sites. Whereas increased frost severity possibly plays a role in determining seedling numbers at high altitudes, competition from other plant species is very unlikely, as plant cover at higher altitudes consists almost entirely of *A. selago* cushions (Huntley, 1971). At lower altitudes, the reversed situation occurs, i.e. *A. selago*, which is known to be a stress-tolerator, has been suggested to be out-competed by other species (Rautenbach, 2007; see also Callaghan and Carlsson, 1997), but frost severity plays a less important role than at high altitudes. It is possible that at the mid-altitude sites, the combined effect of frost action and competition have a more negative effect on seedling establishment and survival than the individual factors alone at low and high altitudes. In addition, seedling abundance could be very site specific, with small scale local variation in microclimates and exposure playing an important role at higher altitudes. Overall, however, *A. selago* cushion abundance (for all individuals larger than

seedlings) was not related to altitude, supporting the findings of Phiri (2008) of very site specific variation below 670 m a.s.l. Mean cushion densities per altitude ranged between 0.69 and 0.73 cushions/m<sup>2</sup>, which is slightly lower than the mean density of 0.81 cushions/m<sup>2</sup> found by Phiri (2008) for sites occupied by discrete cushions (as opposed to continuous mats). However, Phiri (2008) did not restrict her study to grey lava, fellfield habitats. Sites from her study that were in close proximity to sites in this study were mostly on black lava substrate or on different vegetation communities, i.e. not fellfield, and results are therefore not directly comparable. Results from Buwa (2007), however, match those from this study in the sense that higher altitude sites on Skua Ridge and related outcrops had higher mean cushion diameters. However, Buwa (2007) selected cushions within a certain size class (37-477 cm circumference) and again, results are therefore not directly comparable.

The only substrate class that was found to be significantly correlated with seedling numbers was grass cover, i.e. a significantly positive correlation was found across all nine sites. However, within the nine study sites, only one site echoed this correlation between seedling number and grass cover. This indicates that, despite sites with higher aerial cover of grass having higher seedling numbers, seedlings and grass were not necessarily found to occur in the same quadrats within a site. Results therefore suggest that seedlings and rocks respond to the same abiotic, site specific variables, e.g. local topography such as the protection provided by a ridge or local scoria outcrop, rather than being indicative of facilitation between the species (le Roux and McGeoch, 2008c).

Numerous authors have reported reversed J-shaped curves for the size class distributions of cushion plant species (Kleier and Rundel, 2004; Zoller and Lenzin, 2006; Fajardo et al., 2008). Reduced frequency of smaller size classes have also been shown in an Andean stem-rosette species, possibly indicating episodic reproduction (Pérez, 1987), although other tropical alpine rosette species show size class distributions where every size is equally represented (Young and Peacock, 1992). Le Roux and McGeoch (2004) found very low numbers of small individuals of *A. selago* on Marion Island (although seedlings were not included in their sampling strategy). This has been attributed to episodic, but frequent temporal recruitment (Mortimer et al., 2008; see also Callaghan and Carlsson, 1997). Furthermore, long-lived plants (such as *Azorella selago*, Ternetz, 1902; le Roux and McGeoch, 2004) have been found to have a relatively high seedling mortality and better survival in adulthood (Fenner, 1987). The results of this study show that seedling recruitment is high, with a drop in *Azorella* numbers for subsequent size classes, indicating high mortality as expected. There was, however, not one specific size class that was consistently underrepresented at all nine sites, suggesting that successful seedling establishment and survival is largely controlled by unaccounted site specific properties. The importance of unaccounted site specific properties relative to altitudinal variation is further emphasised by the finding that the highest altitude sites had both

the highest and lowest numbers of cushions as well as the largest and smallest mean diameters of cushions.

The importance of vegetative reproduction in high latitude (and altitude) environments has often been mentioned (Bliss, 1971; Grulke and Bliss, 1983). According to Callaghan and Carlsson (1997) clonal reproduction dominates over seedling recruitment in the sub-Arctic and low Arctic. However, seedling recruitment has been suggested to be more important in higher latitude, barren, open landscapes than at more vegetated lower latitudes in the sub-Arctic (Callaghan and Carlsson, 1997). In addition, studies on cushion plant species specifically suggest that sexual reproduction is dominant for this life form (Frenot and Gloaguen, 1994; Bergstrom et al., 1997; Fajardo et al., 2008). As microsite conditions clearly play an important role in seed germination and seedling establishment, further quantification of such microsite requirements is important for understanding cushion plant population dynamics.

## Conclusions

Although there appears to be some altitudinal trend in *Azorella selago* seedling abundance, with the highest numbers of seedlings consistently found at the lowest altitudes, no significant relationship between altitude and seedling numbers was found. Instead, seedling abundance varied greatly between sites and therefore appears to be largely dependent on unaccounted site specific properties. Seedling abundance was independent of sediment substrate size, but was significantly correlated with grass cover across the nine study sites. The absence of such a correlation within the study sites, however, suggests that seedlings and grass respond to the same abiotic variables, rather than being indicative of facilitation. No size classes were consistently underrepresented from the size-class distributions, suggesting that *A. selago* growth dynamics is largely dependent on unaccounted site specific properties. However, seedlings constituted the largest proportion of cushions at all sites, indicating high recruitment and reduced survival into subsequent size classes as indeed expected.

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Table 1. Altitudes and coordinates of the nine study sites. Values in brackets are GPS error estimates.

Site name	Altitude (m a.s.l.)	Coordinates (South)	Coordinates (East)
Stoney Low	120 ( $\pm 5$ )	46° 54.855'	37° 51.861'
Stoney Mid	200 ( $\pm 5$ )	46° 54.949'	37° 50.720'
Stoney High	300 ( $\pm 5$ )	46° 54.521'	37° 49.593'
Skua Low	127 ( $\pm 5$ )	46° 52.037'	37° 50.357'
Skua Mid	220 ( $\pm 5$ )	46° 52.568'	37° 49.097'
Skua High	307 ( $\pm 5$ )	46° 53.126'	37° 48.474'
Longridge Low	144 ( $\pm 5$ )	46° 51.210'	37° 48.382'
Longridge Mid	200 ( $\pm 5$ )	46° 51.379'	37° 47.964'
Longridge High	346 ( $\pm 5$ )	46° 51.955'	37° 47.772'

Table 2. Variation in *Azorella selago* seedling and cushion characteristics across the nine study sites. Total number of *A. selago* excludes seedlings, but includes cushions < 15 cm. Cushion diameters are given as means  $\pm$  S.D. and were calculated excluding seedlings, but including cushions smaller than 15 cm diameter.

Site	Total no. seedlings (20 m <sup>2</sup> )	Total no. <i>A. selago</i> (400 m <sup>2</sup> )	Cushion diameter (cm)
Stoney Low	60	254	42.2 $\pm$ 43.1
Stoney Mid	6	229	21.8 $\pm$ 22.5
Stoney High	36	256	38.5 $\pm$ 46.2
Skua Low	63	364	38.7 $\pm$ 55.9
Skua Mid	22	212	47.0 $\pm$ 37.7
Skua High	4	98	125.3 $\pm$ 77.1
Longridge Low	37	261	46.3 $\pm$ 54.0
Longridge Mid	18	381	39.8 $\pm$ 43.4
Longridge High	30	488	10.1 $\pm$ 35.1

Table 3. Spatially explicit ( $v_i$ ) index of aggregation and p-values for seedling distributions at the nine study sites.

Site	$v_i$	P( $v_i$ )
Stoney Low	0.93	0.61
Stoney Mid	0.97	0.50
Stoney High	1.19	0.12
Skua Low	1.23	0.08
Skua Mid	0.85	0.89
Skua High	0.89	0.76
Longridge Low	1.28	0.07
Longridge Mid	0.98	0.45
Longridge High	1.23	0.08

Table 4. Substrate distributions at the nine study sites. Values are in m<sup>2</sup> and add up to approximately 20 m<sup>2</sup> (the total area assessed at each site). Only “grass” was found to be significantly correlated with seedling numbers ( $\rho = 0.78$ ,  $p < 0.05$ ). St = Stoney Ridge, Sk = Skua Ridge, Lo = Longridge. VCG = very coarse gravel, CG = coarse gravel, MG = medium gravel, FG = fine gravel.

Site	Seedlings	Boulder	Cobble	VCG	CG	MG	FG	Sand	<i>A. selago</i>	Moss	Grass
St Low	60	1.33	5.21	4.03	4.30	1.70	0.63	0.70	1.51	0.02	0.54
St Mid	6	0.66	2.59	2.37	4.73	4.98	3.91	0.64	0.10	0.01	0.01
St High	36	4.70	7.89	1.27	1.04	0.69	0.09	0.47	3.35	0.03	0.45
Sk Low	63	1.11	2.42	2.11	3.08	2.80	1.74	1.19	3.94	0.53	0.88
Sk Mid	22	3.96	4.33	2.03	2.29	2.33	1.21	2.00	1.20	0.27	0.38
Sk High	4	2.00	7.01	2.86	2.74	2.08	0.47	0.28	2.52	0.00	0.03
Lo Low	37	0.97	6.84	4.02	2.69	1.11	0.18	0.11	3.70	0.00	0.39
Lo Mid	18	1.63	6.28	3.80	3.13	1.47	0.21	0.09	2.90	0.01	0.48
Lo High	30	4.06	5.53	2.13	1.89	1.53	1.78	1.08	1.08	0.73	0.19

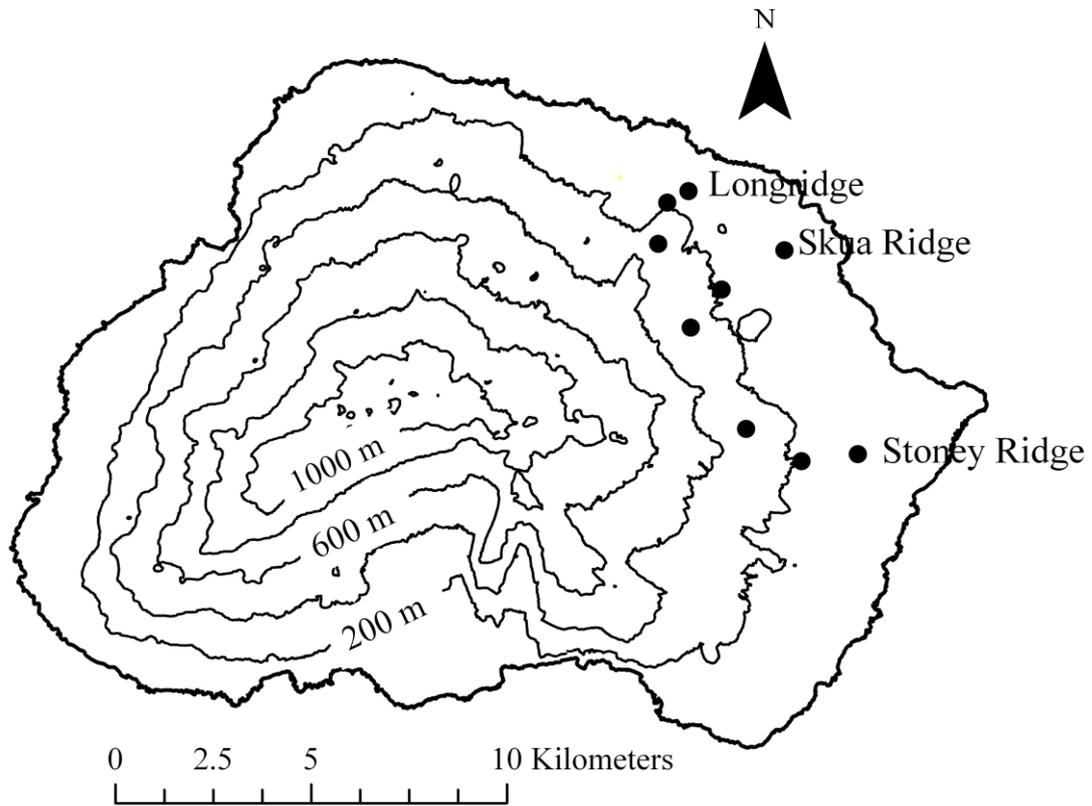


Figure 1. Location of the three grey lava ridges and the nine study sites on Marion Island. Contour lines are at 200 m intervals.

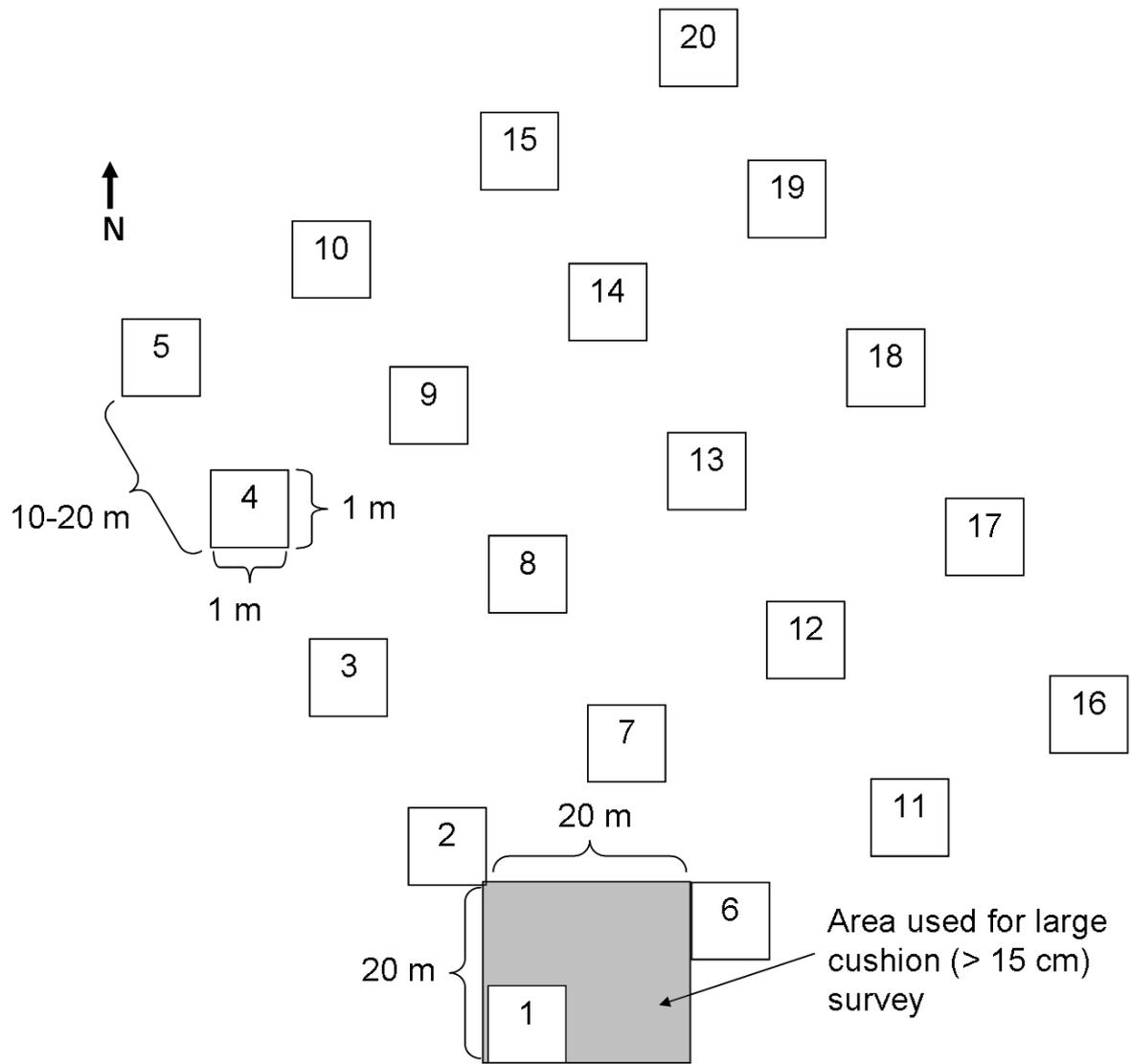


Figure 2. Layout of the sampling scheme. Note that the diagram is not drawn to scale.

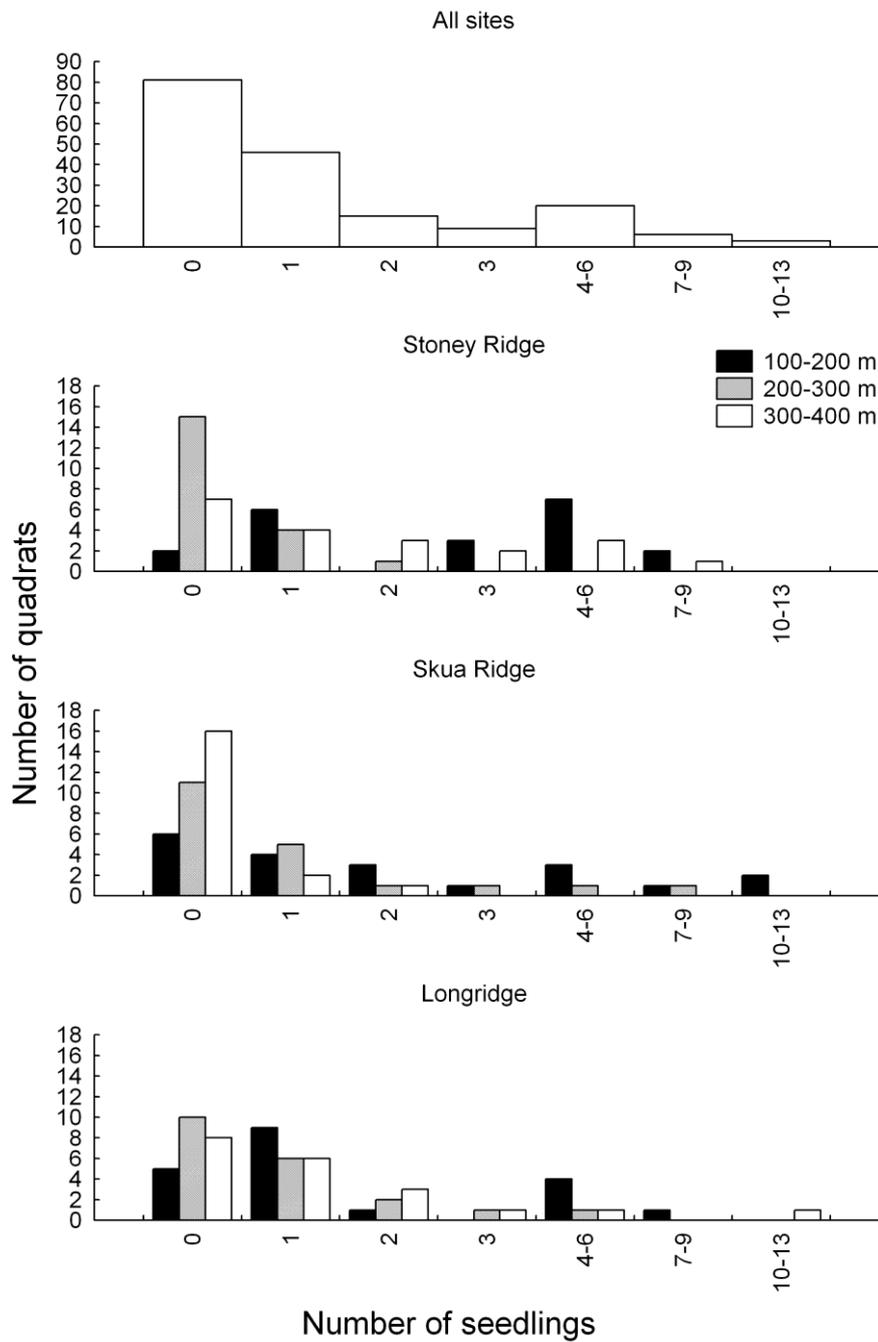


Figure 3. Frequency distributions of seedling numbers per quadrat for all nine sites combined, as well as per site (grouped per ridge). Graph legend indicates metres above sea level.

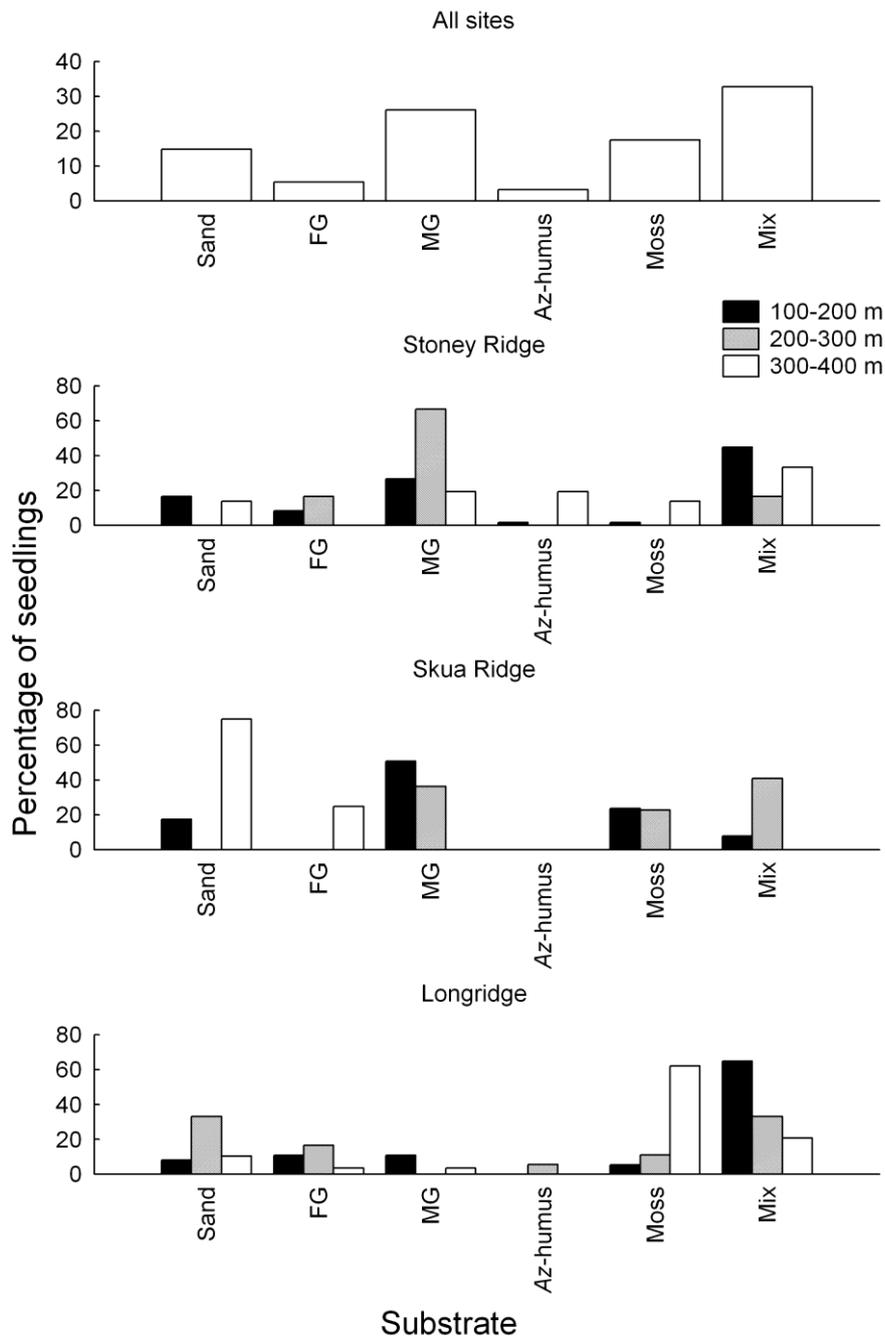


Figure 4. Bar plots of the various substrates that seedlings were found to be rooted in for all nine sites combined as well as per site (grouped per ridge). FG = fine gravel, MG = medium gravel, Az-humus = dark humic material from broken off *Azorella* cushion, Mix = mixture of substrates. Graph legend indicates metres above sea level.



Figure 5. Examples of substrates that seedlings were found to be rooted in: a.) sand, b.) fine gravel, c.) medium gravel and d.) moss.

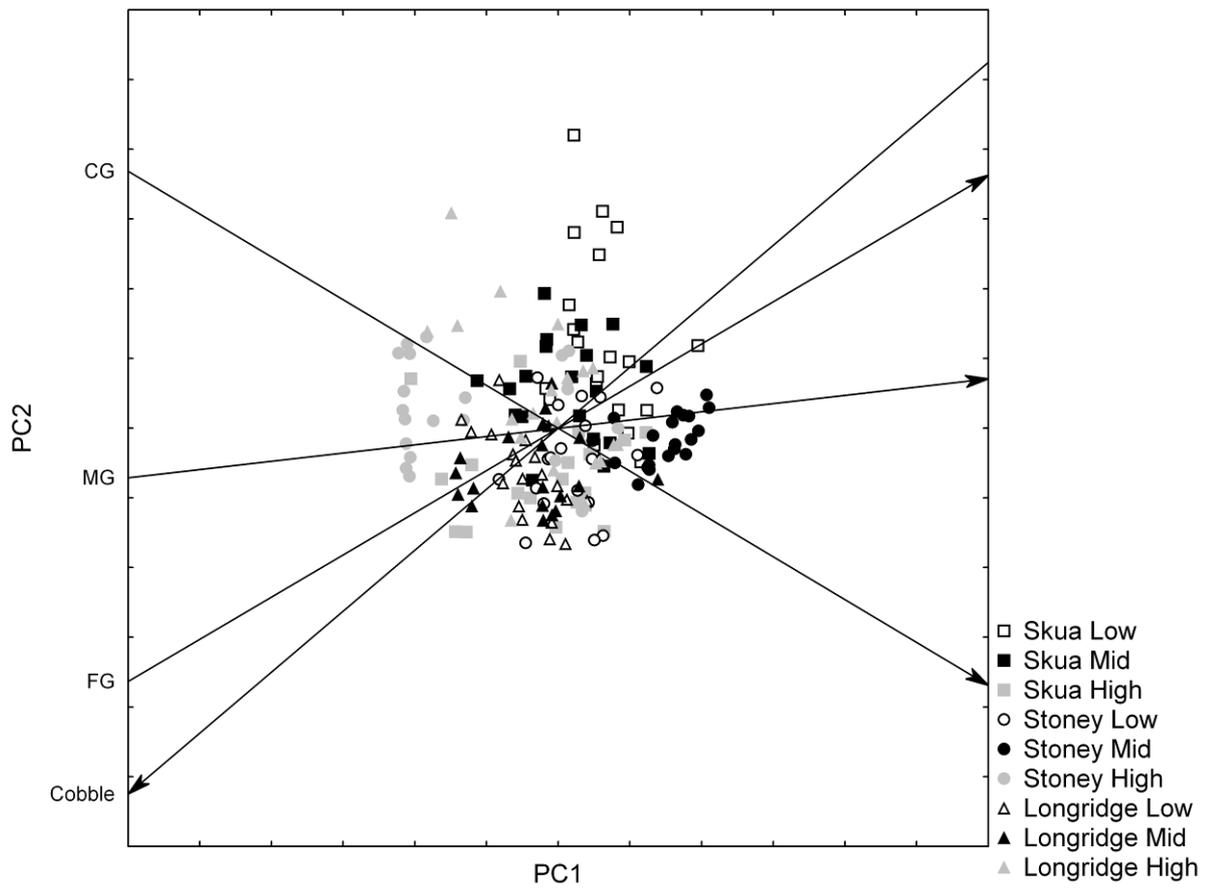


Figure 6. Species-by-samples biplot showing the relationship between the nine study sites and the four substrate classes for which more than 50 % of the variation was explained by the first two PCA axes. FG = fine gravel, MG = medium gravel and CG = coarse gravel.

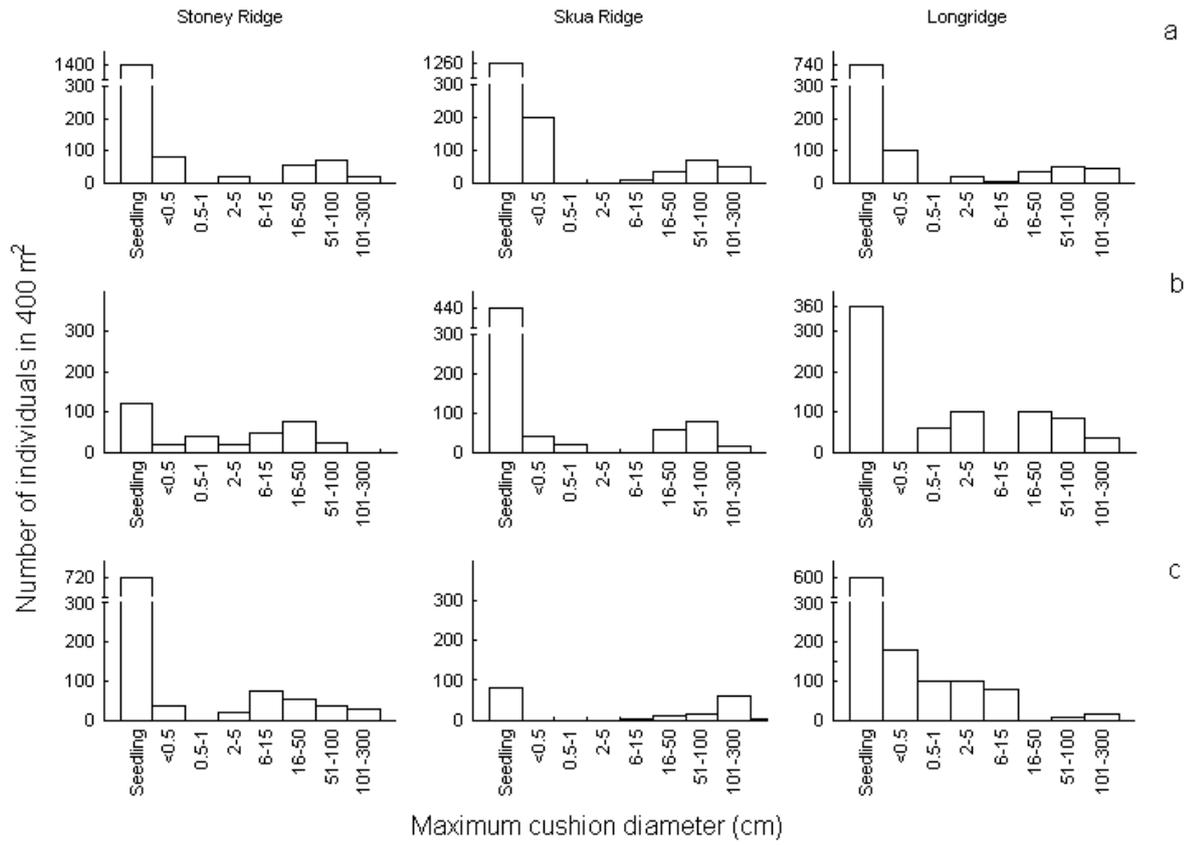


Figure 7. Frequency distributions of cushion sizes at a.) 100-200, b.) 200-300 and c.) 300-400 m a.s.l. Notice the scale break in the y-axis on some of the plots.

## Chapter 6 – $^{10}\text{Be}$ application to soil development on Marion Island\*

### Introduction

Marion Island (46° S, 37° E) is located in the southern Indian Ocean and together with its smaller neighbour, Prince Edward Island, constitutes the Prince Edward Islands Group. The island's area is approximately 290 km<sup>2</sup> and the highest peak is at 1230 m a.s.l. (de Villiers, 1976). Precipitation at the South African Meteorological Station on the eastern side of the island has steadily decreased from more than 2500 mm during the 1960s to just above 2000 mm during the 1990s (le Roux and McGeoch, 2008; Smith, 2002).

The island is the summit of a shield volcano that emerged from the Southwest Indian Ridge system (Verwoerd, 1971). Two lava successions, an older sequence of grey lava, of which the oldest parts have been dated at 450 000 ± 10 000 years and a younger sequence of black lava (10 000 years to present, McDougall et al., 2001) shaped the island. Striated, grooved and smoothed features on older grey lava provide evidence of a period of glaciation in between the two lava successions (Verwoerd, 1971). These relict features are often well-preserved, indicating insignificant in situ bedrock weathering during the Holocene. The period of glaciation is believed to have ended around 10 000 years ago (McDougall et al., 2001) providing a maximum age for soil development. These conditions are promising for the assessment of  $^{10}\text{Be}$  accumulation ages and their applications to soil erosion studies.

In light of this, a small pilot study was conducted to explore the potential of  $^{10}\text{Be}$  as a dating/tracing tool on the island. It was designed to assess the applicability of this type of approach and gain understanding into the kinds of problems this type of research application might present. One such potential problem is the presence of vegetation, such as cushions in fellfield habitats, which could affect  $^{10}\text{Be}$  concentrations of the soil profile (see for example Neal et al., 1992). In this pilot study the  $^{10}\text{Be}$  accumulation time for a glaciated surface on Marion Island was estimated using  $^{10}\text{Be}$  concentrations from two soil profiles and monthly precipitation. Furthermore, to gain understanding into the implications of *A. selago* cushions for accumulation times, samples were taken through and next to a cushion. In addition to shedding light on the applicability of this approach on the island, as well as the influence of vegetation on  $^{10}\text{Be}$  concentrations, the results contribute to the southern hemisphere  $^{10}\text{Be}$  database, which is largely underrepresented in the global beryllium inventory.

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## Methods

A site for this study was selected from the Tafelberg area (Chapter 1, Figure 1), on the eastern side of the island, at approximately 300 m a.s.l. (Figure 1). The Tafelberg area is underlain by pre-glacial grey basalts dated at approximately  $147\,000 \pm 14\,000$  years (McDougall et al., 2001). Surface material consists of a matrix-supported, unsorted glacial till. Samples were taken from a near-flat surface ( $< 2^\circ$  slope angle) to minimise any effects of erosion on the estimation of the  $^{10}\text{Be}$  accumulation period. Although previous research has shown that extensive erosion does occur on near flat surfaces (chapter 3), the location for this study was chosen very specifically to identify a stable in situ soil profile rather than an open slope system. The site was therefore selected from a small plateau with a level surface and a slight basin shape.

Soil samples were collected at one cm interval depths from two unvegetated soil profiles, one 40 cm from the edge of an *Azorella* cushion, the other not associated with a cushion. In addition, an *Azorella selago* cushion itself was spliced through the centre (Figure 2) and samples taken through the cushion and the underlying soil profile, also at one cm intervals.

Because of time and cost constraints samples from comparable depths were selected from the three profiles for preparation and analyses. These depths were: 0-1, 1-2, 7-8, 8-9, 11-12, 12-13 and 17-18 cm. The sample from the cushion itself was taken 7-9 cm from the soil surface and consisted of a mixture of decaying plant matter and intercepted mineral soil particles. Furthermore, six precipitation samples were taken from rainfall events spanning April 2007 to February 2008. Although these rainwater samples were not taken at Tafelberg, but at the research base station on Marion Island, there was no reason to suspect that  $^{10}\text{Be}$  concentrations in the rainwater samples might vary over such small spatial scales.

Sample clean-up and extraction followed the procedure of Aldahan and Possnert (1998). All soil samples were left to dry overnight at  $105^\circ\text{C}$  and subsequently ignited at  $900^\circ\text{C}$  for two hours. Hereafter one gram of sample was combined with 0.5 ml of 1 mg/ml Be-carrier and the mixture was digested using  $\text{H}_2\text{SO}_4$  and HF. Removal of hydroxides was performed using  $\text{NH}_3$  and subsequently filtrated.  $^{10}\text{Be}$  was extracted from the samples using a cation column separation where further elution of Be was done with 4M HCl.  $\text{Be}(\text{OH})_2$  was precipitated by  $\text{NH}_3$ , the solution was centrifuged and conversion to BeO was performed at  $600^\circ\text{C}$  for 2 hours.

The extraction of Be from precipitation samples was performed on 1 l combined with 0.5 mg Be-carrier. Ion exchange column separation was performed using Bio-Rad Poly-Prep pre-filled chromatography columns and the recovered Be-hydroxide was converted to BeO.

For the accelerator mass spectrometric measurements, the BeO was mixed with Nb powder (to enhance beam current) and pressed in aluminum cathodes. The measurement of  $^{10}\text{Be}$  was carried

out using the Uppsala 5 MV Pelletron accelerator with an instrumental and statistical error of < 10% at 1 standard deviation and background  $^{10}\text{Be}/^9\text{Be}$  of  $10^{-15}$ . The NIST SRM 4325 ( $^{10}\text{Be}/^9\text{Be} = 3 \times 10^{-11}$ ) was used for calculating absolute values of measured samples.

## Results and Discussion

$^{10}\text{Be}$  concentrations in precipitation ranged from  $1.5 \times 10^4$  to  $5.4 \times 10^4$  atoms/g (see Table 1). These values represent an important addition to data on  $^{10}\text{Be}$  concentrations in precipitation, especially as the southern hemisphere is largely underrepresented and data for the sub-Antarctic islands beyond  $45^\circ \text{S}$  are completely absent. Estimation of the  $^{10}\text{Be}$  precipitation flux, using the average of all precipitation samples and an annual precipitation rate of 2215 mm/year, produces a value of approximately  $35\,000 \times 10^{-27} \text{ kg/m}^2/\text{s}$ . This value is 5-6 times larger than the combined wet and dry deposition values ( $6000\text{-}7000 \times 10^{-27} \text{ kg/m}^2/\text{s}$ ) simulated by Field et al. for the sub-Antarctic area (Field et al., 2006). Field et al. (2006) used a general circulation model to model the effect of changing climate on  $^{10}\text{Be}$  deposition. However, finer scale variations in precipitation could result in areas of locally increased  $^{10}\text{Be}$  input. Determining local precipitation (rainfall and snow) amounts and patterns is therefore of utmost importance in studies dealing with atmospheric  $^{10}\text{Be}$  (see for example Morris et al., 2003). The high annual precipitation received by Marion Island may partly explain the high flux value. In addition, as storms effectively mix  $^{10}\text{Be}$ -rich air from their regions of production in the stratosphere into the troposphere, increased wet deposition is associated with midlatitude storm tracks (Field et al., 2006).

The  $^{10}\text{Be}$  concentrations obtained for the two unvegetated soil profiles varied between  $0.5 \times 10^8$  and  $7 \times 10^8$  atoms/g (Table 2; Figure 3a and b). A relatively high concentration of  $^{10}\text{Be}$  ( $16.4 \times 10^8$  atoms/g) was found in the material inside the *Azorella* cushion (Figure 3c) and a somewhat lower concentration in the soil layer immediately below the cushion when compared to the bare soil profiles. The general  $^{10}\text{Be}$  concentration trend in the soil profiles shows a decrease with depth. As these soil profiles are expected to be younger than 10 000 years and  $^{10}\text{Be}$  has a half life of  $1.5 \times 10^6$  years, the observed trend cannot be related to isotopic decay. Other alternative explanations could be related to: 1) physical (particle related) and/or chemical (water penetration) transport of  $^{10}\text{Be}$  from the lower horizons; 2) extensive removal of  $^{10}\text{Be}$  from the deeper soil layers that has developed at an earlier phase of the soil development history and 3) an inherited  $^{10}\text{Be}$  concentration in the till that represents supply from the ice during glacial melting that is partly preserved in the lower part of the soil, but overridden by Holocene input in the upper parts.

To utilize  $^{10}\text{Be}$  as a tracer of soil development history, the mean precipitation concentration was used as an approximation of the expected  $^{10}\text{Be}$  inventory in the soil. The  $^{10}\text{Be}$  inventory was

calculated as the number of  $^{10}\text{Be}$  atoms in a 1 x 1 m soil layer with 20 cm thickness, according to equation 1

$$i = \rho \cdot v \cdot c \dots\dots\dots \text{equation 1}$$

where  $i$  = the  $^{10}\text{Be}$  inventory in atoms,  $\rho$  = the density of soil in  $\text{g}/\text{cm}^3$  (taken as  $1.5 \text{ g}/\text{cm}^3$ ),  $v$  = the volume of soil for which the inventory is calculated in  $\text{cm}^3$  and  $c$  = the measured concentration of  $^{10}\text{Be}$  in the soil in atoms/g.

The inventory was calculated both using the mean  $^{10}\text{Be}$  concentration of all the soil samples and using the  $^{10}\text{Be}$  concentration inside the *Azorella* cushion as the primary depositional value. From these two inventory calculation approaches, using an annual precipitation rate of 2215 mm/year (1960s – 1990s), the  $^{10}\text{Be}$  accumulation time was estimated at approximately 2000 and 7000 years respectively, according to equation 2.

$$T = i / (C \cdot w) \dots\dots\dots \text{equation 2}$$

where  $T$  = the total accumulation time in years,  $i$  = the  $^{10}\text{Be}$  inventory in atoms,  $C$  = the concentration of  $^{10}\text{Be}$  in rain water in atoms/liter and  $w$  = the yearly volume of rainfall received by a 1 x 1 m area in liter/year.

The calculated  $^{10}\text{Be}$  accumulation time of the soil seems to be underestimated when considering the notion that the island was covered with ice around 10 000 years ago. These relatively lower than expected values may relate to a possible washout of  $^{10}\text{Be}$  from the soil profile.  $^{10}\text{Be}$  usually adsorbs to fine (clay-sized) particles that could have extensively washed out of the glacial deposits in the early stage of soil development on the island. Another possible reason is an overestimated  $^{10}\text{Be}$  flux, which is dependent on the amount and intensity of precipitation (Brown et al., 1989; Gosse and Phillips, 2001). This may have varied during the Holocene. In addition, calculations of the  $^{10}\text{Be}$  flux were based on annual precipitation values at the research base, which is expected to vary slightly from those at Tafelberg. Such variations are, however, expected to be minimal compared to temporal variation during the Holocene, especially when considering recent large-scale changes in precipitation (le Roux and McGeoch, 2008). Furthermore, although the site was specifically selected as a stable in situ soil profile and therefore minimal frost creep- or runoff-induced erosion is expected to have occurred at the site, wind transport of sediment cannot be excluded as a contributing factor to explaining the low  $^{10}\text{Be}$  concentrations. Lastly, the *Azorella selago* cushion was observed to have intercepted mineral soil particles.  $^{10}\text{Be}$  concentrations of this mineral material inside the cushions suggest an effective trapping of  $^{10}\text{Be}$  in the local vegetation

that may cause loss of the isotope upon erosion. This ability of vegetation to intercept and affect local  $^{10}\text{Be}$  concentrations has also been demonstrated for forests in Wales (Neal et al., 1992). This could potentially have profound consequences for the  $^{10}\text{Be}$  inventory obtained in other places globally, especially where the local vegetation may become an effective  $^{10}\text{Be}$  sink.

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Table 1.  $^{10}\text{Be}$  concentrations of the precipitation samples. Values are means  $\pm$  S.E. (n = 3).

Sampling period	Concentration ( $10^4$ atoms/g)
August 2007	$1.5 \pm 0.18$
September 2007	$2.0 \pm 0.16$
November 2007	$3.3 \pm 0.23$
December 2007	$5.1 \pm 0.23$
January 2008	$5.4 \pm 0.45$
February 2008	$2.4 \pm 0.27$

Table 2.  $^{10}\text{Be}$  concentration of the soil samples. Values are means  $\pm$  S.E. (n = 3).

Depth (cm)	Sampling location	Concentration ( $10^8$ atoms/g)
-1	Not related to <i>Azorella</i>	$4.89 \pm 0.15$
-2	Not related to <i>Azorella</i>	$6.77 \pm 0.17$
-8	Not related to <i>Azorella</i>	$2.95 \pm 0.10$
-9	Not related to <i>Azorella</i>	$5.21 \pm 0.13$
-12	Not related to <i>Azorella</i>	$5.85 \pm 0.18$
-13	Not related to <i>Azorella</i>	$4.51 \pm 0.16$
-18	Not related to <i>Azorella</i>	$1.59 \pm 0.06$
7	Under <i>Azorella</i>	$16.44 \pm 0.36$
-2	Under <i>Azorella</i>	$2.69 \pm 0.08$
-8	Under <i>Azorella</i>	$7.99 \pm 0.18$
-9	Under <i>Azorella</i>	$4.86 \pm 0.14$
-12	Under <i>Azorella</i>	$3.41 \pm 0.10$
-13	Under <i>Azorella</i>	$0.17 \pm 0.01$
-1	40 cm from <i>Azorella</i>	$4.25 \pm 0.12$
-2	40 cm from <i>Azorella</i>	$7.47 \pm 0.19$
-8	40 cm from <i>Azorella</i>	$1.55 \pm 0.06$
-9	40 cm from <i>Azorella</i>	$0.63 \pm 0.03$



Figure 1. Overview of the sampling site showing the spliced-through *Azorella* cushion in the foreground.



Figure 2. Photograph of the spliced-through *Azorella selago* cushion, showing the intercepted mineral soil and decayed organic matter inside.

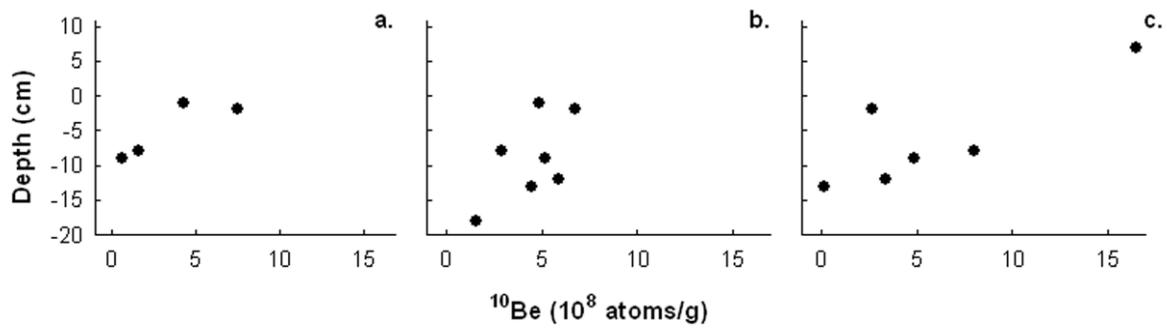


Figure 3.  $^{10}\text{Be}$  concentration of a profile a.) 40 cm from the edge of an *Azorella* cushion, b.) not associated with an *Azorella* cushion and c.) through an *Azorella* cushion and underlying soil. The sample with a positive depth value was taken inside the cushion.

## Chapter 7 – Biogeomorphology: challenges and options for integrating research approaches\*

### Introduction

Since the term “biogeomorphology” emerged in the late 1980s to describe the interactions between organisms and geomorphology (Viles, 1988), a number of reviews have appeared on the progress, emerging problems and suggested directions for future research in the field (Naylor et al., 2002; Urban and Daniels, 2006; Molau, 2008; Viles et al., 2008; Reinhardt et al., 2010). For example, Naylor et al. (2002) suggested a number of future foci, ranging from replication and sampling design improvements to a shift from single species orientated research to studying community dynamics. Others have addressed scale-related problems (Phillips, 1995; Molau, 2008), highlighted the importance of two-way interactions and interdependency between the fields (Stallins, 2006; Reinhardt et al., 2010) and addressed the inclusion of biotic effects in geomorphological modelling (Dietrich and Perron, 2006; Reinhardt et al., 2010).

One of the main challenges that biogeomorphology is faced with, that has to my knowledge only been brushed over (see Naylor et al., 2002; Renschler et al., 2007; Molau, 2008), is how to deal with the different scientific approaches to data collection and validation that ecologists and geomorphologists commonly follow. Having been involved in both fields for the past three years, I encountered a discrepancy in the use of statistics and significance testing between the fields that often made integration quite challenging. Indeed, often it has not so much been the underlying theoretical concepts that have made these fields seem irreconcilable, but trying to combine a rigid statistics-based ecology strategy with a more descriptive geomorphology approach. I found that this discrepancy in the use of statistics and significance testing had not been addressed explicitly within the biogeomorphology framework before (but see Naylor et al., 2002; Molau, 2008), despite seeming quite obvious and important to those involved in both fields.

The objective of this study was therefore firstly to quantify these perceived differences in scientific approach between ecology and geomorphology through a literature review of studies from both fields. My intention was not to compile an extensive comparison between the myriad of modelling and statistical approaches used by the two fields. Instead, I decided to explicitly focus on significance testing and related parameters, as this was where I noticed a fundamental discrepancy between the two fields. Next, I provide possible reasons for the development of these different scientific approaches. I then discuss the status of and advantages to interdisciplinary

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biogeomorphological research and also highlight some potential challenges. Lastly, I provide recommendations for dealing with these challenges when integrating the two fields and approaches.

## Methods

To compare approaches employed in ecology and geomorphology studies, papers were selected from two geomorphology journals, *Geomorphology* and *Earth Surface Processes and Landforms* (hereafter *ESPL*), and two ecology journals, *Ecology* and *Journal of Ecology* (hereafter *JE*). These journals were chosen as representative of the fields based on the broad range of topics within the respective fields that they cover. Papers were selected from 2005-2008. *Geomorphology*, *ESPL* and *Ecology* publish issues monthly. One paper was selected randomly from each month's issue, by scrolling to the paper in the approximate centre of the issue online. *JE* publishes every two months; therefore two papers per issue were selected randomly. In total 48 papers from each journal were selected (12 papers per year x 4 years).

For each paper I classified the method of data collection, either as 1.) unmanipulated field measurements or field monitoring, 2.) experimental procedures, i.e. procedures employing some form of manipulation to obtain data (this category was subdivided as field experiments and laboratory experiments), 3.) a combination of field measurements and experimental procedures or 4.) using existing data sets. I then documented the number of study sites, whether replication was used or not and the maximum total number of samples that were used.

Study sites were identified as areas for which the same measurement protocol was followed, with the explicit intention of either comparing the process/relationship between the sites or increasing the spatial extent for which the results hold. When the intention was not to compare the different sampling areas or increase the spatial extent of the research, these were not documented as different sites, but rather as replicates. For example, when an author wanted to establish the relationship between river meander width and flux and measured these parameters for four rivers with the explicit aim of comparing the four rivers, these were seen as sampling sites. When the same procedure was followed, but the four rivers were treated as replicates for the same analysis, e.g. regression, these were treated as replicates.

Replicates were defined as repeated (in time or space), independent measurements or measuring units. The number of replicates was often not easy to determine because of, for example, different numbers of replications used per treatment or different levels of replication used. Therefore this variable was only noted as present or absent, and only the main study aim was considered in doing so. For example, when the aim of the study was to compare the water chemistry of streams dissecting different lithologies, the study might have used one stream per lithology.

Replicate water samples from each stream might have been used to calculate the concentrations of the different compounds of interest, but as the main aim was to compare the chemistry of different lithologies (and not of the specific streams), replication was noted as absent. The maximum total number of samples was defined as the total number of samples used to answer the main study question, therefore including different levels of replication. When there was more than one main study question, the number of samples for the study question employing the largest sampling scheme was noted.

I also noted the statistical approach employed by the study, focussing explicitly on statistical validation. Therefore, a mathematical modelling approach was seen as a non-statistical approach (or a descriptive statistical approach if descriptive statistics were used), unless the study explicitly tested the model's performance statistically, e.g. using regression parameters or Akaike's Information Criterion. I also noted whether the study reported significance (p) values and if test statistics were reported.

Lastly, I noted the number of authors and the origin (country of the affiliated university) of the authors. If the research was a collaboration between different countries, the origin was noted as "multiple".

## Results

Three papers from *Geomorphology*, two from *ESPL* and one from *JE* were excluded from this study, as these were literature reviews, consisting only of theoretical discussions and no actual analyses of data sets.

The method of data collection differed vastly between the fields. Significantly more ecology than geomorphology studies employed some form of experimental component ( $X^2 = 33.9$ ,  $df = 1$ ,  $p < 0.0001$ , Table 1). Approximately 50% of studies in ecology used an experimental approach, whereas less than 10% of studies in geomorphology made use of experiments. In contrast, 81% of studies in geomorphology, as opposed to 47% of studies in ecology, made use of unmanipulated field measurements to obtain data. Both fields made limited use of existing data sets (Figure 1).

In a number of cases, the number of study sites was not relevant to the study. This was mainly the case for studies employing experimental sampling designs, such as laboratory experiments. These studies were therefore excluded from analyses of site numbers. In total, nine studies from *Ecology*, nine from *JE*, one from *Geomorphology* (number of sites not mentioned) and five from *ESPL* were excluded from site number analyses. Furthermore, sampling schemes were sometimes poorly described and total sample sizes could therefore not be inferred. In these cases they were excluded from sample size analyses. This amounted to the exclusion of two studies from

*Ecology*, three from *JE*, ten from *Geomorphology* and nine from *ESPL*. Although the number of study sites per study did not differ between fields (Kolmogorov-Smirnov two sample test,  $D = 0.13$ ,  $p > 0.05$ ), there was a significant difference in the maximum total number of samples (Kolmogorov-Smirnov two sample test,  $D = 0.40$ ,  $p < 0.001$ ), with the mean number of samples for geomorphology studies being smaller than those for ecology studies (Table 1).

Most studies from both fields employed replication. However, there were more studies without replication from geomorphology journals than from ecology journals ( $X^2 = 8.2$ ,  $df = 1$ ,  $p = 0.004$ , Table 1). The number of studies employing no statistics or only descriptive statistics was greater for geomorphology studies ( $X^2 = 46.9$ ,  $df = 1$ ,  $p < 0.0001$ ) than for ecology studies (Table 1). This was reflected in the percentage of studies reporting p-values ( $X^2 = 66.7$ ,  $df = 1$ ,  $p < 0.0001$ ) and test statistics ( $X^2 = 43.8$ ,  $df = 1$ ,  $p < 0.0001$ ), with significantly more studies reporting these values in ecology than in geomorphology (Table 1).

The number of authors per study did not differ significantly between ecology and geomorphology journals (Kolmogorov-Smirnov two sample test,  $D = 0.04$ ,  $p > 0.05$ , Table 1). However, the journal *Geomorphology* had more single-author papers (20%) than the other three journals (between 6.5 and 10.6%, results not shown). Furthermore, the percentage of authors from the USA was greater for the ecology journals ( $X^2 = 10.1$ ,  $df = 1$ ,  $p < 0.001$ ) than for the geomorphology journals, although this could also be an artefact of the journals chosen, rather than being representative of the fields (Figure 2).

## Discussion

The results suggest that geomorphologists typically employ smaller sample sizes, more often do not use replication and are less prone to using experiments than ecologists. The results further suggest that geomorphologists place less emphasis on significance testing and uncovering patterns through statistical means than ecologists, but rather focus on a more descriptive (albeit still mathematical) approach. According to Richards (1996) two types of research can be distinguished, namely large replication studies, which uncover patterns through statistical, empirical means and more detailed, smaller replication studies, drawing conclusions based on theoretical reasoning (based for example on the laws of physics and other theories that are generally accepted at the time and go beyond the limits of available data (Brown, 1996; see also Kuhn, 1962)). The results suggest that, at least for the journals studied, the former approach is more commonly employed in ecology, whereas the latter approach is more commonly employed in geomorphology. Brown (1996) also juxtaposes purely empirical, observation-based research with a more theory-dependent approach within geomorphology. He discusses positivism, postpositivism and Popper's classic falsification

theories in this context and explains the development of the mainstream, empiricist line of reasoning. As Richards (1996) rightfully points out, sampling theories and the development of the classic empirical approach of hypothesis generation and significance testing are well-known and the merits and drawbacks of this approach have been widely debated (Anderson et al., 2000; Martínez-Abraín, 2008) and will not be discussed here. Some suggest that this approach still often forms the basis of research design in ecology (Koricheva, 2003) and argue in favour of “new” developments such as Akaike’s Information Criteria (AIC) or Bayesian statistics within ecology (Boyce, 2002). Regardless of the exact approach followed, as the results demonstrate, ecologists, and indeed biologists in general, have been found to commonly employ extensive, large replication studies with the emphasis on uncovering patterns in data statistically (Boyce, 2002; Koricheva, 2003; Molau, 2008). It has even been said that statistics originated within the biological fields and that “statistics dominate how biologists do science” (Boyce, 2002).

In contrast, geomorphologists often do not set out to uncover patterns statistically, but instead aim to increase their understanding of patterns and processes through theoretical knowledge and reasoning combined with intensive, detailed measurements of multiple parameters (Richards, 1996). In the process they employ smaller sample sizes and place less emphasis on statistical validation, replication and other related parameters, as results from this study validate. Whereas extensive, large replication studies demonstrate general patterns through statistical means, intensive, smaller replication studies aim to understand the mechanisms responsible for creating those patterns (Yatsu, 1992; Richards, 1996). In these cases, statistical relationships should not be confused with process-based explanations, as a good empirical fit does not necessarily reveal much about the underlying mechanisms (Cox, 2007).

### A case of different natures

One of the main reasons for this discrepancy between the two sciences is the very different nature of the research questions that they ask which to a large extent determines the paradigms that define a discipline (Renschler et al., 2007). Although both ecology and geomorphology study both patterns and processes, the emphasis in geomorphology is often on explaining certain processes, i.e. understanding the underlying mechanisms. This often necessitates detailed monitoring of a wide range of interdependent parameters (see Richards, 1996). Richards (1996) refers to this approach as a “mutually reinforcing explanatory system”. For example, detailed measurements of soil temperature and moisture, needle ice and related sediment movement and wind patterns around a single terrace or a small number of terraces are useful to understand the mechanisms and interactions responsible for creating frost-related sediment sorting patterns. Such monitoring set-ups

are often both time and cost intensive and replication therefore not feasible. In ecology, on the other hand many processes, such as competition or facilitation, are inferred from studying patterns (McIntire and Fajardo, 2009) and also what is seen as the mechanisms responsible for these processes (such as various mechanisms of facilitation) can often be inferred from patterns. However, the objective in ecology is very seldomly to know exactly how a mechanism operates, e.g. understanding how vegetation-banked terraces affect energy budgets, thereby changing temperature regimes and facilitating seedling establishment.

Up until the 1950s (and often still today as results from this study suggest) the aim in geomorphology was quite descriptive, whether it was to describe a certain landform feature or a process involved in creating that feature. This descriptive process often includes a mapping component. When describing and discussing the profile of the Mississippi River or mapping the distribution of karst formations, significance testing is inappropriate, despite replicate measuring/observation points being not only possible, but necessary. In addition, in geomorphology, it is often not merely mean trends and relationships that are of interest. Instead the shapes of curves and the rates of change during specific events are of importance to understand the dynamics of the underlying processes responsible for these trends. For example, when comparing frost environments under different types of plant cover, it is often not merely the mean or minimum temperatures reached during frost cycles that are of interest, but the actual rate of temperature change and small scale fluctuations during freezing that provide information about the conditions during soil frost. Such information will be lost when data are averaged in statistical significance testing and therefore the whole time series has to be studied.

### Case studies vs generalisations

The aim in geomorphology is often to describe and discuss a specific landslide, watershed or part of a glacier, as opposed to landslides, watersheds or glaciers in general. In this regard, an inherent sense of uniqueness of place often makes statistical significance testing inappropriate, if not impossible. Even when a mathematical relationship adequately describes a pattern or process in one case, natural variations make it very difficult to generalise across cases. Data from one case therefore rarely fit equations from another (Pitty, 1971). Another example: when studying the rate of sedimentation, a geomorphologist might focus his research on a specific reservoir and want to know how this specific reservoir fits into the broader picture of certain reservoirs types in general. A single value will then be used directly for comparisons with other reservoirs. It does not make sense to calculate the rate more than once (unless there is a temporal component to the study) in order to have replicates and compare it statistically to other case studies. Ecologists, on the other

hand, often set out to test general trends and relationships, albeit for a specific species, or compare different treatment groups. As the results indicate, they often employ some form of experimental component in the process. Such “controlled” conditions make it possible to have “ideal” sample sizes and therefore facilitate statistical testing.

### Historical developments

Differences in statistical approach and significance testing between the two fields demonstrated in this study can possibly be attributed to different historical development between the fields. Both ecology and geomorphology are relatively new scientific fields (Rhoads and Thorn, 1996; Egerton, 2001) with little separation between the fields until the early 20<sup>th</sup> century (Molau, 2008). In addition, both fields (and indeed most sciences) started out as very descriptive disciplines (Renschler et al., 2007). Amongst the first observations of the relationships between organisms and their environment were those of von Humboldt and Darwin on their exploratory expeditions. Such observations were initially only descriptive accounts of observed patterns and relationships for specific case studies. As ecology developed, probability theory and significance testing were adopted to describe a pattern as a generality and new hypotheses could in turn be formulated to explain the observed patterns and trends. It might be noticed, for example, that plants with more colourful flowers produce more fruit and a hypothesis can subsequently be formulated concerning pollination. Such broader-scale principles or generalisations are then in turn often tested for specific species.

In geomorphology, on the other hand, many of the bench-mark observations, such as those by Powell, Hayden and Gilbert on the evolution of sparsely vegetated landscapes, were geohistorical in nature and by virtue therefore more descriptive. Data on the genesis of the landforms under study could therefore often not be obtained directly and their inferences therefore not tested statistically, as they were based on events that occurred in the past (Rhoads and Thorn, 1996). Much the same can be said of the theory-dominated, descriptive approach of the geological time-scale slope evolution models of Davis, Penck and King. Such descriptive approaches dominated geomorphological research for much of the first half of the 20<sup>th</sup> century (Renschler et al., 2007; Tooth, 2009) and are still commonly used today.

In the 1950s geomorphology developed from being a more descriptive field to a more quantitative field, developing numerical models for a host of landscape processes (Renschler et al., 2007). In contrast to ecology, once general patterns had been described in geomorphology, a shift, from a statistically-based, empirical approach to more detailed case studies, often followed to understand the underlying mechanisms (Richards, 1996). Thus, once empirical relationships

between climate and erosion rates had been established, more detailed case studies in specific environments provide information on the mechanisms responsible for the observed relationships. Nowadays, a trend in geomorphology from more specific case studies to empirical generalisations is again emerging (see for example approach by Ridefelt et al., 2008). Global issues such as climate change and human environmental impact have placed a renewed emphasis on synthesis studies at the landscape scale. This is also reflected in the emergence of Earth System Science and The Critical Zone as new concepts aimed at integrating the study of complex natural systems and human activity. According to Tooth (2009), however, the classic descriptive or otherwise often “case study” nature of geomorphology has led to the field sometimes unjustly being perceived as unscientific or even as “irrelevant gardening” (see also Yatsu, 1992).

### Modelling approaches

These demonstrated differences in statistical approach between the fields often translate into different approaches to numerical modelling. Modelling techniques are commonly used by both fields, but the statistical approach and model validation differ vastly. In ecology models are mostly referred to in a statistical context. A model might therefore be constructed based on collected data and subsequent stepwise statistical deletion of variables that do not significantly contribute towards explaining variation. Models based on theoretical reasoning are also often constructed. Again, criteria such as AIC or significance testing and p-values are used to assess how well the model fits the observed data.

In geomorphology, on the other hand, calculations are often based entirely on mathematical relationships. For example, flood sizes can be estimated from calculations of discharge values from preserved bank deposits. For certain channels and under certain conditions, these values can be fairly straightforward to calculate and palaeo-flood reconstruction is therefore a simple mathematical procedure. Furthermore, models are often constructed based on a priori theoretical knowledge or previous research on the relationships between the input parameters, such as process calculations for flow simulation models (Cox, 2006) and then calibrated using field data. Although subsequent model validation is often performed, studies do not always report a quantitative measure of how well their model performed or whether their validation was statistical. When statistics are used, regression and related methods have been by far the most commonly used approach (Cox, 2007). Renschler et al. (2007) stresses the importance of assessing the accuracy of models in biogeomorphology (see also Reinhardt et al., 2010) and Cox (2006) addresses this problem by discussing methods of assessing agreement in geomorphology.

### Scale-related differences: Truth or fiction?

Problems related to scale (both spatial and temporal) have been discussed quite extensively within biogeomorphology (Phillips, 1995, Renschler et al., 2007; Molau, 2008). When specifically considering the practicalities involved with replication, the spatial dimensions associated with studying plants or animals intuitively seem smaller than those associated with studying landform features or processes. This might make large replication, extensive surveys, with a strong experimental aim appear more practical in ecology than in geomorphology and could therefore seem a plausible explanation for the difference in the use of experimental procedures between the fields demonstrated by the results from this study. However, the actual unit of replication in ecology is seldom a plant or an animal. When studying forest species composition or fish population dynamics, for example, the unit of replication is not a tree or fish species, but a sample of trees or fish, representing the forest or fish population as a whole. Furthermore, even if the study subject were to be bigger in geomorphology than in ecology, the study subject in geomorphology is seldom the unit of replication. For example, for a study describing a specific volcano, the study subject is clearly the volcano. The unit of replication, on the other hand, would be the specific landform features studied on the volcano in order to describe it. To generalise across volcanoes within a single project, however, would be an expensive and impractical task.

### The status of interdisciplinary biogeomorphological research

According to van den Besselaar and Heimeriks (2001), a research discipline can be defined as “a group of researchers working on a specific set of research questions, using the same set of methods and a shared approach” (see also Kuhn, 1962). When such research disciplines are combined, research is said to be multidisciplinary. Whereas multidisciplinary research combines fields without the explicit integration of theoretical perspectives or findings, interdisciplinary research encompasses combining theoretical concepts, principles and approaches, leading to a more integrated, holistic approach (van den Besselaar and Heimeriks, 2001).

Unfortunately, studies that really integrate both fields and accompanying approaches and philosophies and require a sound knowledge of both ecological and geomorphological principles are, to my knowledge, largely still lacking (but see Kreyling et al., 2008 for an example of such a study). Often adding a “bio” component to a geomorphological study constitutes as biogeomorphology. However, the approach is still completely “geomorphological” and expertise from ecologists is often completely absent. The reverse situation, i.e. ecologists practicing biogeomorphology, is altogether less common, probably as biogeomorphology is regarded more as

a sub-discipline of geomorphology than ecology. This said, many ecologists have added abiotic variables, such as soil temperature or moisture to their studies. However, again geomorphological knowledge is often not required and the methods employed are mostly strictly “ecological”.

This lack of integration in biogeomorphological research has both advantages and shortcomings. On the one hand, because the two fields speak such different languages, integration might slow down research at first and communication might be somewhat difficult. By continuing to use the sampling designs and techniques with which the respective fields are familiar, conflicting research approaches are avoided (see also Renschler et al., 2007). On the other hand, by having input from both ecologists and geomorphologists, shortcomings to a specific study, which might not be recognised if only one of the disciplines were present, can be recognised. For example, when comparing soil moisture around plants on different aspects of a hill, an ecologist might not take all the important geomorphological site characteristics into account. Similarly, a geomorphologist might not take seed dispersal patterns into account when trying to establish how frost severity affects seedling distributions. By combining the experience and expertise of both fields (and thereby taking biogeomorphology from multi- to interdisciplinary), biogeomorphological research can be optimised (see also Naylor et al., 2002; Renschler et al., 2007). However, true integration of two fields that use such different approaches will almost certainly not happen without stumbling blocks and pitfalls and it is important that we are aware of these potential challenges.

### Challenges, pitfalls and suggestions

As discussed, the different natures of the two fields often require that different approaches be used. Therefore, although the stepwise approach of hypothesis generation, data collection, statistical testing and arriving at a conclusion based on a p-value is fairly straightforward to follow, it requires large sample sizes and extensive surveys, which is often not practically possible or appropriate in geomorphology. Similarly, as ecologists follow a more rigid, stepwise protocol in deriving conclusions, they might struggle to familiarise themselves with the seemingly more intuitive geomorphological approach.

To facilitate integration between the fields, firstly being aware of the different approaches when setting up sampling schemes and research protocols is very important. By familiarising oneself with the type of research and techniques the “other field” applies, communication efficiency can be increased. One potential challenge is then deciding which part of the research requires which approach. It is important to agree beforehand at which level more extensive replication is necessary and possible, when a more intensive, case study approach is required or, alternatively, when new approaches are necessary to facilitate integrated, holistic research (Naylor et al., 2002; Dollar et al.,

2007). If not, one runs the risk of trying to do rigorous ecology statistics with a geomorphology experimental set-up largely lacking in replicates. Conceptual frameworks can serve as excellent organisational structures in this regard (e.g. Dollar et al., 2007). Furthermore, common interests, such as the use of remote sensing and GIS (Renschler et al., 2007; Molau, 2008; Reinhardt et al., 2010) should be utilised more as a platform for increasing integration.

According to Naylor et al. (2002), geomorphologists can often learn from ecologists when it comes to question framing and methodological rigour. Research questions in geomorphology are often posed very broadly, which hinders the formulation of a clear, unambiguous scientific approach. Broad questions such as “How do soil frost features and vegetation patterns interact?” could be framed more specifically, i.e. “Do sorted stripe widths differ between vegetated plots and non-vegetated plots?” or “Is there a relationship between the rate of freezing during a frost event and degree of die-back in a plant?”

Lastly, biogeomorphological research as it is practiced at the moment is often from the start biased towards either one of the fields and approaches, simply as a result of the background training of those involved. In addition to biogeomorphology teams consisting of both geomorphologists and ecologists, unbiased “biogeomorphologists” are needed, that have a broad background training. Such biogeomorphologists should have enough relevant knowledge and expertise from both fields to recognise potential shortcomings, act as translators between the two fields and take biogeomorphology from multi- to interdisciplinary.

## **Conclusions**

Ecologists and geomorphologists follow very different approaches to data collection and validation. As a result, truly interdisciplinary biogeomorphology, requiring the input of both ecologists and geomorphologists, might be slow at first. Such research is necessary, however, if we want to benefit maximally from the knowledge, experience and approaches of both fields. Ecologists and geomorphologists wishing to facilitate such integration should familiarise themselves with both fields and accompanying approaches. In addition, biogeomorphological studies should place emphasis on narrowly framed research questions and good communication between the fields, so that it is clear which approach will be followed to answer the various research questions or alternatively when new approaches are needed. Lastly, impartial “biogeomorphologists” are needed to translate between the two research fields and facilitate unbiased, integrated biogeomorphological research.

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Table 1. Comparison of studies from ecology and geomorphology journals. Numbers that are not percentages are means  $\pm$  S.D. Bold numbers represent statistically significant differences. \* $p < 0.01$ , \*\*  $p < 0.001$ , \*\*\* $p < 0.0001$ . JE = Journal of Ecology, ESPL = Earth Surface Processes and Landforms.

	Ecology		Mean $\pm$ S.D.	Geomorphology		
	Ecology	JE		Geomorphology	ESPL	Mean $\pm$ S.D.
Number of studies	48	47		45	46	
% with experimental component	56.3	38.3	<b>47.4***</b>	2.2	15.2	<b>8.8***</b>
Sites/study	5.6 $\pm$ 15.6 (n=39)	3.1 $\pm$ 5.0 (n=38)	4.4 $\pm$ 11.6	3.2 $\pm$ 6.1 (n=44)	1.7 $\pm$ 1.5 (n=41)	2.5 $\pm$ 4.5
Samples/study	3870 $\pm$ 10477 (n=46)	4323 $\pm$ 21358 (n=44)	<b>4091 <math>\pm</math></b> <b>16611**</b>	3371 $\pm$ 15552 (n=35)	982 $\pm$ 4336 (n=37)	<b>2144 <math>\pm</math></b> <b>11260**</b>
% without replication	2.1	2.1	<b>2.1*</b>	8.9	17.4	<b>13.2*</b>
% non- statistical or descriptive statistics	2.1	10.6	<b>6.3***</b>	44.4	58.7	<b>51.6***</b>
% p-values reported	91.7	85.1	<b>88.4***</b>	35.6	23.9	<b>29.7***</b>
% test statistic reported	87.5	85.1	<b>86.3***</b>	42.2	37.0	<b>39.6***</b>
Authors/study	3.3 $\pm$ 1.8	3.0 $\pm$ 1.5	3.2 $\pm$ 1.6	2.9 $\pm$ 1.7	3.5 $\pm$ 1.9	3.2 $\pm$ 1.8

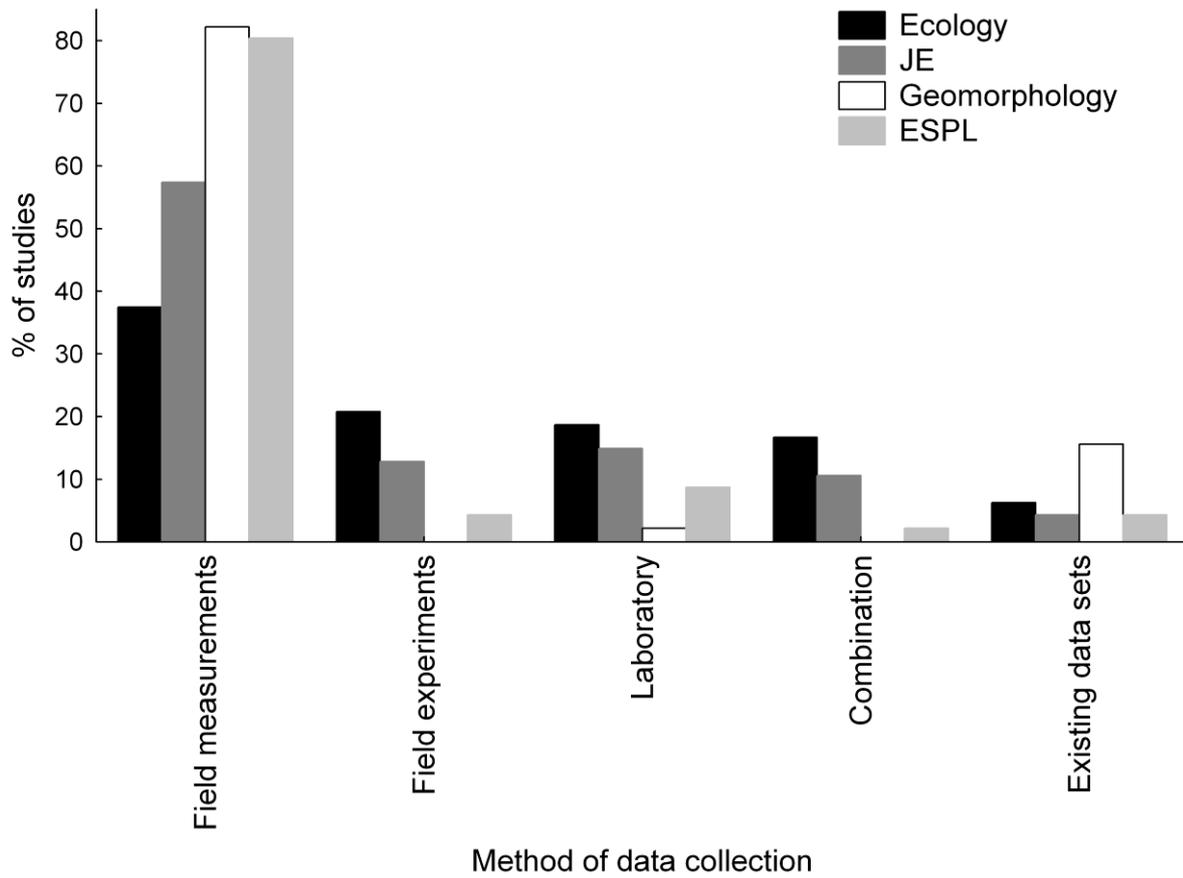


Figure 1. The method of data collection differed between studies from ecology journals (Ecology (n = 48) and Journal of Ecology (JE, n = 47)) and geomorphology journals (Geomorphology (n = 45) and Earth Surface Processes and Landforms (ESPL, n = 46)).

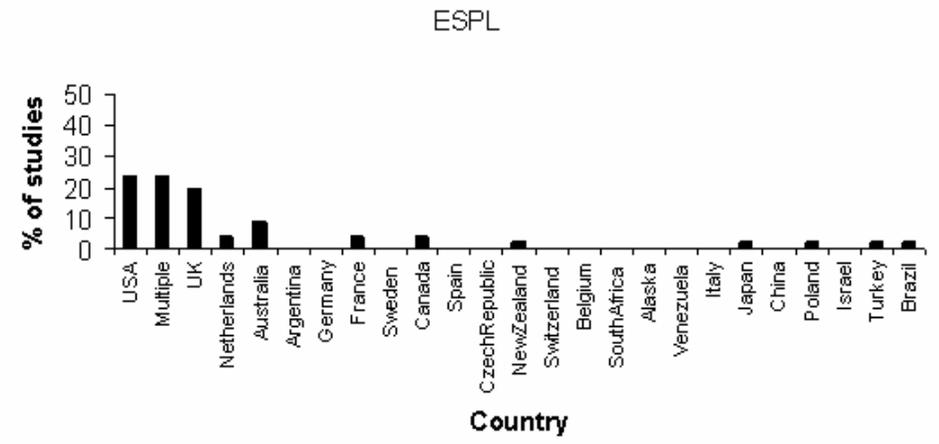
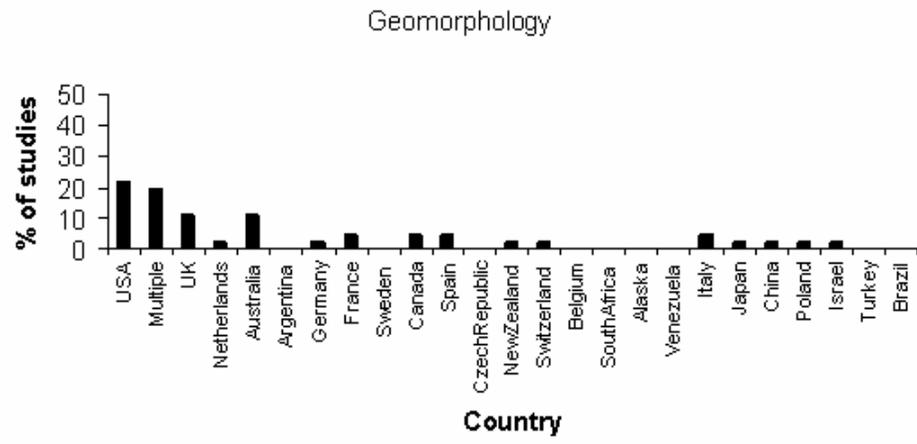
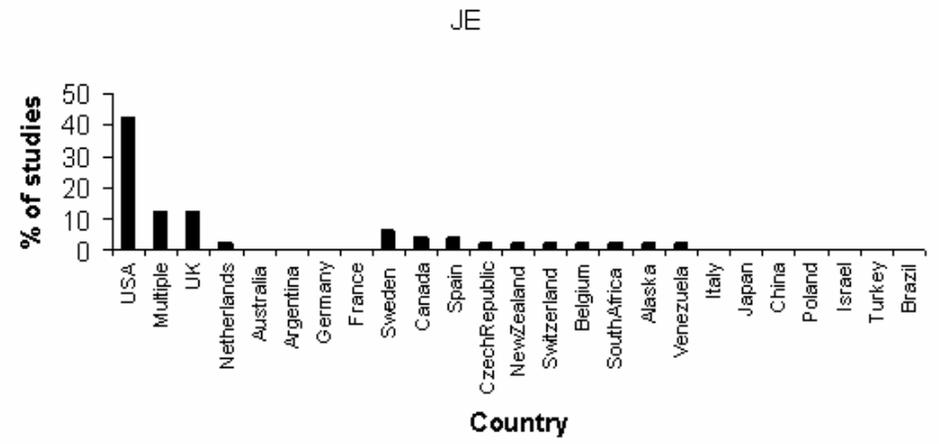
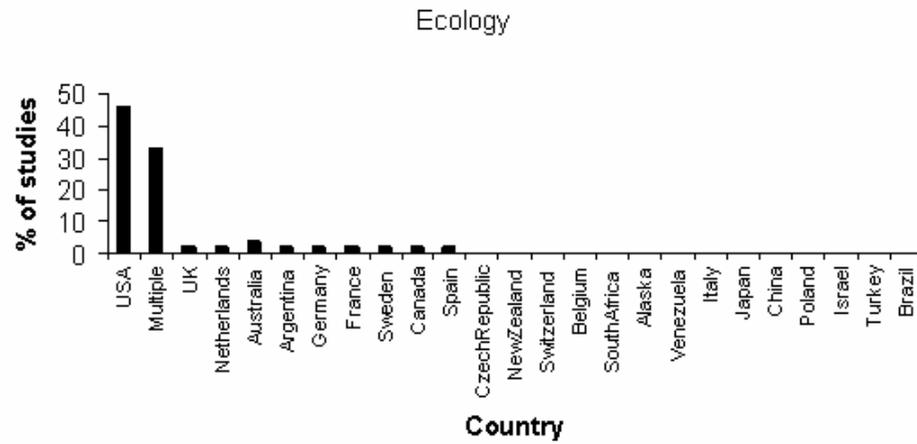


Figure 2. Origin of authors for studies from two ecology journals, Ecology (n = 48) and Journal of Ecology (JE, n = 47) and two geomorphology journals, Geomorphology (n = 45) and Earth Surface Processes and Landforms (ESPL, n = 46).

## Chapter 8 – General conclusion

Since the emergence of biogeomorphology as a formal research field in the late 1980s (Viles, 1988), an ongoing awareness in the scientific community of the importance of multidisciplinary research has led to a large number of studies explicitly exploring the ways in which ecology and geomorphology interact (Naylor et al., 2002; Dietrich and Perron, 2006; Renschler et al., 2007; Viles et al., 2008; Reinhardt et al., 2010). Such interactions are especially important in the light of climate change. Not only are landform properties and processes likely to influence how biota respond to a changing environment, but biota are also likely to influence the way in which landscapes respond to global climate change. However, despite a tight coupling between organisms and their environment in glacial and periglacial regions (Kennedy, 1995) and a high sensitivity of these regions to climate change (Barrett et al., 2006; Turner et al., 2007), these areas have been largely underrepresented as biogeomorphological platforms (Hjort and Luoto, 2009). This thesis studied the two-way interactions between the cushion plant, *Azorella selago*, and its abiotic environment on sub-Antarctic Marion Island. It not only looked at some of the two way interactions between *A. selago* and the surrounding geomorphological processes and landforms (chapters 2-5), but also at the implications of this keystone plant species for a previously unexplored geomorphological measuring technique, namely  $^{10}\text{Be}$  dating (chapter 6). Lastly, as a corollary of the research, a synthesis is provided on the different approaches employed within geomorphology and ecology (chapter 7). In this last data chapter a philosophical reflection is provided on the development of the two fields; and suggestions are provided, based on experiences gained during the course of the PhD, to facilitate future biogeomorphological research.

The results demonstrate that *A. selago* cushions not only affect the surrounding geomorphology, such as sediment distribution patterns, terrace formation (chapter 2) and soil frost regimes (chapter 3), but they also affect geomorphological tracing tools, such as accumulation of the cosmogenic isotope  $^{10}\text{Be}$  (chapter 6). In addition, by changing their abiotic surroundings (chapter 3), *A. selago* cushions act as ecosystem engineers, modifying microclimates in such a way that they create habitats, thereby facilitating plant establishment not only on the cushion plant itself, as previously described (Huntley, 1972; McGeoch et al., 2008), but also in the surrounding soil (chapter 4). Such associations of *A. selago* seedlings with cushions (and *A. magellanica* seedlings with both cushions and rocks, chapter 4) demonstrate the importance of “safe sites” for seedling establishment in climatically severe environments.

Recent climate changes on Marion Island (Smith, 2002; le Roux and McGeoch, 2008) have raised renewed concern for the conservation status of the island. In addition to the potential direct effects of continued drying and warming on *Azorella* cushions (le Roux et al., 2005) on the one

hand, and on frost activity and slope stability on the other hand (Sumner et al., 2004), this study highlights potential indirect consequences as a result of interactions between these two biotic and abiotic components. Therefore, as *A. selago* both affects and is affected by the surrounding abiotic properties and processes of fellfield habitats, climate change could potentially not only affect *A. selago* integrity directly, as suggested by le Roux et al. (2005), but would also indirectly affect terrace formation (chapter 2), microclimate (chapter 3) and resulting microhabitats (chapter 4).

Despite seemingly increased recruitment of *A. selago* seedlings at milder frost climates (chapter 5), suggesting increased seedling numbers under warming scenarios, the establishment and propagation of alien invasive plant species is also believed to be favoured by climate change (Kennedy, 1995; Chown et al., 1998; Frenot et al., 2001). As *A. selago* has been shown to be a poor competitor, being outcompeted by more resilient species at lower altitudes (Rautenbach, 2007), such establishment is likely to have negative impacts on cushion numbers and integrity. Lastly, increased activity of introduced house mice with climate change (see Chown and Smith, 1993; Bergstrom and Chown, 1999) has led to detrimental effects on *A. selago* vitality (Phiri et al., 2008). As a result of these complex interactions, coupled with the complex biogeomorphological interactions demonstrated in this thesis, the total effect of disturbances, such as climate change, on this keystone sub-Antarctic species is difficult to predict. In addition, as *Azorella selago* is widespread across the sub-Antarctic and the genus *Azorella* is native not only to the Southern Ocean islands, but also to tropical alpine regions of South America, biogeomorphological interactions related to *Azorella* cushions are potentially important determinants of landscape evolution, not only on Marion Island, but across a far broader geographic range.

Globally, a renewed interest in biogeomorphological interactions has arisen lately, as is evident from the number of recent review articles (Naylor et al., 2002; Viles et al., 2008; Reinhardt et al., 2010). The search for a “topographic signature of life”, i.e. whether there are landforms that would not exist without life (see Dietrich and Perron, 2006; Reinhardt et al., 2010) has received a lot of interest lately, emphasising biosphere-geosphere interactions on a global (and even universal, see Dietrich and Perron, 2006) scale. Other studies highlight, for example, vegetation effects on channel morphology in riparian systems (Gran and Paolo, 2001; Tal and Paolo, 2007), sediment displacement by burrowing organisms (Gabet, 2000; Gabet et al., 2003; Yoo et al., 2005), or vegetation impacts on sediment transport and vice versa (see review by Murray et al., 2008). All of these studies demonstrate how biotic and abiotic components interact. However, little attention has been paid to how ecologists and geomorphologists interact (although some reviews do highlight common measuring tools and techniques - Dietrich and Perron, 2006; Renschler et al., 2007; Reinhardt et al., 2010). To facilitate truly integrated biogeomorphological research, however, interaction between ecologists and geomorphologists is important. In this regard,

biogeomorphological research can be complicated by the different scientific approaches to data collection and statistical data validation that ecologists and geomorphologists commonly follow. Ecologists often employ a more statistics-based approach, with emphasis on empirical significance testing, whereas geomorphologists place less emphasis on replication and significance testing and focus on a more descriptive approach and theoretical reasoning (chapter 7). Combining theoretical concepts, principles and approaches is necessary for integrated biogeomorphology and a shift from multi- to interdisciplinary research.

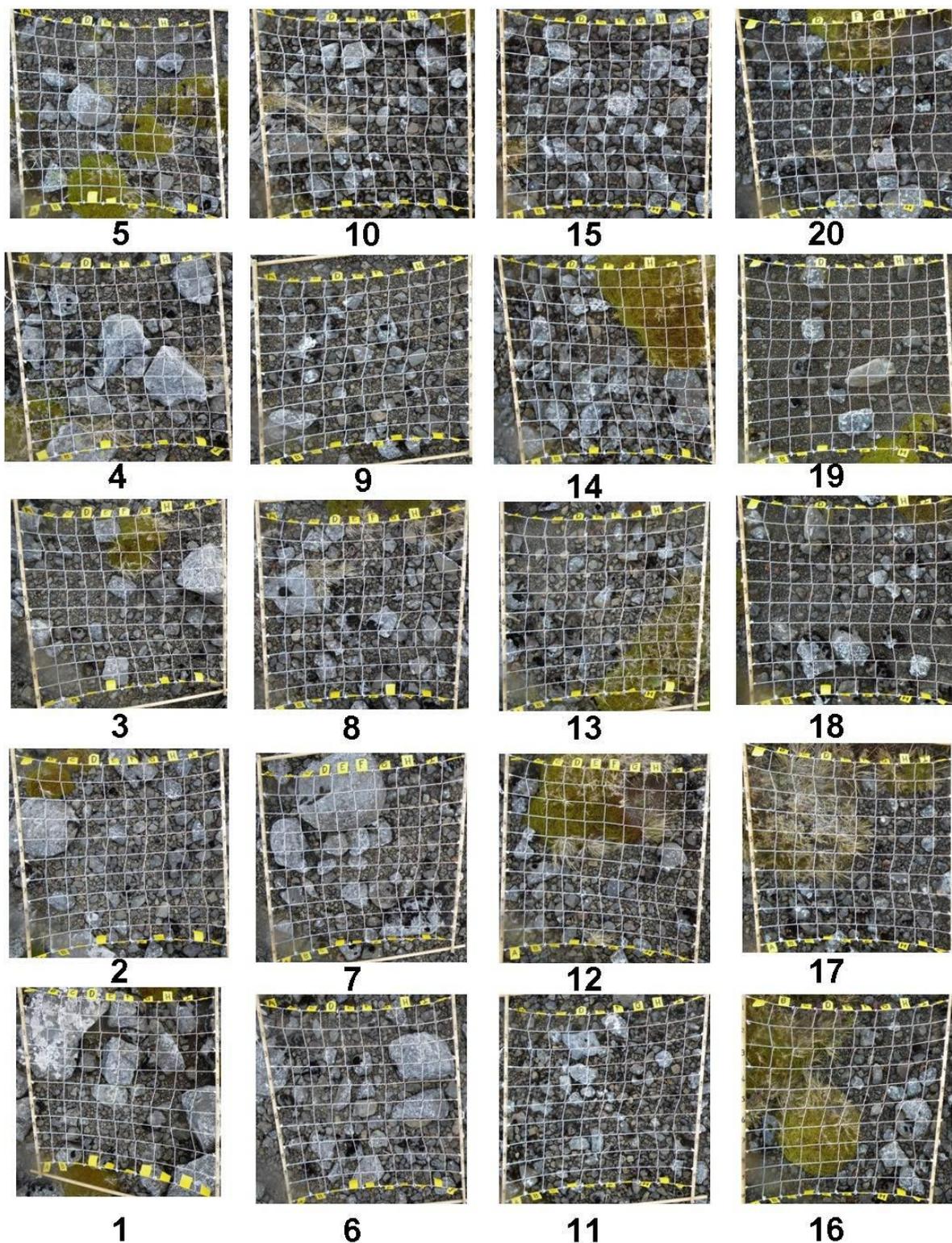
In conclusion, to predict the responses of both landscapes and biota to natural or human-induced ecosystem disturbance, such as climate change, more accurately, biogeomorphological research is necessary. Such research is facilitated not only through theoretical knowledge of the principles of both ecology and geomorphology and the interactions between the fields, but also through an increased understanding of the philosophies and approaches underlying the respective disciplines. The research and experiences presented in this thesis aimed at contributing to such an understanding.

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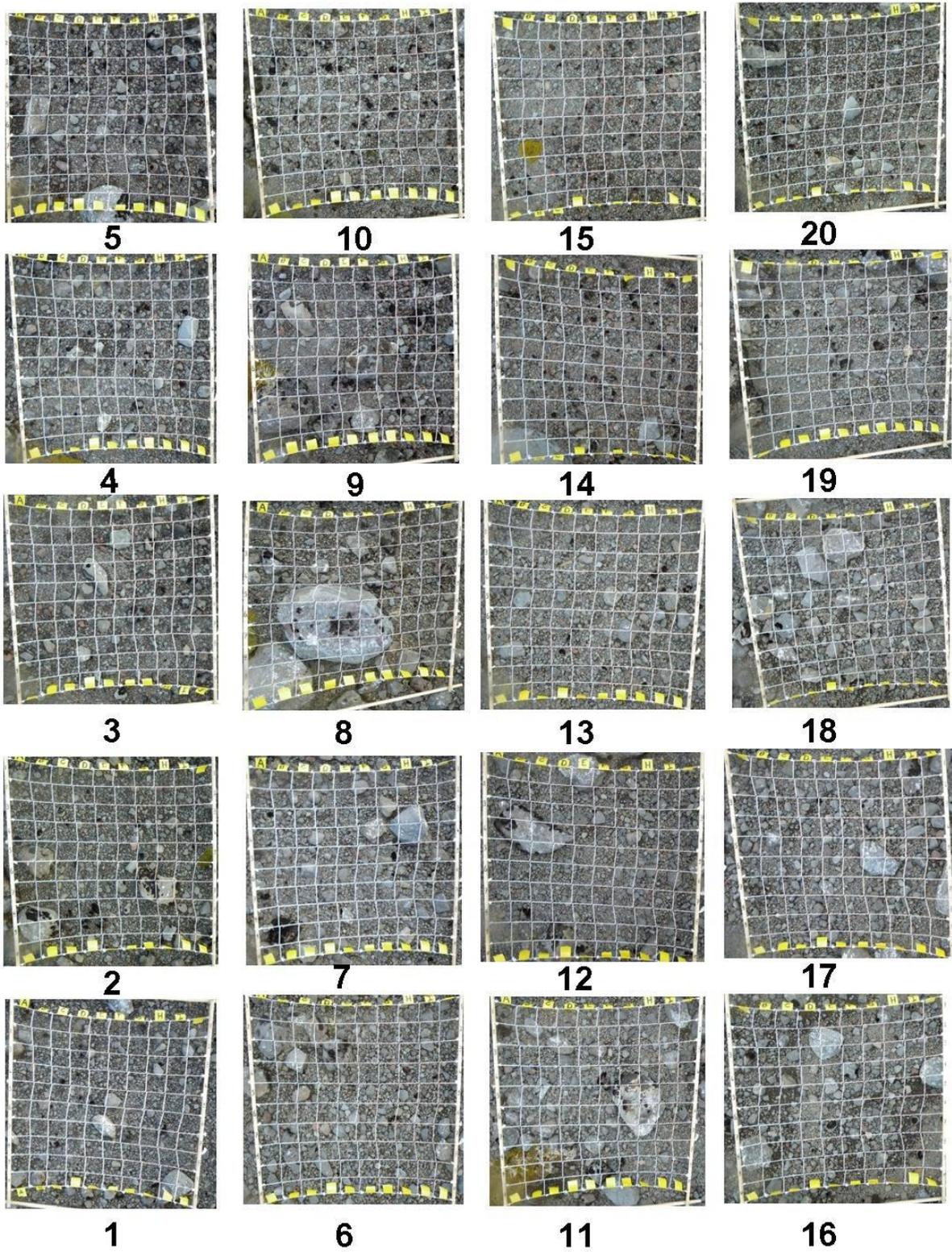
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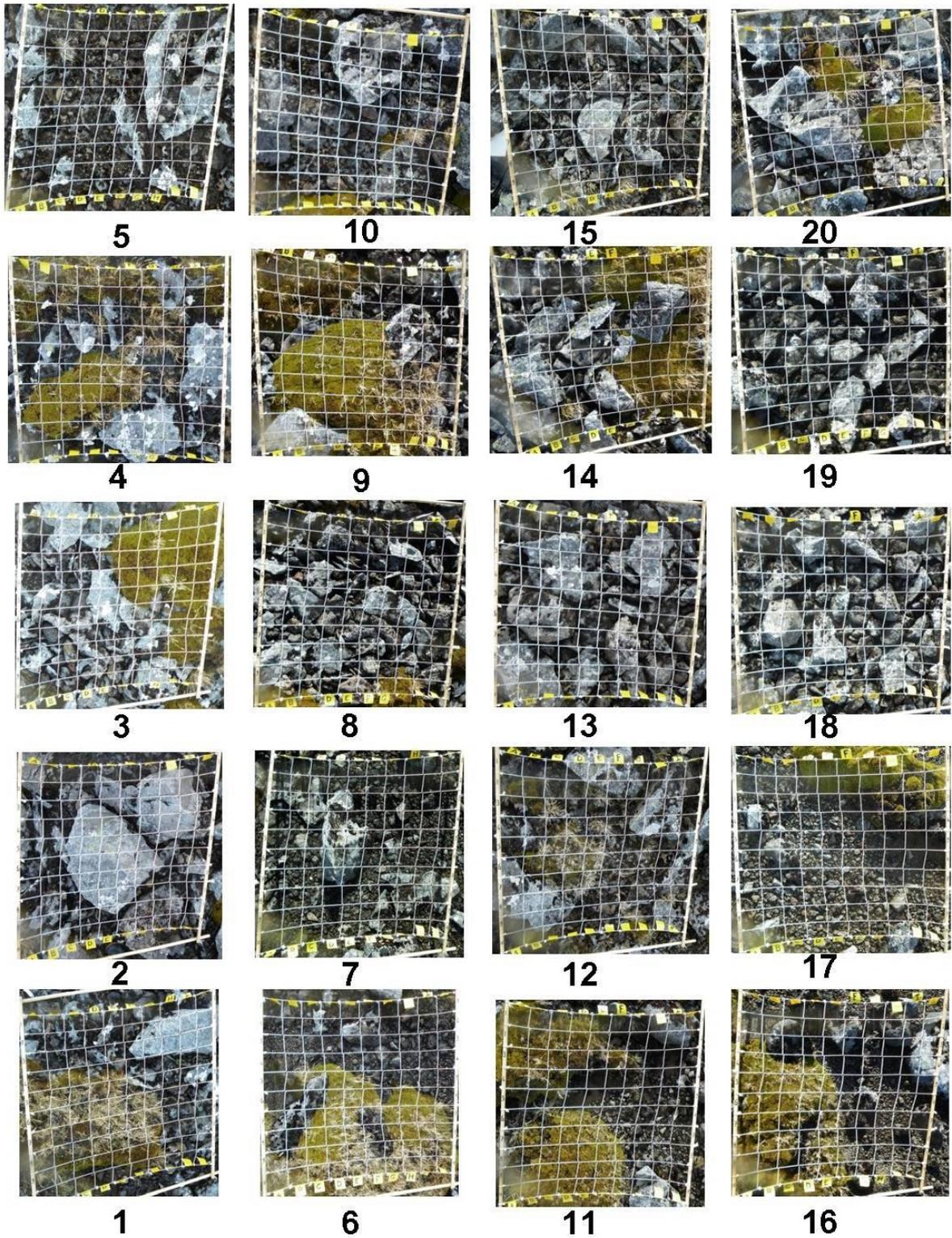
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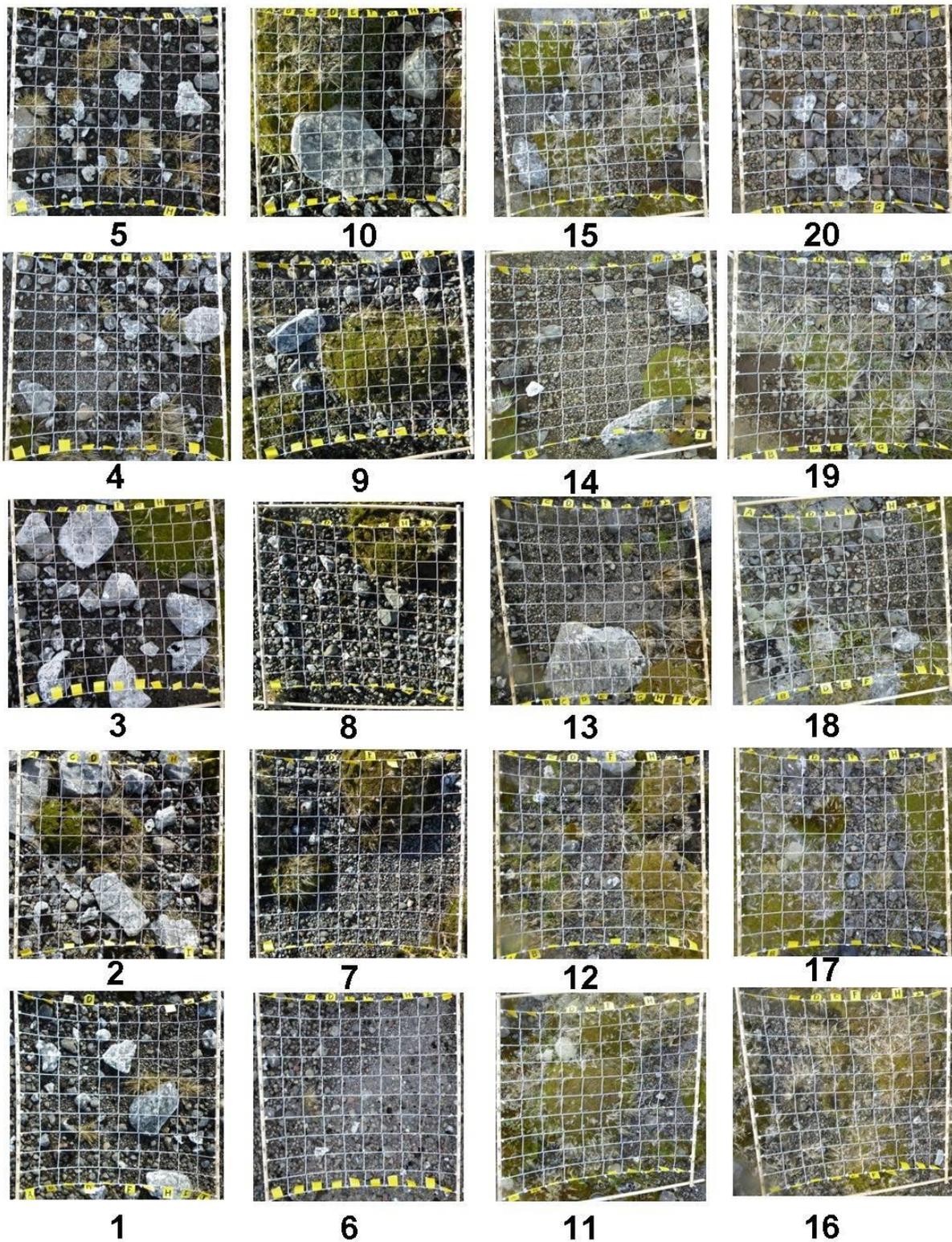
Appendix A. Photographs of the twenty 1 x 1 m quadrats at the Stoney Ridge low altitude site. The altitude of the site was  $120 \pm 5$  m a.s.l.



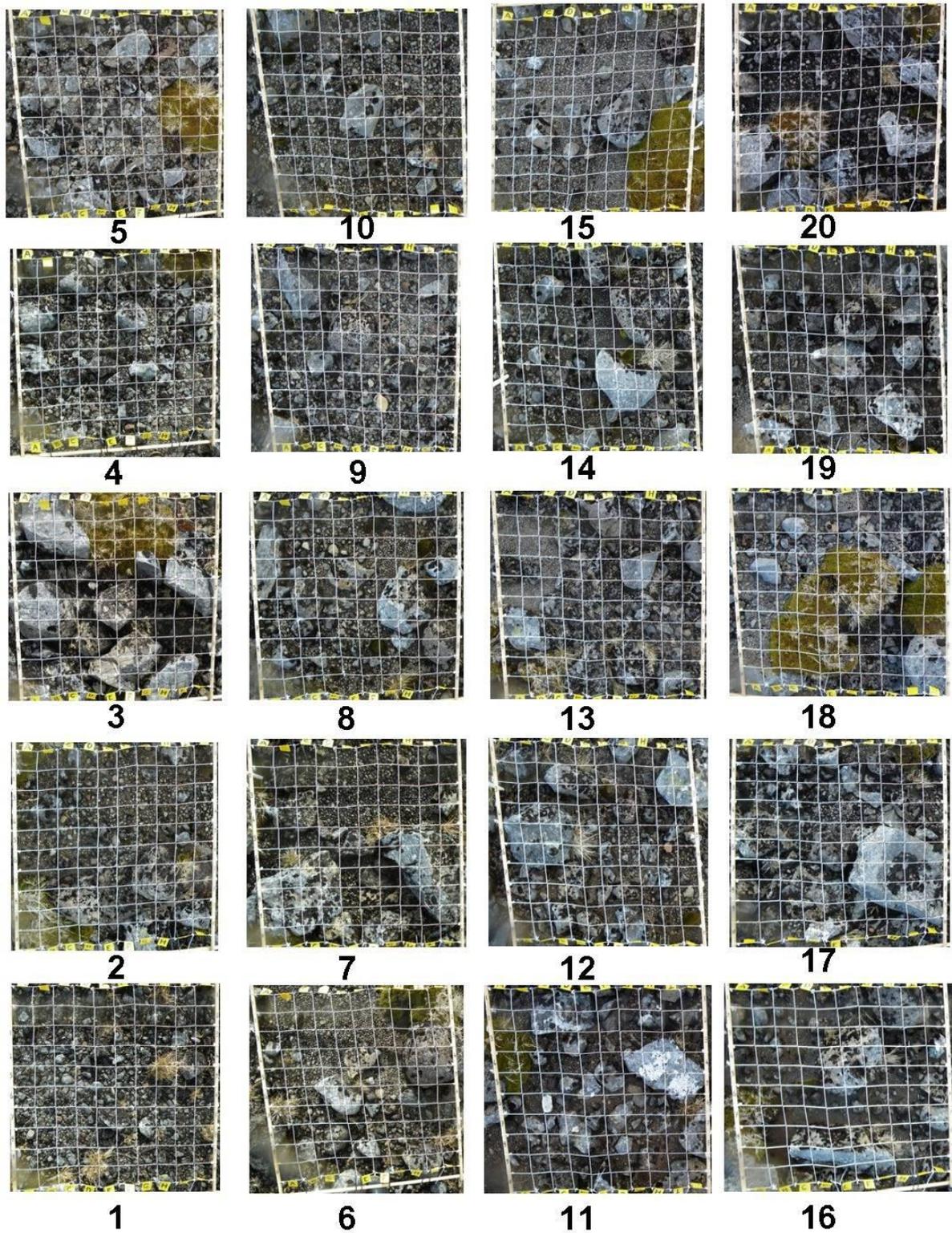
Appendix B. Photographs of the twenty 1 x 1 m quadrats at the Stoney Ridge mid-altitude site. The altitude of the site was  $200 \pm 5$  m a.s.l.



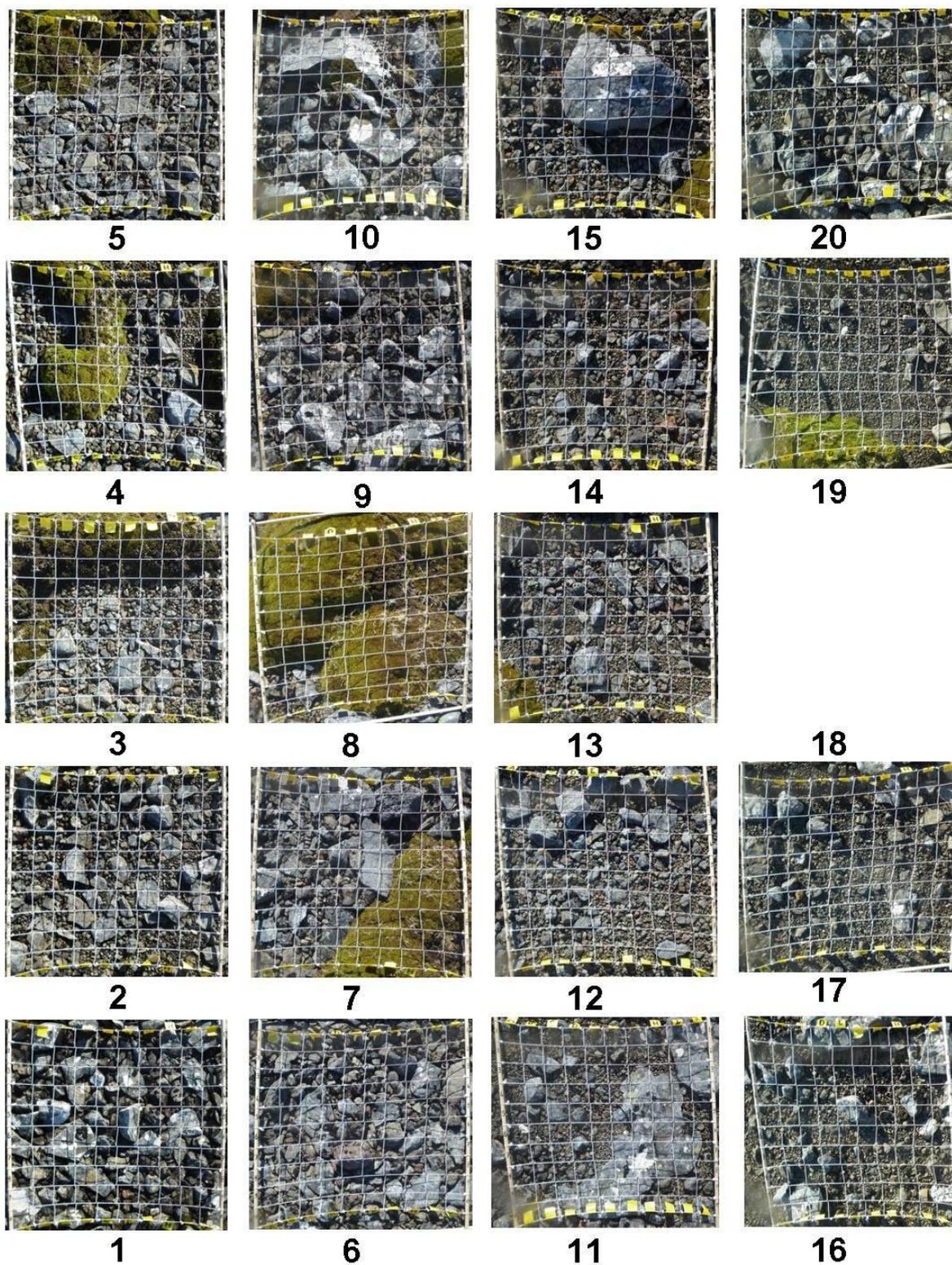
Appendix C. Photographs of the twenty 1 x 1 m quadrats at the Stoney Ridge high altitude site. The altitude of the site was  $300 \pm 5$  m a.s.l.



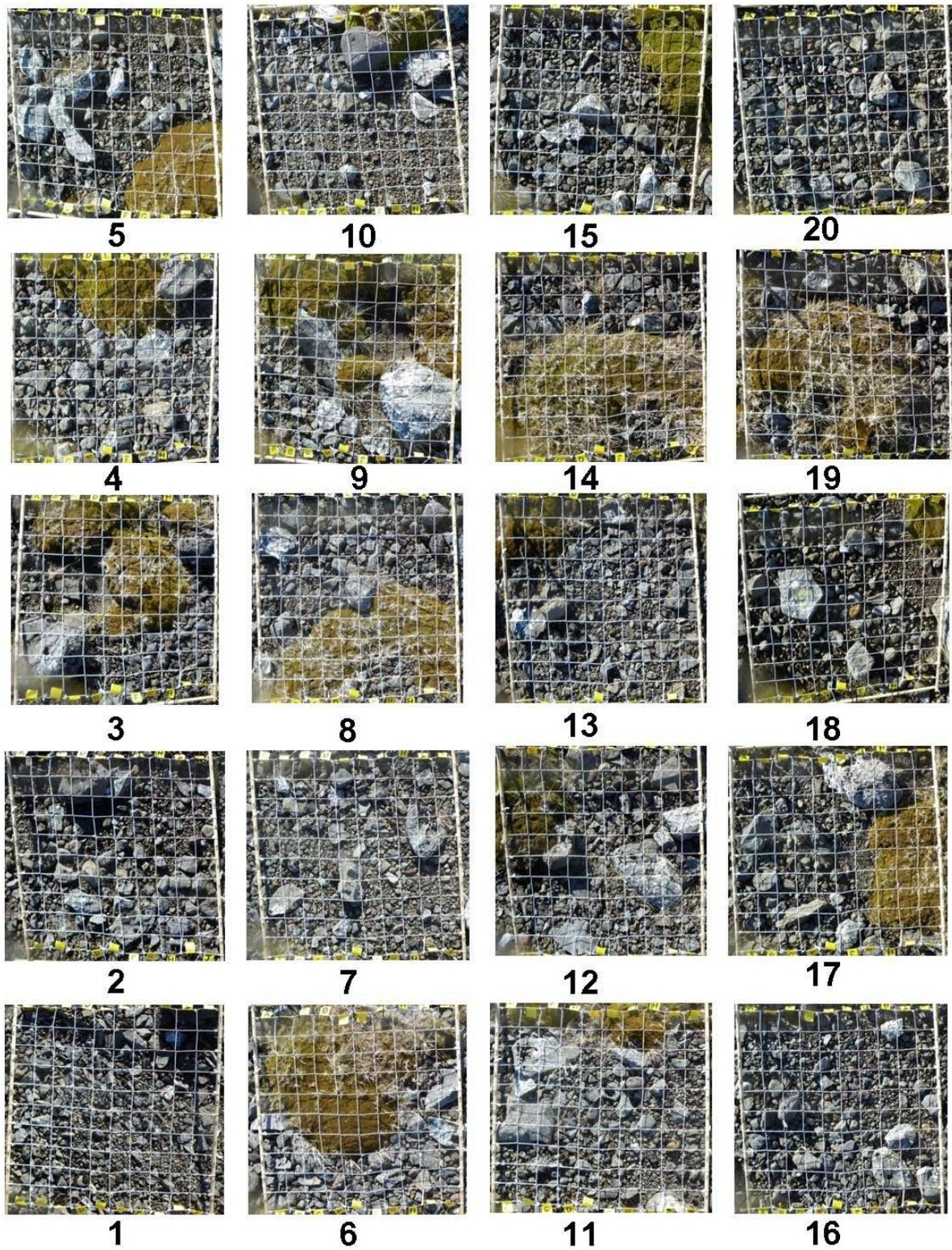
Appendix D. Photographs of the twenty 1 x 1 m quadrats at the Skua Ridge low altitude site. The altitude of the site was  $127 \pm 5$  m a.s.l.



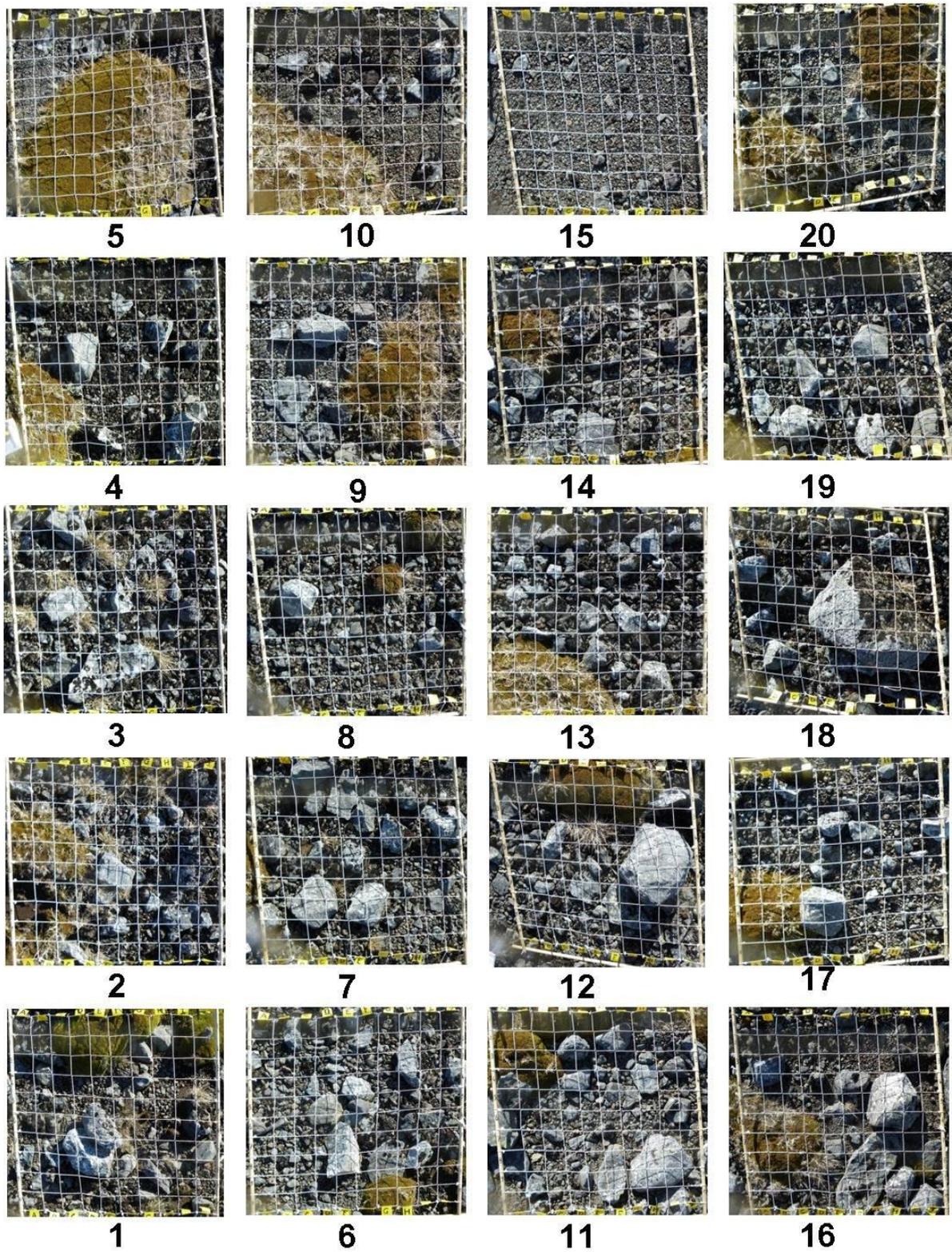
Appendix E. Photographs of the twenty 1 x 1 m quadrats at the Skua Ridge mid-altitude site. The altitude of the site was  $220 \pm 5$  m a.s.l.



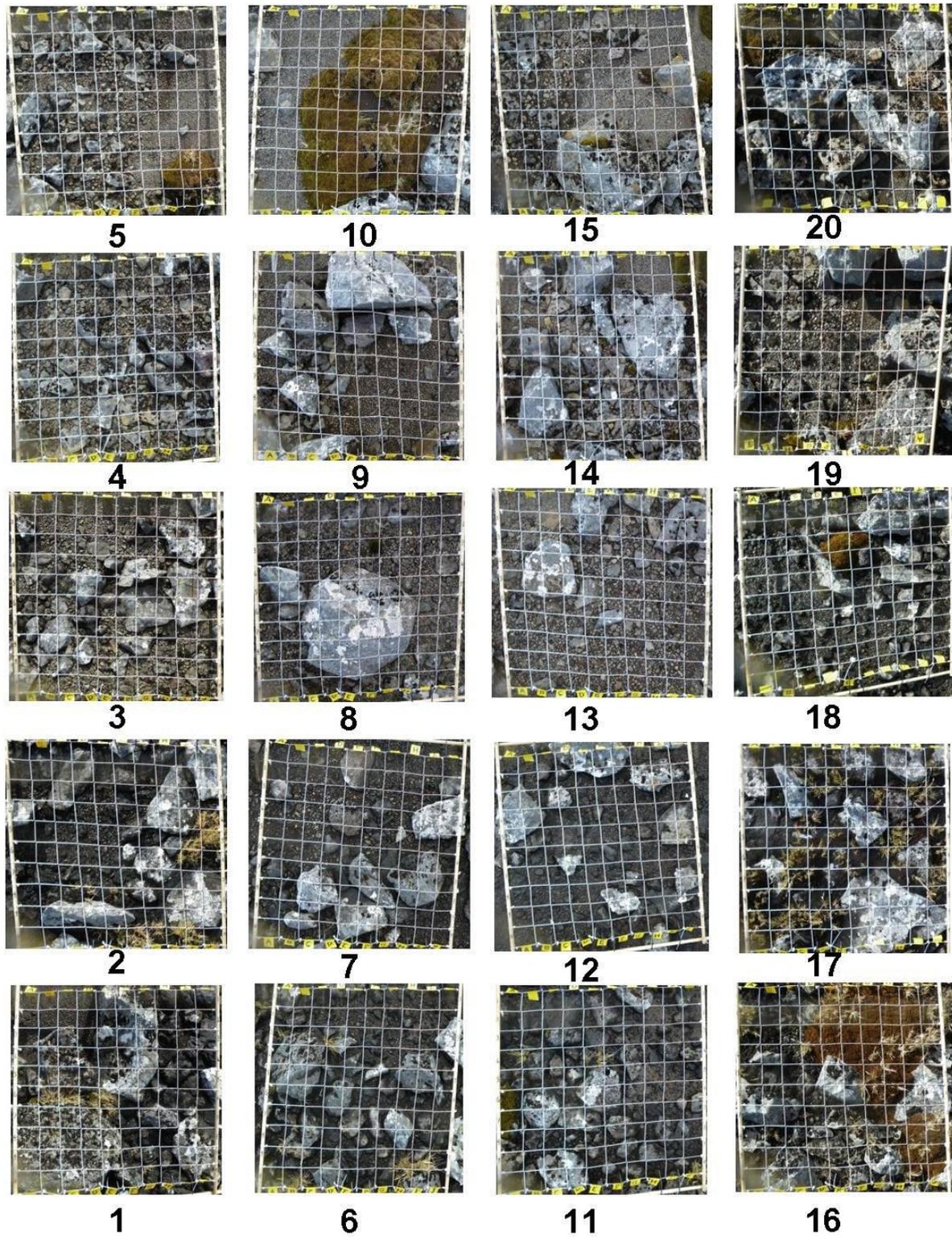
Appendix F. Photographs of the twenty 1 x 1 m quadrats at the Skua Ridge high altitude site. The altitude of the site was  $307 \pm 5$  m a.s.l. Note that one of the photographs is missing.



Appendix G. Photographs of the twenty 1 x 1 m quadrats at the Longridge low altitude site. The altitude of the site was  $144 \pm 5$  m a.s.l.



Appendix H. Photographs of the twenty 1 x 1 m quadrats at the Longridge mid-altitude site. The altitude of the site was  $200 \pm 5$  m a.s.l.



Appendix I. Photographs of the twenty 1 x 1 m quadrats at the Longridge high altitude site. The altitude of the site was  $346 \pm 5$  m a.s.l.

<b>5</b> 1:0	<b>10</b> 0:0	<b>15</b> 1:0	<b>20</b> 4:0
<b>4</b> 7:0	<b>9</b> 3:0	<b>14</b> 1:0	<b>19</b> 4:0
<b>3</b> 5:0	<b>8</b> 8:1	<b>13</b> 3:1	<b>18</b> 5:0
<b>2</b> 4:0	<b>7</b> 4:0	<b>12</b> 1:0	<b>17</b> 0:0
<b>1</b> 1:2	<b>6</b> 4:0	<b>11</b> 1:0	<b>16</b> 3:0

Appendix J. Seedling to small cushion (< 15 cm maximum diameter) ratios at the Stoney Ridge low altitude site. Numbers in bold are the quadrat numbers.

<b>5</b> 2:0	<b>10</b> 1:0	<b>15</b> 0:1	<b>20</b> 0:0
<b>4</b> 0:0	<b>9</b> 0:0	<b>14</b> 0:0	<b>19</b> 0:0
<b>3</b> 1:0	<b>8</b> 0:1	<b>13</b> 0:0	<b>18</b> 1:1
<b>2</b> 0:1	<b>7</b> 0:0	<b>12</b> 0:0	<b>17</b> 0:0
<b>1</b> 0:0	<b>6</b> 0:1	<b>11</b> 0:1	<b>16</b> 1:0

Appendix K. Seedling to small cushion (< 15 cm maximum diameter) ratios at the Stoney Ridge mid-altitude site. Numbers in bold are the quadrat numbers.

<b>5</b> 1:0	<b>10</b> 0:1	<b>15</b> 1:1	<b>20</b> 0:0
<b>4</b> 1:1	<b>9</b> 0:0	<b>14</b> 2:0	<b>19</b> 2:0
<b>3</b> 0:0	<b>8</b> 7:1	<b>13</b> 0:0	<b>18</b> 0:0
<b>2</b> 0:0	<b>7</b> 5:0	<b>12</b> 1:2	<b>17</b> 3:0
<b>1</b> 2:0	<b>6</b> 4:0	<b>11</b> 4:0	<b>16</b> 3:0

Appendix L. Seedling to small cushion (< 15 cm maximum diameter) ratios at the Stoney Ridge high altitude site. Numbers in bold are the quadrat numbers.

<b>5</b> 0:0	<b>10</b> 0:0	<b>15</b> 0:0	<b>20</b> 0:0
<b>4</b> 2:0	<b>9</b> 12:0	<b>14</b> 6:0	<b>19</b> 2:0
<b>3</b> 1:0	<b>8</b> 1:0	<b>13</b> 0:0	<b>18</b> 6:0
<b>2</b> 1:0	<b>7</b> 0:0	<b>12</b> 3:0	<b>17</b> 7:0
<b>1</b> 1:0	<b>6</b> 6:0	<b>11</b> 13:4	<b>16</b> 2:6

Appendix M. Seedling to small cushion (< 15 cm maximum diameter) ratios at the Skua Ridge low altitude site. Numbers in bold are the quadrat numbers.

<b>5</b> 0:0	<b>10</b> 0:0	<b>15</b> 3:0	<b>20</b> 0:0
<b>4</b> 1:1	<b>9</b> 0:0	<b>14</b> 4:0	<b>19</b> 0:1
<b>3</b> 0:0	<b>8</b> 0:0	<b>13</b> 1:0	<b>18</b> 1:0
<b>2</b> 2:0	<b>7</b> 1:0	<b>12</b> 0:0	<b>17</b> 0:1
<b>1</b> 0:0	<b>6</b> 1:0	<b>11</b> 8:0	<b>16</b> 0:0

Appendix N. Seedling to small cushion (< 15 cm maximum diameter) ratios at the Skua Ridge mid-altitude site. Numbers in bold are the quadrat numbers.

<b>5</b>	<b>10</b>	<b>15</b>	<b>20</b>
2:0	0:0	0:0	0:0
<b>4</b>	<b>9</b>	<b>14</b>	<b>19</b>
0:0	0:0	0:0	0:0
<b>3</b>	<b>8</b>	<b>13</b>	<b>18</b>
0:0	0:0	0:0	0:0
<b>2</b>	<b>7</b>	<b>12</b>	<b>17</b>
1:0	0:0	0:0	0:0
<b>1</b>	<b>6</b>	<b>11</b>	<b>16</b>
0:0	0:0	1:0	0:0

Appendix O. Seedling to small cushion (< 15 cm maximum diameter) ratios at the Skua Ridge high altitude site. Numbers in bold are the quadrat numbers.

<b>5</b>	<b>10</b>	<b>15</b>	<b>20</b>
0:0	1:0	1:0	0:0
<b>4</b>	<b>9</b>	<b>14</b>	<b>19</b>
2:0	1:0	0:1	0:0
<b>3</b>	<b>8</b>	<b>13</b>	<b>18</b>
4:0	1:0	1:0	1:0
<b>2</b>	<b>7</b>	<b>12</b>	<b>17</b>
4:2	1:7	8:2	6:0
<b>1</b>	<b>6</b>	<b>11</b>	<b>16</b>
1:1	0:0	1:0	4:0

Appendix P. Seedling to small cushion (< 15 cm maximum diameter) ratios at the Longridge low altitude site. Numbers in bold are the quadrat numbers.

<b>5</b>	<b>10</b>	<b>15</b>	<b>20</b>
0:0	0:0	0:0	1:0
<b>4</b>	<b>9</b>	<b>14</b>	<b>19</b>
2:0	0:0	0:0	5:0
<b>3</b>	<b>8</b>	<b>13</b>	<b>18</b>
1:0	0:0	1:0	1:0
<b>2</b>	<b>7</b>	<b>12</b>	<b>17</b>
1:0	0:0	0:1	3:0
<b>1</b>	<b>6</b>	<b>11</b>	<b>16</b>
2:0	1:6	0:0	0:1

Appendix Q. Seedling to small cushion (< 15 cm maximum diameter) ratios at the Longridge mid-altitude site. Numbers in bold are the quadrat numbers.

<b>5</b> 0:0	<b>10</b> 1:0	<b>15</b> 0:2	<b>20</b> 2:9
<b>4</b> 0:0	<b>9</b> 0:0	<b>14</b> 1:0	<b>19</b> 4:3
<b>3</b> 1:0	<b>8</b> 0:0	<b>13</b> 1:0	<b>18</b> 0:0
<b>2</b> 2:0	<b>7</b> 1:0	<b>12</b> 0:0	<b>17</b> 0:6
<b>1</b> 1:1	<b>6</b> 2:0	<b>11</b> 11:1	<b>16</b> 3:1

Appendix R. Seedling to small cushion (< 15 cm maximum diameter) ratios at the Longridge high altitude site. Numbers in bold are the quadrat numbers.