

Ecology of the declining *Olearia lineata* and not-threatened *Olearia bullata* in human-modified environments and implications for their conservation



Olearia lineata population in Gorge Creek, Alexandra.

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By

Michelle Teresa Lambert

School of Biological Sciences,

University of Canterbury,

Christchurch, New Zealand

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Abstract

Globally, human modification of land and the human-aided introduction of exotic species are considered to be the main drivers behind species decline and extinction. Human colonisation of New Zealand and subsequent development resulted in the conversion of native forests and shrublands into productive land, which together with the introduction of invasive species has caused the decline of many species, and many more are now threatened with extinction. This issue is particularly prevalent in the lowland eastern areas of the South Island, in which there has been intensive land development. One strongly affected group are species within the genus *Olearia*, in which several species are threatened with extinction, including nationally declining *Olearia lineata*. In contrast, other species in this genus, such as non-threatened *O. bullata*, are seemingly not as strongly impacted.

My study investigated the mechanisms behind why *O. lineata* is nationally declining in comparison to the non-threatened congener *O. bullata*. To do this, I investigated two main research questions; one question investigated the demographic structure of populations to determine if regeneration is occurring and the vegetation composition of the surrounding community. Sampled populations indicated regeneration failure in *O. lineata* populations but also in *O. bullata* populations, despite its non-threatened status. I found that a high proportion communities contained exotic grasses, therefore, the second question was how the presence of the exotic grass- *Agrostis capillaris*, affected recruitment of *O. lineata* and *O. bullata*. Two glasshouse experiments investigated how the presence or absence of grass affected germination and growth of seedlings. Both *Olearia* species were found to germinate in the presence of grass, but seedlings grew significantly better in the absence of grass.

Olearia are also important native Lepidoptera hosts as a suite of native moths feed exclusively on this genus. Therefore, a third research question investigated the abundance of larvae and the community composition of Lepidoptera on *O. lineata* and *O. bullata* in comparison to another

Lepidoptera host *Coprosma propinqua*. Moth larvae were collected and some species successfully reared to find there was higher larvae abundance on *O. lineata* and high species overlap between *O. lineata* and *O. bullata* with little species overlap between the two *Olearia* species and *C. propinqua*. Overall, my research found that exotic invasive grasses potentially cause regeneration failure in both *O. bullata* and *O. lineata*. However, the largest impact in the difference of threat status is due to *O. lineata* populations occurring in the most developed lowland areas of the eastern South Island, whereas *O. bullata* populations occur in less human modified, higher altitude areas. The further development of these areas through human activity threatens the future persistence of these *Olearia* species and the future of the *Olearia* Lepidoptera specialists.

Chapter 1: Introduction



Olearia lineata population in Gorge Creek, Alexandra

Background

Biodiversity decline and key drivers

Biodiversity decline is a major issue that is experienced worldwide and has critical consequences (Chapin III *et al.* 2000, Sala *et al.* 2000, MEA 2005). Species numbers have been declining, not only affecting the persistence of natural ecosystems and their species, but also the livelihoods of people who depend on natural systems for food production and jobs associated within those industries (MEA 2005). Biodiversity is important as it allows for ecosystems to provide ecosystem services people rely on daily (Diaz *et al.* 2006). Diverse ecosystems provide pollinators and seed dispersers for plants that we eat, the control of agricultural pests and diseases, which affect human health, and can aid in the production clean water through nutrient cycling (Diaz *et al.* 2006). Species extinctions are occurring at an unusually rapid rate due to anthropogenic drivers of change (Chapin III *et al.* 2000, Sala *et al.* 2000, MEA 2005). The actions of humans have resulted in the extinction of 5-20% of the species in some groups of species (Chapin III *et al.* 2000). Two of the main drivers affecting biodiversity loss are land use change, such as conversion from natural forest, shrubland or grassland to agriculture or plantation and biotic exchange where new species native or exotic invade an area that is outside their normal range (Chapin III *et al.* 2000, Didham *et al.* 2007, Murphy & Romanuk 2014). These drivers can work in isolation or in concert , as it has been seen that increased land modification allows for the invasion of new species into an area causing negative effects for biodiversity (MacDougall & Turkington 2005, Didham *et al.* 2007, Murphy & Romanuk 2014).

Land-use modification

An important cause of biodiversity loss is vegetation change through land-use modification (Chapin III *et al.* 2000, Bockerhoff *et al.* 2008, Murphy & Romanuk 2014). A 2014 meta-analysis found that land-use change had the largest effect on species richness compared with other biodiversity drivers

(species invasion, habitat loss, nutrient addition and temperature increase) investigated (Murphy & Romanuk 2014). Globally, land-use change has caused 24.8% of species richness loss when compared with other drivers of biodiversity decline (Murphy & Romanuk 2014). Populations can become isolated and restricted to fragments resulting in lower pollinator visits causing reproductive failure and reduced fitness due to inbreeding depression (Kearns *et al.* 1998, Willi *et al.* 2005, Chi & Molano-Flores 2014, Ison & Wagenius 2014). Small fragments are seen to hold less native species than large fragments with edge effects causing a reduction in habitat quality (Fischer & Lindenmayer 2007, Kuussaari *et al.* 2009). Yet some types of habitat degradation may be difficult to detect as the effect of the degradation may not be immediately evident and could create fragments of non-regenerating communities forming an extinction debt (Fischer & Lindenmayer 2007, Kuussaari *et al.* 2009). For example, in a Swedish study there was a 50-100 year time lag before any extinction effect on the native ecosystem became evident (Kuussaari *et al.* 2009).

Biotic exchange- invasion of exotic species

Biotic exchange is another important driver of biodiversity and species loss (Chapin III *et al.* 2000, Murphy & Romanuk 2014). The previously mentioned 2014 meta-analysis, found species invasions had the second largest impact on species richness decline of 23.7%, behind the effect of land-use change (Murphy & Romanuk 2014). With increasing globalisation, it has been easier for species to move from place to place (Chapin III *et al.* 2000, Murphy & Romanuk 2014). Exotic species are able to reach new locations, with some species becoming established and spreading quickly in new environments becoming invasive (Chapin III *et al.* 2000, Levine *et al.* 2003). Invasive species can cause regime shift affecting the functioning of a system (Levine *et al.* 2003, Gaertner *et al.* 2014). An increase in exotic grass density increases the abundance of fuel, possibly causing a regime shift through the increase in the frequency of fires in an ecosystem (Rossiter *et al.* 2003, Gaertner *et al.* 2014). For example, in northern Australia, an increase density of exotic grass *Andropogon gayanus*,

created conditions required to cause a fire regime shift (Rossiter *et al.* 2003, Gaertner *et al.* 2014). Invasive species can also competitively exclude the native species resulting in its decline and in rare cases the extinction of a native species (Levine *et al.* 2003, Thomson 2005, Diaz *et al.* 2006). This has been seen in where exotic grass *Bromus diandrus* suppressed recruitment in the Antioch Dunes primrose (*Oenothera deltoids* ssp. *howellii*) causing its decline (Thomson 2005).

Interactive effects of land-use change and biotic exchange

Land-use change and the invasion of exotic species can also interact to cause biodiversity loss (Didham *et al.* 2007). Often, land-use change causes the degradation of land, which makes it easier for exotic species to invade that area causing further degradation of ecosystems (Didham *et al.* 2007). For example, in New Zealand, coinciding with the dramatic changes of land-use, there was the arrival of many exotic animal and plant species (Craig *et al.* 2000). Poor management of new farms resulted in the invasion of many weeds and browsing animals such as rabbits, further increasing land degradation (Craig *et al.* 2000). However, are invasive species directly causing the declines in native species or are invasive species acting as passengers to the already human modified and disturbed land (Didham *et al.* 2005, MacDougall & Turkington 2005, Didham *et al.* 2007)? In the field, it is difficult to draw conclusions on the specific mechanisms, such as habitat degradation, land-use change or invasive species, behind native species decline (Didham *et al.* 2005, Didham *et al.* 2007). Correlation between any of these mechanisms and species decline does not necessarily imply causation (Didham *et al.* 2005, Didham *et al.* 2007). An experimental approach is needed to determine if the invasion of exotic species is causing a direct negative competitive effect on native species or if the invasive species are just filling gaps produced by the modification and degradation of land (MacDougall & Turkington 2005, Didham *et al.* 2007).

How species differ in their response to environmental change

The response of species to environmental change can vary from species to species (Diaz *et al.* 2006). Some species can succeed in modified habitats, whilst others are detrimentally affected (Diaz *et al.* 2006). Species that succeed in the face of environmental change tend to be those that are well adapted to many different environmental conditions and can easily spread and establish in new areas (Diaz *et al.* 2006). A number of successful species tend to be exotic, although, not all exotic species are invasive, and some become invasive as they are often pre-adapted to human modified and disturbed systems (Levine *et al.* 2003). Conversely, the species that tend to lose in the face of environmental change are those that require specific habitat conditions to establish and regenerate or are slow to establish and are therefore outcompeted by exotic species (Diaz *et al.* 2006). Invasive species can also change the aspects of a habitat making it no longer suitable for native species (Widyatmoko & Norton 1997, Chapin III *et al.* 2000). Even species in the same genus can respond differently to human-caused environmental change (Hedges 1998), therefore it is important to study individual species to determine why these differences may occur.

Biodiversity loss and plant-animal interactions

Land-use modification causes the loss of habitat and the creation of fragments reducing the number, size and quality of the remaining habitats (Tscharntke & Brandl 2004, Fischer & Lindenmayer 2007). The features of a habitat such as distance from another fragment and size can affect species richness, but also the species interactions (e.g. plant and herbivore or plant and pollinator) within the habitat (Tscharntke & Brandl 2004, Fischer & Lindenmayer 2007, Tylianakis *et al.* 2008). Therefore, a reduction in these features can cause a negative impact not only on the community but the interactions that make up the community (Tscharntke & Brandl 2004). There are many examples

of plant-animal dependencies involving trophic or mutualistic interactions (Leimu & Lehtilä 2006, Drummond *et al.* 2010, Anderson *et al.* 2011). Some of these interactions, as a consequence, cause the specialization of animals to their host plant and vice versa (Patrick 2000, Drummond *et al.* 2010, Anderson *et al.* 2011). A study on the declining moth *Lycaena dispar batavus* in Europe shows it has become specialized to feeding on species in the genus *Rumex* (Martin & Pullin 2004). This resulted in the specialization towards declining fenland habitats where *Rumex* is found, thus causing the decline in the moth species itself (Martin & Pullin 2004). Anderson *et al.* (2011) noted extinction and decline of bird pollinators resulted in reduced pollination in *Rhabdothamnus solandri* causing seed limitation and resulting in regeneration failure. Plant- animal interactions can also cause speciation such as in the yucca moth *Prodoxus coloradensis*, in which speciation has occurred ,where multiple species can coexist on one yucca tree due to specialization of feeding on different parts of the tree such as fruit, flowers or leaves (Drummond *et al.* 2010). It is important in a system that the plant-animal interaction are both present as they are inextricably linked so the removal of one partner in the interaction, such as the extinction of the plant, can cause the extinction of the other partner, such as a reliant moth species (Patrick 2000, Martin & Pullin 2004). This has implications on future survival of both species in the interaction. As part of my study, I will investigate a plant-herbivore interaction involving the abundance of larvae and community composition of native herbivore Lepidoptera species found on my two study plant species (Chapter 4).

Land-use change and species invasion in New Zealand

In New Zealand, land use change and the invasion of species are seen as main drivers behind biodiversity loss (Brockerhoff *et al.* 2008, Walker *et al.* 2008). The colonisation of New Zealand resulted in dramatic changes of land-use (Craig *et al.* 2000, Ewers *et al.* 2006, McWethy *et al.* 2010). There was a reduction of native forest cover from pre-human arrival of 78% to 23% coverage, since the arrival of both Maori and European settlers (Ewers *et al.* 2006, Wiser *et al.* 2011). With

colonisation came the settlement and expansion of towns and cities along with the development of agriculture and forestry having great impacts on biodiversity (Ewers *et al.* 2006, Walker *et al.* 2006a, Brockerhoff *et al.* 2008). There are now more introduced exotic plants than natives in New Zealand with exotic plants continuing to invade (Craig *et al.* 2000). This can cause more competition for native plant species on land that is already challenging for species establishment and regeneration (Rogers 1996b, Widyatmoko & Norton 1997).

Increasing environmental change has resulted in the decline of New Zealand's endemic biota (Ewers *et al.* 2006, Walker *et al.* 2006a, Brockerhoff *et al.* 2008, de Lange *et al.* 2010). In 2009, a revised list of threatened and uncommon plants in New Zealand was released (de Lange *et al.* 2009). It describes the conservation status of 898 indigenous vascular flora listing 180 taxa as 'threatened' and 651 as 'at risk' (de Lange *et al.* 2009). The largest proportion of listed plants were from lowland habitats (30%) followed by those from montane habitats (24.3%) (de Lange *et al.* 2009, de Lange *et al.* 2010). Particular genera were also more affected than others, with the most affected species such as *Myosotis*, *Leptinella* and *Olearia*, being found in the most threatened habitat types (de Lange *et al.* 2009). It is likely these trends are due to continual land-use change and range expansion of invasive exotic species experienced in New Zealand today (Ewers *et al.* 2006, de Lange *et al.* 2009, de Lange *et al.* 2010). This has dire consequences for species as seen in *Gnaphalium luteoalbum* var. *compactum* which has experienced a serious decline in population numbers due to land use alteration; or through invasive grasses and herbs outcompeting native plants causing populations, such as *Carmichaelia* and *Olearia* species, to suffer from regeneration limitation (de Lange *et al.* 2009).

Demographics of native species

One way to determine the status of a species, is to determine the demographic structure of the species populations (Rogers 1996b, Gruner 2003). The demographic structure can indicate whether a population contains young individuals and is regenerating or whether the population contains mostly mature individuals and regeneration is not occurring within the population (Rogers 1996b, Widyatmoko & Norton 1997, Gruner 2003). This is important to know because populations may exist but the population may not be contributing to the future persistence of the species (Gaertner *et al.* 2009, Kuussaari *et al.* 2009). For instance, if a population persists in a farmland area but does not have any young individuals present it may not be contributing to the future persistence of the species, but rather it may be part of an extinction debt in that, as soon as the older mature individuals have disappeared, the population will become extinct (Gaertner *et al.* 2009). Therefore, the demographic structure of a population is useful to determine if a species can persist for the long term future or if it is part of an extinction debt (Gaertner *et al.* 2009, Kuussaari *et al.* 2009). So by completing this comparative study I will investigate how a nationally declining species *O. lineata*, survives in the face of environmental change compared with a non- threatened species in the same genus *O. bullata*. It is important to measure demographics in addition to proximate causes of decline. I investigate the effects of land-use modification and invasive species by using a case study of *Olearia lineata* (Kirk) Cockayne 1911 and *Olearia bullata* H.D. Wilson & Garn.-Jones 1992. I will give details below on the biology of the species and then explain why I have chosen *O. lineata* and *O. bullata* as a case study.

Why study these species?

Biology and ecology of *Olearia bullata* and *Olearia lineata*

The genus *Olearia* or 'tree daisies' are part of the Asteraceae family and are endemic to Australasia with 130 species present in this genus (Rogers 1996b, Heads 1998). *Olearia* is one of the more

species rich plant genera in New Zealand with 38 species with a range of large-leaved and small-leaved trees and shrubs (Heds 1998, Derraik *et al.* 2003). Within this genus of woody/shrubby growth forms is the group *Olearia* section *Divaricaster* (Heds 1998). *Olearia* section *Divaricaster* displays characteristics such as divaricating branches, small clustered leaves in opposite pairs, flowers with purple style arms and singular or grouped flower heads and hosts a distinct insect fauna (Heds 1998).

This group of *Olearia* has been significantly impacted by the effects of human activity such as land-use conversion resulting in habitat loss (Heds 1998, Patrick 2000, Department of Conservation 2007). This has caused a majority of the species in this group to be ranked as ‘at risk’ or ‘threatened’ (Rogers 1996b, Heds 1998, Conservation 2007, de Lange *et al.* 2009, de Lange *et al.* 2010). It is not known why *O. bullata* is still relatively common and *O. lineata* is rare so a comparison of population structure and regeneration abilities is important to determine why this occurs.

***Olearia bullata* H.D. Wilson & Garn.-Jones 1992**

Olearia bullata is non-threatened and endemic to the South Island of New Zealand (Wilson & Galloway 1993, Heds 1998, de Lange *et al.* 2009). It occurs south from Kaikoura on the east coast of the South Island, Southland and Fiordland but is absent on the west coast (Figure 1.1a). This species is found in habitats of montane shrubland, and is especially common in the mountains of the Canterbury region where it is usually associated with seepages and other damp sites (Wilson & Galloway 1993, Heds 1998). It can grow up to 2m in height and leaves are in opposite clusters on their branches (Figure 1.2). Little is known of the ecology of *O. bullata* but several studies have been undertaken on invertebrate richness associated with this plant (Derraik *et al.* 2002a, Derraik *et al.* 2003, Derraik *et al.* 2005). These studies found that *O. bullata* is a host to a diverse assemblage of

invertebrate species such as beetles, moths, true bugs and flies showing its importance as an invertebrate host (Patrick & Dugdale 2000, Derraik *et al.* 2002a, Derraik *et al.* 2005).

***Olearia lineata* (Kirk) Cockayne 1911**

Olearia lineata is nationally declining and endemic to the South Island of New Zealand where it is present south of Kaikoura occurring on both the east coast and west coast of New Zealand, and Southland, but is absent from Fiordland (Figure 1.1b) (Wilson & Galloway 1993, Heads 1998, Conservation 2007, de Lange *et al.* 2009, Dawson & Lucas 2012). *Olearia lineata* is found in dynamic habitats such as lowland to lower montane shrubland, scrub and on river terraces (Wilson & Galloway 1993, Heads 1998, Dawson & Lucas 2012). It can grow to 6m tall and has leaves in opposite clusters but the leaves are thinner, longer and do not display distinctive wrinkling, such as that seen in *O. bullata* (Figure 1.2) (Heads 1998). There is a lack of research on the ecology of *O. lineata* with only little known about the moth fauna associated with this species (Patrick 2000). It is likely that *O. lineata* is experiencing regeneration failure, which may be causing the decline in this species (Wilson & Galloway 1993, Heads 1998, Conservation 2007, Dawson & Lucas 2012). This decline is hypothesized to be due to competition with invasive grasses (Figure 1.2) (Department of Conservation 2007).

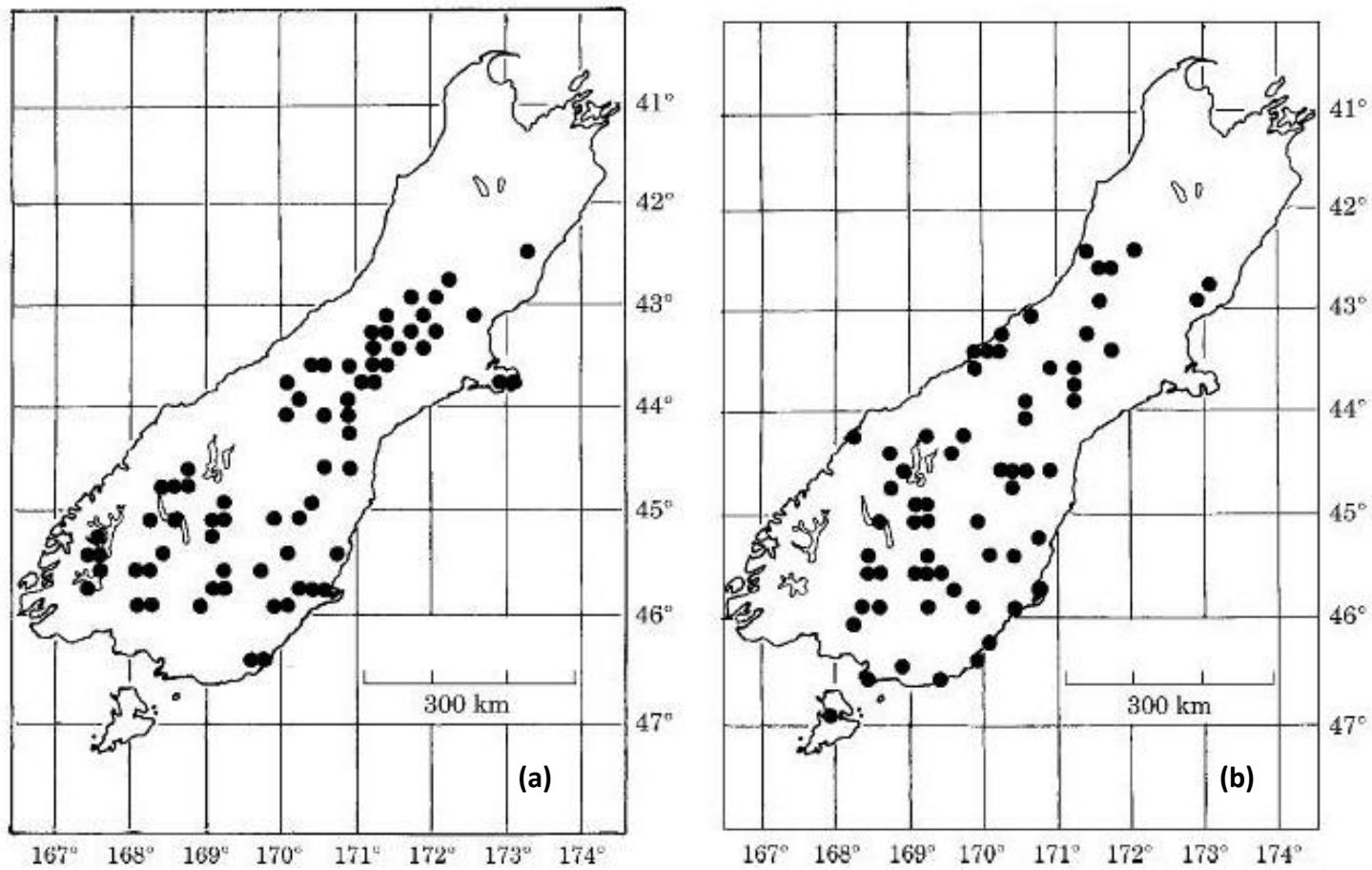


Figure 1.1: (a) Distribution of *O. bullata* (Heads 1998) p. 260. (b) Distribution of *O. lineata* (Heads 1998) p. 262.



Figure 1.2: Leaf characteristics and habit of *O. lineata* and *O. bullata*. **A.** Habit of *O. lineata*. Also note the invasive grasses present at the bottom of this photo. **B.** *O. lineata* leaf form. **C.** *O. bullata* leaf form. **D.** *O. bullata* habit. (Photo credits A-D: David Norton, Michelle Lambert, John Barkla, John Barkla.)

Importance of *Olearia lineata* and *Olearia bullata*

The genus *Olearia* has an unusually high number of threatened and at risk species, especially in the South Island of New Zealand (de Lange *et al.* 2009, de Lange *et al.* 2010). I will focus on two species in this genus- *O. lineata* and *O. bullata* as the effects of land use and invasive species have not been previously studied in these species. *Olearia bullata* and *O. lineata* both occupy habitats which are heavily impacted by human activity although one species is common and the other species is declining (Heads 1998). These species are important parts of the community as they are significant

hosts for endemic invertebrate fauna, reduce soil erosion, provide nesting sites for native birds, and being part of a shrubland community they aid in the successional process towards forest growth and establishment (Heads 1998, Merrett *et al.* 2007). I will introduce each of these roles below.

Importance of Olearia bullata and Olearia lineata for Invertebrates

O. bullata and *O. lineata* not only support a wide array of invertebrate species but also act as hosts to moss, algae and lichen communities providing a habitat and more complex resources for invertebrate taxa (Patrick 2000). There is a high rate of endemism at the species level in the New Zealand invertebrate fauna (Patrick 1994). *Olearia bullata* supports a rich suite of invertebrate taxa (Derraik *et al.* 2002a, Derraik *et al.* 2003, Derraik *et al.* 2005). In a 2003 study it was found that *O. bullata* had significantly more associated insects compared with *Coprosma propinqua* (Derraik *et al.* 2003). *O. bullata* harbored 69 invertebrate taxa including six species of spider, three species of beetles, three species of true bugs and one species of fly, while *C. propinqua* contained only 30 taxa (Derraik *et al.* 2003). This indicates not only is *O. bullata* an important host for Lepidoptera but it is equally as important as a host for other native invertebrates. More studies are required on moth presence in areas that harbor large proportions of threatened native moths such as Canterbury, Marlborough, Otago, Southland and Wellington (Patrick 2000, Patrick & Dugdale 2000). The data required includes moth presence/absence data, and host preference and habitats so the protection of land can be implemented to protect these native moth species while also protecting the host plants (Patrick 2000, Patrick & Dugdale 2000). Lepidoptera form New Zealand's third largest order of Insecta (Patrick 2000, Patrick & Dugdale 2000). Lepidoptera include many taxa which are highly threatened and 80% of the 114 species identified in this study were found to be threatened in a study on the conservation status of native Lepidoptera (Patrick & Dugdale 2000). There is a high level of host plant specificity in the New Zealand moth fauna (Patrick 2000). This is seen in the genus *Olearia* where a wealth of herbivorous moth species feed on this genus and 41 species feed on the

Olearia section *Divaricaster*, within which *O. bullata* and *O. lineata* are classified (Patrick 2000).

Twenty of these moths are specialists with 17 restricted specifically to feeding on this host group (Patrick 2000). These moths employ feeding strategies that include leaf mining, feeding on flowers, dead bark and new live foliage (Patrick 2000). However, these moths are very reliant on their host species and now show patchy distributions due to the fragmented nature of their host species populations (Patrick 2000).

Importance of Olearia bullata and Olearia lineata for ecosystems

Olearia lineata and *O. bullata* also provide many benefits to ecosystems. *Olearia lineata* and larger *O. bullata* individuals can also provide nesting sites for birds. Numerous birds such as the silvereye build nests within these trees (pers. obs.). The provision of nesting sites therefore provides additional ecosystem benefits, as these birds are important pollinators of the New Zealand flora (Anderson *et al.* 2011, Pattemore & Wilcove 2012). *Olearia lineata* has also been observed as a host of 'at risk' native mistletoe species *Korthalsella clavata* (pers.obs.). These examples all highlight that these *Olearia* species are a vital part of the ecosystem as they support many other native species.

Importance of Olearia bullata and Olearia lineata for succession

Lastly, *O. lineata* and *O. bullata* are an integral part of shrubland communities (Heads 1998, Merrett *et al.* 2007). There are approximately 380-400 species of shrubs making up 16% of New Zealand's total native flora (Merrett *et al.* 2007). Shrubs are important as they play a major role in successional pathways from abandoned pasture to the formation of native shrublands, or the eventual formation of canopy forests (Merrett *et al.* 2007). Shrublands tend to be located on forest margins and lowland regions which are significantly affected by deforestation and land degradation, therefore, a proportionally large number of shrubs are of conservation concern (Heads 1998, Patrick 2000, Merrett *et al.* 2007, Department of Conservation 2007).

Aim of Research

The aim of my thesis is to determine the effect of two human-mediated changes, land-use modification and invasion of exotic grasses, on native New Zealand species that differ in their threat status. To do this I am using *Olearia lineata* and *Olearia bullata* as a model system. Specifically, Chapter 2 will investigate the population demographics of these study species to determine whether they are affected by regeneration failure (potentially due to land-use changes and invasive species). It will also look at the vegetation composition of the communities in which these species exist, to determine if there are any co-occurring species that may or may not promote the presence of these *Olearia*.

Chapter 3 builds on the population demographics and community structure of these species, presented in Chapter 2, by investigating experimentally the effect of the most common exotic grass in the region, *Agrostis capillaris*, on the germination and growth of seedlings in these two *Olearia* species. Chapter 4 investigates the Lepidoptera community present on these two *Olearia* species, and compares it with another plant host species of a similar habit and another species in the same family Asteraceae. Chapter 5 will synthesise the results from each of these chapters to determine the response of *O. lineata* and *O. bullata* to human-induced change and provide future research suggestions and recommendations on management techniques to ensure the persistence of these *Olearia* species.

Chapter 2: Population Demographics and Community Composition of *Olearia lineata* and *Olearia bullata*



Olearia bullata population at Speight's Saddle, Cass.

Introduction

Humans are altering the world at an unprecedented rate as agents of change in the natural global environment (Chapin III *et al.* 2000). Human land-use modification through the conversion of native vegetation cover into agriculture land, forestry or alternatively for urbanisation, causes the decline or loss of many species (Chapin III *et al.* 2000, Ewers *et al.* 2006, Walker *et al.* 2006a, Fischer & Lindenmayer 2007). Further, there has been an increase in biotic exchange, especially human-aided (Grauver *et al.* 2008, Norton & Reid 2013), resulting in many species now being able to travel and establish in new locations (Chapin III *et al.* 2000, Sala *et al.* 2000). This influx of new species into an areas becomes a problem when they establish and become invasive, outcompeting native species in their natural range (Corbin & D'Antonio 2004). One example of this is the exotic shrub *Lonicera maackii* which is able to outcompete native herbs *Galium aparine*, *Impatiens pallida* and *Pilea pumila* in the Eastern United States, resulting in reduced survival and fecundity of these native herbs (Gould & Gorchov 2000). Both of these processes can result in the fragmentation of populations from a local to a landscape level (Fischer & Lindenmayer 2007).

Human land-use modification and the establishment of invasive species is also a pressing concern in New Zealand. Colonisation by people has caused many land-use changes resulting in the conversion of native forest, shrubland and grassland into farming and forestry (Ewers *et al.* 2006, Walker *et al.* 2006a). Forests covered 78% of New Zealand before the arrival of humans, but now only cover 23% (Craig *et al.* 2000, Ewers *et al.* 2006). The building and expansion of towns and cities linked by road networks further decreased native forest cover. In New Zealand, this human land-use change was especially intensive in the eastern and lowland parts of the country, resulting in 50% of New Zealand being converted into pasture (Craig *et al.* 2000). Increasing development facilitated the invasion of exotic species into these lowland areas causing further change to ecosystems in these intensively modified environments (Ewers *et al.* 2006). The spread of exotic grasses increased rapidly with the

planting of species such as brown top (*Agrostis capillaris*) for stock consumption, which is now found in native ecosystems throughout the country (Edgar & Connor 2000).

A high proportion of native shrubs are found in lowland areas where they would have occurred in successional and forest margin habitats naturally (Merrett *et al.* 2007). They are an important part of shrubland ecosystems as they provide important ecosystem services by establishing in the soil, making it more habitable for other species to establish, and stabilising ground to prevent erosion (Merrett *et al.* 2007). However, given the large-scale transformation of lowland areas these species are particularly threatened (Merrett *et al.* 2007, de Lange *et al.* 2009, de Lange *et al.* 2010). Some traits such as fast growth and adaptation to low nutrient soils allow certain species (e.g. *Discaria toumatou*) to persist in these modified landscapes, though many shrubs have similar life history traits (Widyatmoko 1994). In spite of this similarity, related species may differ in the extent to which they are threatened by landscape changes. For example, two related lowland-montane species *Olearia lineata* and *Olearia bullata*, with a similar eastern South Island distribution, differ in the extent to which they are considered to be threatened (Heads 1998, de Lange *et al.* 2009).

Olearia lineata is a nationally declining tree that is found on lowland and montane river terraces (Heads 1998). *Olearia bullata* is non-threatened and found in wetland and flush areas (Heads 1998). What attributes could be driving the differing conservation status? The abiotic and biotic attributes of the community may vary between species, especially due to the differences in the habitats these two species occupy. The vegetative community composition would likely contribute an important role in the differing conservation status as it is expected there will be different species present in the communities. Some of these species may encourage the persistence of the *Olearia* species or they may prevent the persistence of these species through competition (Rogers 1996b). These attributes, in turn, could affect the demographic structure of populations of these species, in which the populations may consist of young and old individuals (i.e. population

regenerating) or be restricted to older mature individuals with a lack of young seedlings (i.e. population not regenerating) (Rogers 1996b). This can be a problem for the future persistence of these species if there are no young seedlings as recruits to sustain the population (Rogers 1996b).

In this chapter my research aims are:

1) To identify which environmental characteristics mechanisms may explain why *O. lineata* is nationally declining and *O. bullata* is non-threatened. A comparative study analysing the abiotic, biotic attributes and vegetative community composition of these species will be used to determine any similarities and/or differences in the environment occupied by these species. A difference is expected in the vegetation community composition and abiotic requirements of both species, as the sites *O. bullata* occupies tends to be in wetland seepage areas whilst *O. lineata* is found in drier areas.

2) The second aim is to investigate the demographic population structure of *Olearia bullata* and *O. lineata*. This is to identify if there are any young seedlings and determine whether the population is young and regenerating or whether there are mature populations with a lack of young seedlings, hence the population is not regenerating. Because *O. bullata* is classified as non-threatened, populations would be expected to have numerous young seedlings and be regenerating. However, *O. lineata* is nationally declining so it should exhibit a lack of small seedlings in its populations indicating regeneration failure.

Methods

Site selection and Sampling

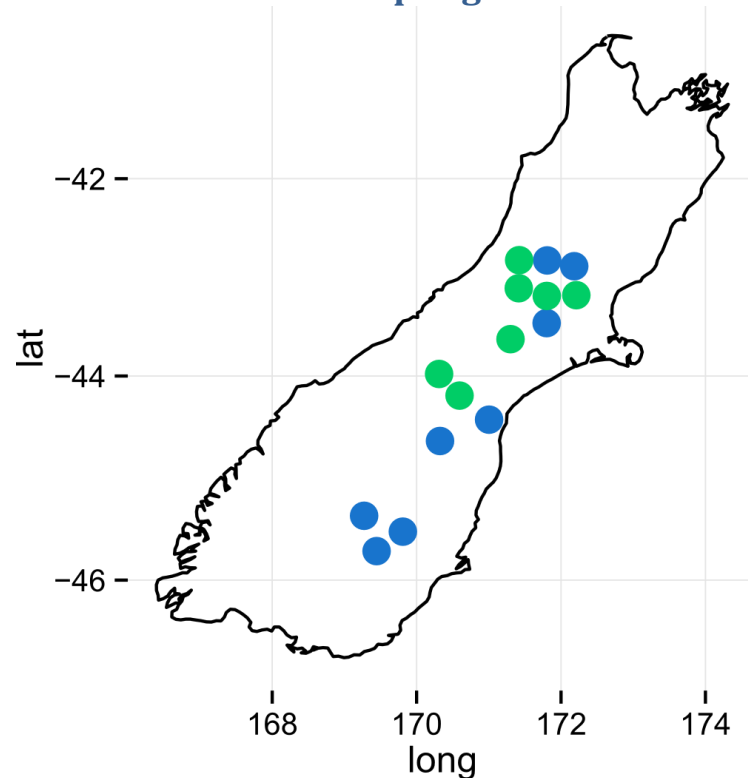


Figure 2.1: *O. lineata* (blue circles, N=8) and *O. bullata* (green circles, N=7) field sampling sites.

Field sites were selected throughout Canterbury and Otago, South Island, New Zealand, where populations of both study species were known to occur (Figure 2.1, Heads 1998). Selection criteria were the same for both species, with each location being easily accessible by road and having a population greater than 20 trees. Sites were found in consultation with the Department of Conservation, the QEII National Trust, locations from published papers and knowledge of the areas from supervisors. Eight sites were sampled for *O. lineata* and seven sites for *O. bullata*, which comprised all the populations I could find that met the above criteria. Except for the Cass Mountain Research Area and sites on road reserves or within the Queens chain, permission was obtained from land owners, or in the case of public conservation land, from the Department of Conservation, before sampling was undertaken. Note: Site 3- Rakaia Island, for *O. lineata* is not included in this

Chapter of the thesis, as it only consisted of one tree but seed from this tree was collected and used for experiments in Chapter 3. At each location, the sample of the population was defined either by sampling all the individuals in the population if there were <50 individuals, or by sampling a subset (50 individuals) of the population, if the population had >50 individuals.

Population Demographic Structure of *O. lineata* and *O. bullata*

To determine the demographic structure of each population, the size of the trees was measured. Because the trees were too small to core and growth rings of these species are known to be often only slightly distinct (Meylan & Butterfield 1978) the trees could not be aged in these ways, and size was used as a surrogate for age. Heights (m) of trees were often greater than 1.5m so trees above that height were measured using a clinometer, with height calculated using trigonometry. Basal diameter (cm), canopy cross section (m) and for *O. lineata*, the distance from the ground to canopy (m) were also measured. The canopy to ground measure was not needed for *O. bullata* as the foliage for this species reaches the ground, so an accurate canopy volume could already be measured. Canopy cross section comprised of two measures perpendicular to each other of the canopy diameter. While none of these measures are directly measures of plant age (Harper 1977), they do provide a relative index of the structure of each population and have been used in studies with similar species (Widyatmoko and Norton 1997, Rogers 1996). The total basal area of multi-stemmed trees was also determined by calculating the basal area for each individual stem and then summing these for the tree. The volume of the tree canopy was calculated by using the volume formula for an ellipsoid (Equation 1). The volume of an ellipsoid was used as this best approximation for the shape of the trees. For *O. lineata*, the ground to canopy measure was subtracted from the height to get a more accurate height value for the volume formula.

$$\text{Volume (m}^3\text{)} = \frac{4}{3} \pi abc \quad (1)$$

Where $\pi = 3.14$ (2 d.p.)

a= height- ground to canopy (*O. lineata*) or height for (*O. bullata*)(m).

b= first canopy cross-section measure (m)

c= second canopy cross-section measure (m)

At one *O. lineata* site (Site 4 -High Peak Station), the heights and ground to canopy measures of some of the trees were measured incorrectly. However, the basal diameter measures were correct so using measurements from a similar site with similar abiotic and biotic attributes (Site 2- Poulter River), the relationship between basal area and height or basal area and ground to canopy using a linear model was established, and the height and ground to canopy values for the incorrectly-measured individuals were estimated at the High Peak Station site.

Abiotic and Biotic Attributes, and Vegetation Community Composition for *O. lineata* and *O. bullata*

At each site the biotic attributes, abiotic attributes and vegetation community composition were recorded using the RECCE plot method (Hurst & Allen 2007). This is the standard method used throughout New Zealand for characterising vegetation communities, and was therefore selected to ensure that the data collected were comparable with other similar studies (e.g. by the Department of Conservation). One temporary 10m x 10m plot was set up at each site (in an area that was representative of the vegetation and landform of the site), within which the RECCE method was applied.

RECCE plot method- Abiotic Attributes

Ground slope was measured using a clinometer in the centre of the plot, taking the midpoint value between an eye level point at the top and bottom of the plot. Drainage was visually estimated and assigned a value of 1 (poor: pooling of water common over site; ground damp and muddy, usually boggy/wetland sites), 2 (moderate: slight pooling of water at site, some areas of the ground is wet) or 3 (good: no pooling of water, ground dry often dusty; usually grassland sites). Altitude was recorded using a GPS. Aspect was recorded using a compass and was corrected for data analysis so that all values were relative to North or South (i.e. East and West had the same value).

RECCE plot method- Biotic Attributes and Vegetation Community Composition

Biotic attributes including species present, canopy cover (canopy cover (%) of all plants greater than 1.3m in height in the plot), non-vascular species percentage ground cover, and average height of the plot vegetation were recorded. All plant species within a plot were identified and unknown species were collected for later identification in the lab. It was not possible to identify all species, as some were missing important identifier characteristics (e.g. flowers, as in cases where they had already flowered or were yet to flower). Each plant was given a percentage cover score depending on how much of the area of the plot it covered in each of the different height tiers in which it was present. Six height tiers were used (0-30cm; >30cm-2m; 2-5m; 5m-12m; 12m-25m) and species were assigned a modified Braun-Blanquet cover abundance score within six cover classes (1=<1%, 2=1-5%, 3=6-25%, 4= 25-50%, 5= 51-75%, 6=76-100%) in each height tier they occurred.

Data analysis

Population demographic and community data were analysed using the packages Vegan (Oksanen, et al, 2013) and Lattice (Sarkar, 2008) for the R environment (R core Team 2012).

Population Demographic Structure of *O. lineata* and *O. bullata*

For both species, histograms of size classes were produced for each of the sites and for all sites combined. Size classes were based on (i) height, (ii) basal area and (iii) canopy volume of individuals. These histograms were used to obtain a visual representation of the structure of the populations. Basal area and canopy volume were log transformed to obtain comparable data between the three population structure categories. The population structures of *O. lineata* and *O. bullata* populations were then compared using Kolmogorov-Smirnov tests (to compare the shape of their distributions), t-tests (to compare their means), and Wilcoxon rank tests (to compare mean ranks, as unlike t-tests this is insensitive to non-normal rank distributions).

Abiotic and Biotic Attributes, and Vegetation Community Composition for *O. lineata* and *O. bullata*

The total number of species per plot, exotic species per plot and native species per plot were counted. T-tests were used to compare the mean differences between *O. lineata* and *O. bullata* sites for each abiotic and biotic (such as total number of species, exotic species and native species per plot) attribute.

Non-metric Multidimensional Scaling (NMDS) was used to compare the plant communities in sites of the two species, and was conducted in R using the package Vegan (Oksanen et al, 2013) in conjunction with Lattice (Sarkar, 2008), and Permute (Simpson, 2014). Prior to analysis, a cumulative cover value was generated for each species in each plot. Cover scores within each height tier were converted to the mid-point for each percentage cover range within each cover class, and summed across all height tiers to give a single value for each species in each plot (Wiser et al, 2011). These cover values were then used in a NMDS ordination to investigate relationships between the sites. Rare species (present in <2 plots), unidentified species and the study species *O. lineata* and *O.*

bullata were removed prior to analysis to determine the relationships between the sites without their influence. Abiotic attributes were also overlain on the NMDS ordination to determine if they influenced species composition, and a permutational multivariate analysis of variance (conducted using the 'Adonis' function in Vegan) was used to test for a difference in the community composition in plots of the two *Olearia* species.

Results

Population Demographic Structure of *O. lineata* and *O. bullata*

While the overall size-class distributions for the three variables (height, basal area, and canopy volume) were broadly similar between *O. lineata* and *O. bullata*, in that most individuals were larger and there was a relative paucity of smaller individuals, there were some differences between the two species (Figure 2.2). When sites were pooled for the total population for *O. lineata* and *O. bullata*, there were differences in height, basal area and canopy volume demographics (Figure 2.2). In particular, there was a slight negative skew in the *O. lineata* population graphs, indicating greater proportion of the population comprised older individuals, compared with *O. bullata*.

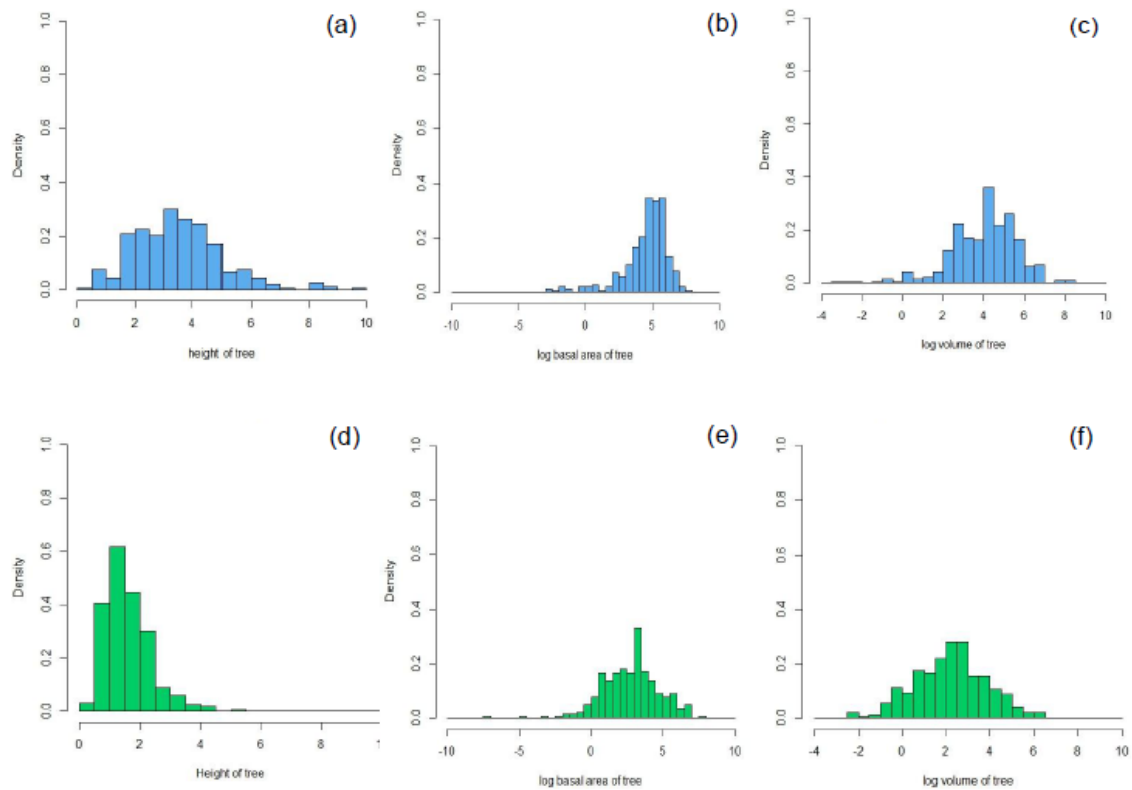


Figure 2.2: Total population structure for *O. lineata* (N=8, blue) and *O. bullata* (N=7, green); Total population height (a,d), log total population tree basal area (b,e) and log total population tree volume (c,f).

When sites were used as replicates to compare the species, *O. lineata* had fewer individuals at lower height classes than *O. bullata* (Figure 2.3a and d). The height distribution and mean height were significantly different (Kolmogorov-Smirnov test: $D = 0.64$, $p < 0.01$; T-test: $t = -19.7$, $p < 0.01$) between *O. lineata* (N=8) and *O. bullata* (N=7) populations.

In general, the distribution (Kolmogorov-Smirnov test: $D = 0.53$, $p < 0.01$) and mean (T-test: $t = -6.39$, $p < 0.01$) of log basal area also differed significantly, as the proportion of the population was the same for both species in the small size classes, but *O. lineata* had larger basal areas for the majority of the total population distribution (Figure 2.3b and f). This indicates an ageing population of *O. lineata*, which has a greater proportion of older (or at least larger) trees.

Mean canopy volume (log transformed) (T-test: $t = -8.10$, $p < 0.01$) and the shape of its distribution (Kolmogorov-Smirnov test: $D = 0.47$, $p < 0.01$) also differed between the two species (Figure 2.3c).

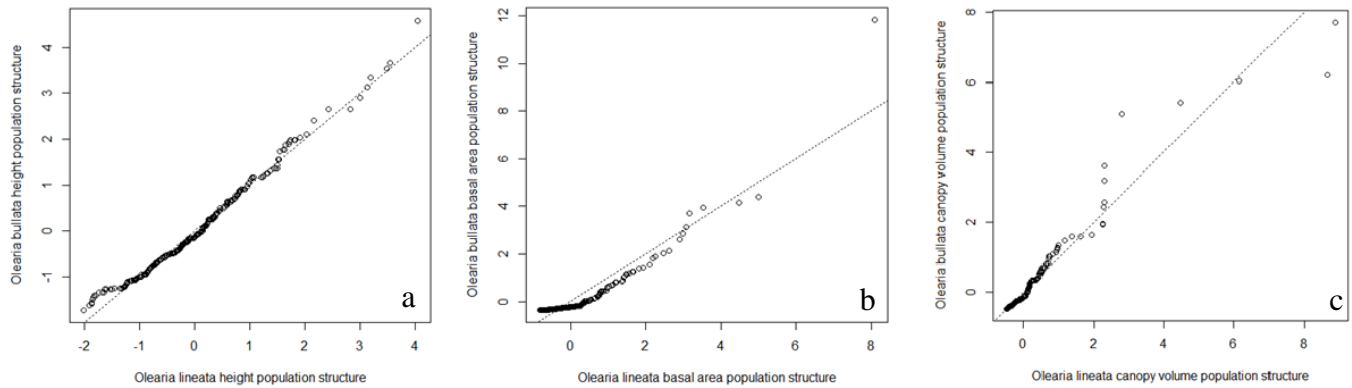


Figure 2.3: Quantile-Quantile plots to compare distributions of *O. lineata* and *O. bullata* total population structure for three measures: a) Height, b) Basal area c) Canopy volume. Both x and y axis are scaled and centred to compare the relative shape of their distributions rather than their raw size values.

Abiotic and Biotic Attributes, and Vegetation Community Composition for *O. lineata* and *O. bullata*

Abiotic attributes:

There were some differences in abiotic attributes between the sites at which the two species occurred. *Olearia lineata* was found at significantly lower altitudes than *O. bullata* (T-test: $t = 4.44$, $p = 0.001$), though the slope and aspect of sites did not differ significantly among the two species ($p = 0.87$, $p = 0.27$ respectively, Table 2.1). *Olearia bullata* also occurred at sites that had poor to moderate drainage, whereas *O. lineata* was found in sites in which there was moderate to good drainage (Fisher's Exact Test: $p = 0.009$). Although comparing multiple variables in this way increases the Type 1 error rate, the significant results presented in (Table 2.1) would remain significant at a Bonferroni corrected alpha of 0.0125.

Table 2.1: Abiotic attributes of *O. lineata* and *O. bullata* sites mean and standard deviation across all sites.

	Abiotic Attributes			
	<i>Olearia bullata</i> (N=7)	<i>Olearia lineata</i> (N=8)	Test statistic (t-stat)	p-value
altitude	586.29 ± 74.11	312.63 ± 155.47	4.44	0.001
slope	18.14 ± 11.41	16.99 ± 74.38	0.16	0.87
aspect	107.43 ± 15.84	74.38 ± 60.20	1.16	0.27
drainage	poor/moderate	moderate/good		0.009

Biotic attributes:

There were no significant differences in the biotic attributes of the communities between the two study species (Table 2.2). The only exception was a significant difference seen between the unidentified species category for the communities of each *Olearia* species (T-test: $t = -2.43$, $p = 0.04$). This may be due to a Type 1 error (this effect would be non-significant if a Bonferroni correction was applied to account for multiple testing) or a slight bias if species at *O. bullata* sites were easier to identify than those at *O. lineata* sites. For example, there may be more rare species at *O. lineata* sites making it difficult to identify all species at those sites compared with *O. bullata* sites. Unidentified species were non-flowering grasses, sedges and other species, which could not be determined to species level with certainty. Nevertheless, these species were too few to alter the non-significance of the total, exotic or native species categories, even if they could be assigned to one of these.

Table 2.2: Biotic attributes of *O. lineata* and *O. bullata* (mean and standard deviation, and results of T-test comparing sites of the two species) across all sites.

	Biotic attributes			
	<i>Olearia bullata</i> (N=7) ± SD	<i>Olearia lineata</i> (N=8) ± SD	<i>t</i>	p-value
Average Top Height	0.63 ± 0.62	0.72 ± 0.81	-0.23	0.82
Canopy cover	17.14 ± 11.50	26.86 ± 23.74	-0.67	0.51
Percentage non-vascular	1.36 ± 1.70	0.56 ± 0.18	1.23	0.26
Total Species	32.43± 12.97	35.75± 16.05	-0.44	0.67
Exotic species	14.43± 3.60	19.13± 7.00	-1.66	0.13
Native Species	16.71± 10.06	12.88± 8.03	0.81	0.43
Unidentified Species	1.29± 1.11	3.75± 2.60	-2.43	0.04

Vegetation Community Composition of *O. lineata* and *O. bullata* sites

The NMDS ordination showed slight floristic separation between *O. lineata* and *O. bullata* sites, however, the separation was not significant in the permutation anova ($p = 0.089$, Figure 2.4). The physical drivers influencing this slight separation are likely to have been significant differences in the drainage ability of water from the site (Fisher's exact test: $p = 0.009$) and the altitude differences of the communities (T-test: $t = 4.44$, $p = 0.001$).

This difference is reflected in the dominance of wetland or water tolerant plants at *O. bullata* sites compared with *O. lineata* sites. Common wetland plants, such as *Schoenus pauciflorus*, along with plants often associated with damper conditions such as *Holcus lanatus* and *Blechnum penna-marina*, were found in *O. bullata* sites, whereas these species were mainly absent from *O. lineata* sites (Table 2.3). The exotic plants *Dactylis glomerata*, *Digitalis purpurea*, *Veronica verna* and *Rumex acetosella*, all plants that are more common on well drained substrates, were more commonly found at *O. lineata* sites than *O. bullata* sites. Native *Rubus schmidelioides* was also only found at *O. lineata* sites.

Some species found in both *O. lineata* and *O. bullata* communities were common native plants

Discaria tomatou and *Coprosma propinqua* or exotic species such as *Agrostis capillaris*,

Anthoxanthum odoratum, *Hypochaeris radicata* and *Trifolium repens*.

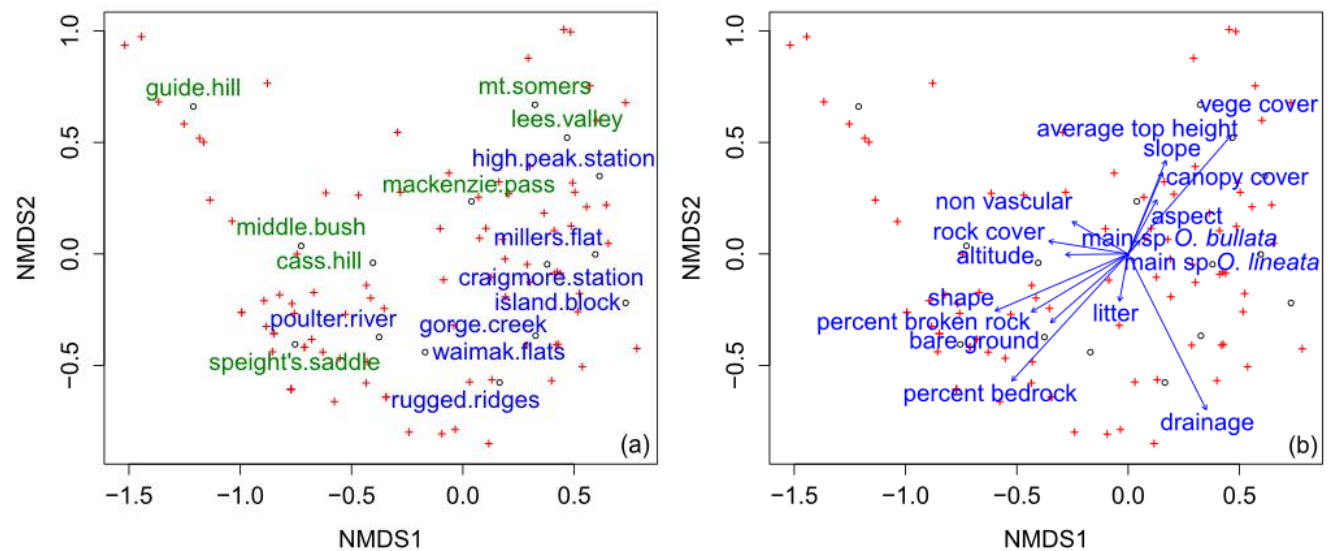


Figure 2.4: (a) Non-metric multidimensional scaling (NMDS) of sites (black circles) and species (red crosses). Site names coloured depending on main *Olearia* species- *O. lineata* (blue) and *O. bullata* (green). (b) same as (a), but with environmental variables overlain. The permutation anova found that site separation by study species *O. lineata* and *O. bullata* was not significant ($p = 0.089$).

Table 2.3

Mean importance value (calculated from the RECCE plot method) and species presence for common species at sites for *O. lineata* and *O. bullata*.

*naturalized species

Species	<i>Olearia bullata</i> (N=7)		<i>Olearia lineata</i> (N=8)	
	Mean importance value	no. sites present	Mean Importance Value	no. Sites present
<i>Discaria toumatou</i>	16.12	7	25.63	7
* <i>Agrostis capillaris</i>	4.29	7	8.12	8
* <i>Trifolium repens</i>	0.45	6	0.34	8
* <i>Anthoxanthum odoratum</i>	3.19	6	2.91	7
* <i>Holcus lanatus</i>	8.71	6	0.66	4
<i>Blechnum penna-marina</i>	0.43	5	0.06	3
* <i>Cerastium fontanum</i>	0.11	5	0.11	6
<i>Coprosma propinqua</i>	8.79	5	7.75	8
<i>Schoenus pauciflorus</i>	18.40	4	0.13	1
* <i>Hypochaeris radicata</i>	0.09	4	0.34	8
* <i>Linum catharticum</i>	0.09	4	0.04	2
<i>Festuca novae-zelandiae</i>	0.88	4	1.11	4
<i>Muehlenbeckia complexa</i>	5.46	3	1.71	3
* <i>Dactylis glomerata</i>	1.51	3	0.54	8
<i>Carex coriacea</i>	12.18	2	10.5	1
* <i>Rosa rubiginosa</i>	1.00	2	4.33	3
* <i>Digitalis purpurea</i>	0.00	0	0.28	4
* <i>Veronica verna</i>	0.00	0	0.09	5

<i>*Rumex acetosella</i>	0.00	0	0.11	6
<i>Rubus schmidelioides</i>	0.00	0	12.14	6

Discussion

Community attributes- abiotic, biotic and species composition characteristics

Across many characteristics, there were ecological similarities in the abiotic site variables and the biotic and vegetative community composition of *O. lineata* and *O. bullata*. Even with these similarities, two abiotic factors, drainage and altitude differed significantly. *Olearia bullata* was found in higher altitude areas and sites with poorer water drainage ability whilst *O. lineata* was present in lower altitude, drier sites. There was a non-significant trend towards site separation between the vegetation communities of *O. lineata* and *O. bullata* (Figure 2.4a), which may be due to the significant difference in the abiotic characteristics (i.e. altitude and drainage ability) of the sites affecting species composition. Wetland species were present in *O. bullata* communities although they were mainly absent from *O. lineata* communities. Common species to both *Olearia* community types were natives *Discaria tomatou* and *Coprosma propinqua* and the exotic species *Agrostis capillaris*, *Anthoxanthum odoratum* and *Trifolium repens*.

Altitude is a significant factor affecting the distribution of *O. lineata* and *O. bullata*. *O. lineata* is found on lowland river terraces and slopes, whereas *O. bullata* is predominantly located in higher altitude flush areas. Drainage is another important driver of difference in the distribution between these two species as *O. bullata* needs its roots to be partially submerged with sufficient moisture to grow in a particular area whereas *O. lineata* can tolerate soil drying on river terraces and slopes, where soil moisture retention is low (Heads 1998). Both species are found in close proximity to rivers and streams (Heads 1998), although *O. lineata* tends to be present in the floodplains of large rivers such as the Waimakariri River or the Clutha River while *O. bullata* is more commonly found beside small streams and in other damp sites such as seepages and flushes. Therefore, *O. lineata* is more likely to tolerate occasional disturbance events from river flooding. River flooding could provide a

disturbance regime to aid in regeneration and henceforth, the persistence of *O. lineata* in this dynamic environment (Merrett *et al.* 2007). However, with human land-use modification, disturbance regimes have been altered, through farming activities and modification of stream channels, removing the landscape level disturbance and the opportunity for species such as *O. lineata* to establish (Corbin & D'Antonio 2004, Merrett *et al.* 2007, Brockerhoff *et al.* 2008, Walker *et al.* 2008). In addition, invasive species now dominate disturbed sites and limit regeneration (further discussed in Chapter Three).

Although some species differed between communities, there was only a slight separation between vegetation communities of *O. lineata* and *O. bullata* indicating these communities are very floristically similar (Table 2.3). Some of the communities that cluster together are in close geographical proximity e.g. all the communities from the Cass/Upper Waimakairi area cluster together in the ordination (Figure 2.4). This shows that geographic location may have an effect on vegetation community composition. Species that were present in communities for both sites were exotic species such as *Agrostis capillaris* and *Anthoxanthum odoratum*. Species that were present in communities for both sites were exotic species such as *Agrostis capillaris* and *Anthoxanthum odoratum*. These species because of their invasive nature may prevent the regeneration of seedlings at sites. Another common species present in communities for both species was native *Discaria toumatou* (Table 2.3). This species is a nitrogen fixer so may encourage the persistence of *Olearia* at these sites by increasing the amount of available nitrogen in these disturbed soils creating more favourable conditions for the establishment (Widyatmoko 1994).

The significant difference in the altitudinal location for these *Olearia* species has implications for persistence of populations in these areas. In lower altitudes, there is a higher proportion of human-induced land modification such as the conversion of easily accessible land from native ecosystems to farming and forestry (Brockerhoff *et al.* 2008, Craig *et al.* 2000, Ewers *et al.* 2006). This is prevalent

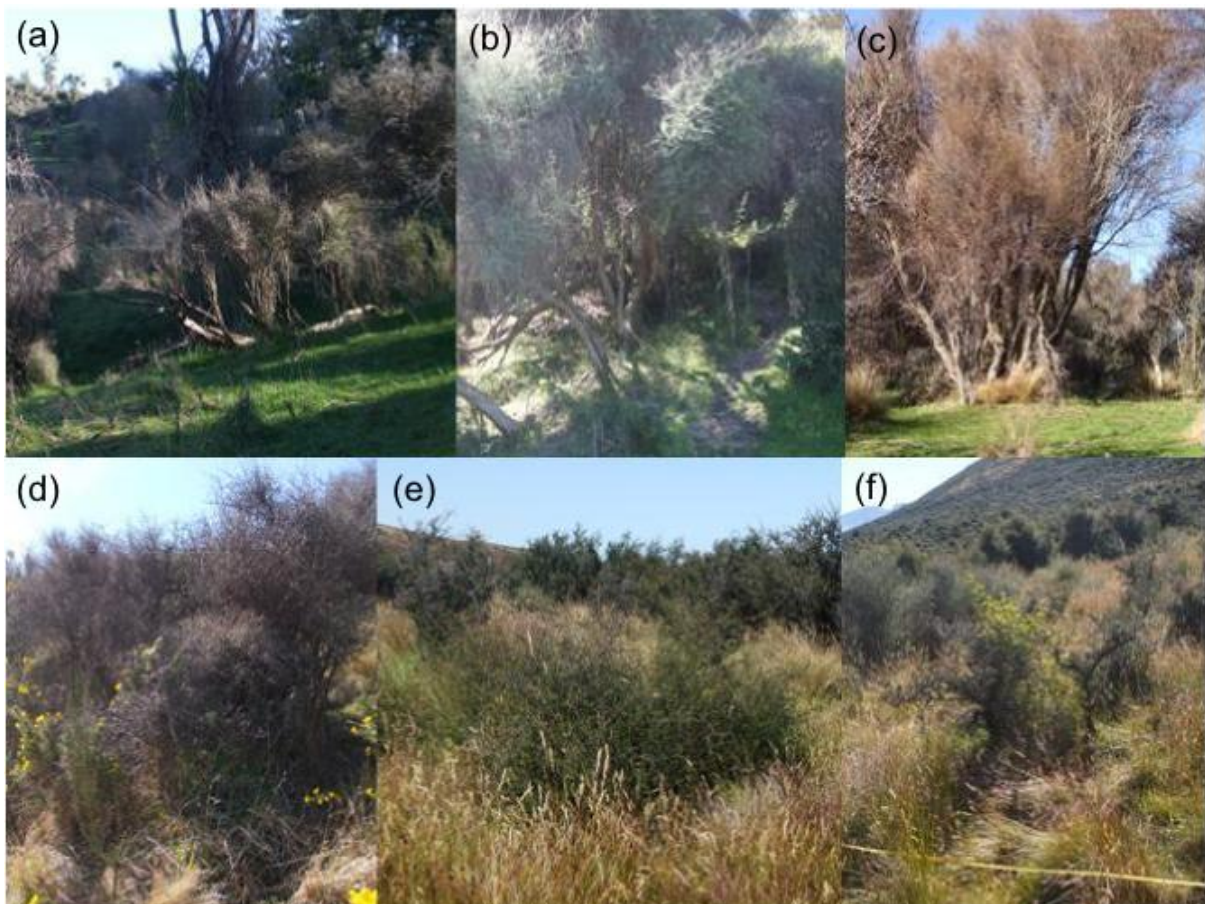
in lowland parts of the Eastern South Island where the majority of populations for both of these species occur (Merrett *et al.* 2007). Further, the development of towns and infrastructure e.g. roads, has increased the accessibility of lowland areas and some higher altitude areas allowing for further land-use changes (Ewers *et al.* 2006). Often within these areas, there are large water courses, which have been modified for irrigation such as channel straightening, possibly altering natural flooding disturbance regimes, hence, restricting *O. lineata* and numerous other native lowland plants to relictual populations (Walker *et al.* 2006b). Human land-use change often results in greater dispersal of exotic species as it is easier for these exotic species to spread into these newly accessible, highly-modified areas (Levine *et al.* 2003, Corbin & D'Antonio 2004). However, the effect exotic plants have on native plants varies from species to species and this combined with land-use changes may have an effect on regeneration of these *Olearia* species (Levine *et al.* 2003, Corbin & D'Antonio 2004). This is further investigated in Chapter Three and discussed in Chapter Five.

Population Demographics of *O. lineata* and *O. bullata*

Overall, there was a relative paucity of smaller individuals in populations of both species but this was more evident in *O. lineata* than *O. bullata*. The population demographics data shows that both species lack smaller, and presumably younger, individuals, and this is especially evident for *O. lineata*. This suggests that nationally declining *O. lineata* is affected by a process preventing the regeneration of its populations. However, some populations (such as sites two, seven, eight and nine) were more affected than others due to the sites being steep or consisting of high exotic species cover (Appendix for Chapter 2 A2.1, A2.3, A2.5, & A2.7). Non- threatened *O. bullata* populations also demonstrated low relative numbers of smaller individuals, therefore implying some lack of regeneration, but they had a greater proportion of small seedlings than *O. lineata*. Noticeably, there was higher exotic species presence in wetland/flush sites than expected, which may have caused lower than expected observations of *O. bullata* seedlings due to competitive

exclusion from these exotic species (Korsten *et al.* 2013). There is also the possibility that in *O. bullata* sites, due to the habit of the other vegetation, smaller seedlings may not have been visible (Figure 2.6). This was not the case for *O. lineata* sites as they consisted of smaller ground cover vegetation in which seedlings would have easily been visible (Figure 2.6). Yet the lack of smaller individuals suggests that recruitment of new individuals is not occurring and this could be due to several factors including (1) a requirement for disturbance to provide conditions for regeneration, (2) interactions with exotic species preventing regeneration e.g. competitive exclusion by exotic grasses or (3) a failure in either pollination or seed dispersal such as insufficient propagule pressure due to small isolated populations (Duncan *et al.* 2009).

Figure 2.6: Ground cover comparison in *O. lineata* sites (a, b, c) and *O. bullata* sites (d,e,f).



Shrubs and trees may need disturbance to provide conditions for regeneration (Merrett *et al.* 2007). For example, disturbance events such as fire, flooding or landslips, clear the land of the current vegetation, hence providing a new site to be colonised by propagules of species which need clear open sites to regenerate (Merrett *et al.* 2007). Often this creates periodic regeneration, through a boom-bust cycle, where a disturbance event creates a new opportunity for recruits to colonise so populations may not be continuously recruiting (Rossi *et al.* 2012). *Olearia lineata* is a light-demanding, colonising species so needs the clearance that a disturbance event creates to colonise (Heads 1998). Therefore, it is likely to exhibit episodic regeneration (Rossi *et al.* 2012). However, landscape level disturbance regimes in these lowland areas where *O. lineata* is present, have been altered through human land-use modification (e.g. conversion to farmland) (Walker *et al.* 2006a, Brockerhoff *et al.* 2008). This has consequences for possible episodic regeneration in *O. lineata*, as the disturbance event may not be frequent or the return interval may have changed, altering recruitment opportunities (Turner 2010). Furthermore, *O. lineata* was not regenerating at the more disturbed, steep sloping locations surveyed such as High Peak Station, Poulter River and Gorge Creek where regeneration would be expected (Heads 1998). The fact that *O. lineata* is not regenerating at the more disturbed sites indicates there may be another limiting factor that is preventing the regeneration of *O. lineata*. In contrast, it seems *O. bullata* does not require a disturbance event to regenerate since the wetland flush sites it is found in are slightly more stable systems than river bed terraces where *O. lineata* persists (Heads 1998).

After a disturbance event, a variety of native and exotic species establish. Therefore, another factor that may be important in regeneration of these *Olearia* species is the interaction with native and exotic species. One such issue in these ecosystems is that *O. lineata* and *O. bullata* are possibly being outcompeted by exotic grasses and herbs for light, space and nutrients (Callaway & Aschehoug 2000, Levine *et al.* 2003, Corbin & D'Antonio 2004). These exotic grasses and herbs may be faster at establishing and at utilising resources in these newly created spaces resulting in competitive

exclusion of native species such as *O. lineata* and *O. bullata*. For example, *Hebe cupressoides* is another recruitment-limited species, which, was found to be outcompeted by exotic grasses (Widyatmoko & Norton 1997). The exotic grasses prevented light from reaching the soil, thereby reducing the seedlings' ability to photosynthesize and resulting in seeds being unable to establish. Moreover, the *H. cupressoides* seedlings that established were unable to compete with the exotic grasses preventing seedling survival (Widyatmoko & Norton 1997). This factor may contribute greatly to inhibiting the regeneration of *O. lineata* and *O. bullata* and is tested experimentally in Chapter three.

Herbivory is another exotic species interaction that may affect regeneration. *Olearia lineata* and *O. bullata* individuals that can establish may be eaten by exotic herbivores such as hares, rabbits and livestock (e.g. cattle and sheep). Almost all of the sites surveyed were in farmland with some intensity of grazing on the land, resulting in the possibility that these species may be establishing and germinating, but were then being eaten before they could contribute to the population.

Herbivory is seen to reduce the number of seedlings and saplings present in a population so could be a possible source of regeneration failure (Morta 2004). However, this was not tested in my research so cannot be dismissed as a possible recruitment issue. Nevertheless, it has been seen in conspecific *O. adenocarpa* that a reduction in herbivory by livestock benefits its persistence (Morta 2004) so this is a plausible explanation for recruitment limitation in the *Olearia* species studied here.

Lastly, failure in pollination or seed dispersal can result in recruitment limitation of a species (Merrett *et al.* 2007, Duncan *et al.* 2009). Due to human-induced land use modification plant populations have become fragmented resulting in difficulty for pollinators to find and pollinate the same plant species (Ghazoul 2005, Merrett *et al.* 2007, Newman *et al.* 2013). Land-use conversion can cause a disruption to the plant-pollinator interaction as the plant populations become fragmented and isolated (Merrett *et al.* 2007, Newman *et al.* 2013). Alternatively, pollinators may

preferentially pollinate the new more common plants in the landscape matrix rather than the native fragmented species (Lopezaraiza-Mikel *et al.* 2007, Merrett *et al.* 2007). Experiments were set up to test pollen limitation in *O. lineata* and *O. bullata*, however, the experiments failed due to a number of factors. Bags to cover the flowers were constructed with fine mesh for three treatments- hand-pollination (a bag covering the flowers to prevent insect pollination, in which the flowers would be manually pollinated by hand), selfing (a bag covering open flowers to investigate if the species could self-pollinate) and natural pollination (control). However, the bags seemed to delay flower opening when compared with the non-bagged flowers in both *O. lineata* and *O. bullata*. *Olearia lineata* flowers opened in the period between the end of November and beginning of December, although, the seeds weren't ripe for collection until mid to end of December. Seeds are ripe when they can easily be removed from the flower head. These factors meant that flowers were unable to be hand-pollinated as I was unable to pollinate the flowers when they opened and seed was collected too early. *Olearia bullata* also had a low flowering year so there were not many flowers available for the experiment to take place.

However, despite the attempted pollination experiment, pollination mutualism failure seems unlikely in *O. lineata* and *O. bullata*, as these species are Asteraceae so have non-pollinator-specific capitula (Heads 1998). *Olearia lineata* and *O. bullata* are both wind dispersed so there is no reliance on a mutualist at this stage of reproduction (Heads 1998). However, there may be years in which the species produce significantly more flowers than others (i.e. masting) resulting in inconsistent reproductive output. The season I studied *O. bullata*, I noticed a low flower output on populations sampled compared to the previous year, so masting could affect regeneration of this species. Dispersal of seed into unsuitable areas can also affect regeneration of a plant population (Duncan *et al.* 2009). This becomes increasingly common as the population gets smaller and fewer seeds are dispersed across the landscape. *Olearia lineata* and *O. bullata* are dispersed by wind (Heads 1998) resulting in a high probability of seeds dispersing into unsuitable areas in which the seeds cannot

germinate. They may disperse into a thick patch of grass (known as a grass sward) resulting in the seed being unable to reach the soil. If the seed can reach the soil, it may not be able to germinate due to intense competition with the exotic grass sward. The effects of grasses on germination are tested in Chapter Three.

Alternatively, a portion of the seed may not be dispersed far instead landing under the parent plant (Freckleton & Lewis 2006, Petermann *et al.* 2008). On one hand, it may be beneficial for the seed to land under the parent plant, as a plant from the same species already grows there, so the site should be suitable for this new seed to successfully grow (Freckleton & Lewis 2006, Petermann *et al.* 2008). However, there are many costs which can outweigh the benefits, such as competition for space, nutrients and light with an already established plant or there could be species specific pathogens in the soil preventing the colonisation of more of the same species under the parent plant (Freckleton & Lewis 2006, Petermann *et al.* 2008). These two *Olearia* species often form quite a dense canopy preventing growth of other species underneath except for small understory, shade tolerant herbs and grasses. No seedlings, for either *Olearia* species, were located under the canopy of another mature individual, although individuals are able to grow within metres of each other (pers. observation). However, it is not known if plants established next to each other are related. Further, it is highly likely any seeds produced by these *Olearia* may disperse into a thick grass sward due to these *Olearia* sites being dominated by exotic grasses and herbs.

Overall, it can be concluded that *O. lineata* and *O. bullata* are experiencing regeneration failure. Regeneration failure is commonly seen in several lowland and montane New Zealand shrubs including other *Olearia* species (*O. hectorii* and *O. adenocarpa*), *Carmichaelia* species, *Hebe armstrongii*, *Hebe cupressoides* and *Muehlenbeckia astonii* (Williams *et al.* 1996, Widyatmoko & Norton 1997, Heenan & Molloy 2004, Barnaud & Houlston 2010). These plants are all present in lowland-montane areas of New Zealand, where the greatest land-use changes have occurred during

conversion into farming and forestry (Craig *et al.* 2000, Ewers *et al.* 2006, Walker *et al.* 2006a, Brockerhoff *et al.* 2008). This fragments populations and increases their susceptibility to regeneration failure (Fischer & Lindenmayer 2007). Although evidence suggests that recruitment limitation due to a combination of the lack of disturbance regime and the introduction of exotic grasses and herbs are the main factors causing regeneration failure in these *Olearia*, alternative factors involving mutualism failure, and the dispersal and establishment of seeds cannot be completely ruled out as limiting recruitment.

Chapter Three further discusses the processes that may be involved in the growth and establishment of *O. lineata* and *O. bullata* seedlings (in the presence of exotic grasses). The effect of exotic grasses and herbs may be important in the recruitment of these *Olearia*, as the modification of disturbance regimes by human activities may be working in concert with the invasion of exotic grasses and herbs to alter the demographics of the population of *O. lineata* and *O. bullata*. These factors, I believe, are important and can be experimentally tested with results applied to restoration of the Nationally Declining *O. lineata*.

Chapter 3:

The effect of an invasive species and light availability on *O. lineata* and *O. bullata*



Olearia lineata and *O. bullata* seedlings in the presence or absence of grass

Introduction

Worldwide one of the biggest threats to biodiversity besides habitat change is the invasion of exotic species (Chapin III *et al.* 2000, Sala *et al.* 2000, Tylianakis *et al.* 2008, Murphy & Romanuk 2014).

Native communities are being invaded by exotic plants which pose a threat to community structure and function and to the individual native species comprising those communities (Chapin III *et al.* 2000, Bellingham & Coomes 2003, Gaertner *et al.* 2009). Invasion by alien species can affect ecosystem processes such as disturbance frequency, nitrogen cycling rates and carbon sequestration (D'Antonio *et al.* 1998, Fagan & Peart 2004). In addition, anthropogenic disturbance can also facilitate biological invasion, further threatening native species diversity (Gould & Gorchov 2000, Corbin & D'Antonio 2004, DiVittorio *et al.* 2007, Catford *et al.* 2012, te Beest *et al.* 2015). These processes can have a negative impact on native species richness due to a decline in species from competition with these new invaders (DiVittorio *et al.* 2007, Bernard-Verdier & Hulme 2015).

Exotic species that are used by humans have an added competitive advantage of large landscape cover and occasionally through additional sowing, therefore, resulting in greater propagule pressure (Bellingham & Coomes 2003, DiVittorio *et al.* 2007, Dorrough & Scroggie 2008). Not only are grasses exotic invasive species but they are actively planted by humans for farmland causing habitat change (DiVittorio *et al.* 2007, Dorrough & Scroggie 2008). They are a common group of invasive species that have had a tremendous effect on native species, with numerous studies in the literature emphasising how grass invasion can lead to native species decline (Williams *et al.* 1996, D'Antonio *et al.* 1998, Gordon & Rice 2000, Miller & Duncan 2004, Thomson 2005). A majority of alien grass species are fast growing, with some being rhizomatous such as *Lolium perenne* and *Cynosurus cristatus*, resulting in easy dispersal ability (Bernard-Verdier & Hulme 2015). These characteristics mean that grasses can have a direct competitive impact on native species (Miller & Duncan 2004). Competition with invasive species, especially grasses, has been demonstrated to inhibit or prevent the growth of several woody species (Rogers 1996b, D'Antonio *et al.* 1998, Gordon & Rice 2000). For

example, in Panama, exotic grass *Saccharum spontaneum* ssp. *spontaneum* has been seen to form dense stands (Hooper *et al.* 2005). This results in above and below ground competition with native woody species negatively affecting the regeneration ability of those native species (Hooper *et al.* 2005). However, sometimes grasses can just fill the gap left by a disturbance and be passengers of land degradation and change rather than the drivers of species decline (Didham *et al.* 2005, MacDougall & Turkington 2005). This indicates that even if grasses are present in an ecosystem, they aren't necessarily the drivers behind decline of a native species (Didham *et al.* 2005, MacDougall & Turkington 2005).

Similar effects of invasive grass have been seen in New Zealand (Widyatmoko & Norton 1997, Gruner 2003, Miller & Duncan 2004), a country in which agriculture involving exotic grasses has caused dramatic land change and degradation (Craig *et al.* 2000, Bockerhoff *et al.* 2008). Species, such as *Olearia hectorii*, have experienced a marked decline in abundance resulting in currently being listed as Nationally Endangered due past habitat loss and presently competition from invasive grasses (Rogers 1996b, de Lange *et al.* 2009). *Olearia lineata*, another species in the same genus, is often found in human modified land in areas with high exotic species density. It is a nationally declining woody species which is regeneration limited (see Chapter 2). The congener *Olearia bullata*, a non-threatened, more common species, also has signs of regeneration failure (see Chapter 2). The specific mechanisms behind regeneration failure in these two species are unclear, however the presence of invasive grasses may be a contributing factor.

Shading or light availability has also been identified as an important factor in shrub seedling establishment (D'Antonio *et al.* 1998). Therefore, the effect of shading from mature individuals of the same or other species may contribute to regeneration failure in these two *Olearia* species as well. From field observations, mature *O. lineata* individuals are seen to form large sprawling canopies with very little vegetation found underneath the canopy. The shading effect, from the

mature tree canopies, may restrict seedling recruitment in the immediate vicinity of these trees. The sprawling *O. lineata* canopy is also observed to prevent exotic grass growth resulting in relatively bare sites for possible seedling recruitment. However, I found no seedlings present under these canopies. *Olearia bullata* mature individuals do not have large sprawling canopies but do co-exist in communities with other shrubby vegetation and tall wetland grasses and sedges that could provide the potential for shading to restrict seedling recruitment. However, the effect of shading has not been investigated with these *Olearia* species in regards to regeneration failure.

The aim of this study was to investigate the potential role of grass presence and the effect of shading on the regeneration of *O. lineata* and *O. bullata*. To do this, two main questions pertaining to the germination ability and growth of seedlings of *O. lineata* and *O. bullata*:

- 1) Does the presence of grass affect the germination of *O. lineata* and *O. bullata*?
- 2) How do the presence of an exotic grass and the degree of shading affect the growth of *O. lineata* and *O. bullata* seedlings? Is there an interaction effect between the grass and varying shade levels causing additional reductions in *Olearia* seedling growth?

As seen from previous literature, it is hypothesized that grass will reduce the germination ability of both *Olearia* species (Williams *et al.* 1996, Widyatmoko & Norton 1997). Reduced germination will be due to the grass preventing light from reaching the soil surface resulting in seeds being unable to harness the light they need to germinate (Williams *et al.* 1996). In addition, grass is expected to have a negative effect on seedling growth for nationally declining *O. lineata* since grass competition is hypothesised as a key mechanism behind regeneration failure in this species (Wilson & Galloway 1993, Department of Conservation 2007, Dawson & Lucas 2012). In contrast, *O. bullata* is listed as non-threatened so is hypothesised to be less affected by grass presence even though it has a paucity

of seedlings in populations (Wilson & Galloway 1993, Dawson & Lucas 2012)(see Chapter 2). While shade is hypothesised to have more of an effect on *O. lineata*, since it is a coloniser of disturbed river terrace habitats meaning it will require a lot of light to grow, *O. bullata* will be less affected by shade due to the vegetation community in which it persists (Heads 1998). *Olearia bullata* grows as part of a community that consists of other shrubby species of similar sizes and tall grasses and sedges (Chapter 2) resulting in some shading effects and the need for *O. bullata* to tolerate some level of shading.

Methods

Seed from *O. lineata* and *O. bullata* was collected from three different populations for each species (*O. lineata* Site 1-Waimakariri Flats, Site 2- Poulter River, Site 3- Rakaia Island, and *O. bullata* Site 4-Mt Somers, Site 5- Mackenzie Pass, Site 6- Guide Hill; Table A2.1). *Olearia lineata* seed was collected in the middle - end of December 2013 and for *O. bullata* at the end of December 2013- middle of January 2014. Seeds were collected when they were ripe as they were easily brushed off and pulled out of the capitula by the pappus (Jason Butt pers. comm.) and in paper bags to reduce the chance of moisture destroying the seeds. To germinate the seeds, they were sown into seed trays on top of potting mix with a thin layer of light gravel on top. The sown seeds were put into the ambient temperature glasshouse and watered daily until and after germination. The seeds were counted into groups of 1000 for each site to determine the germination rate in a preliminary germination experiment. This preliminary experiment was set up to determine how many seeds may need to be used in the following germination experiment. The 1000 seeds and other collected seeds were sown into germination trays with additional seeds set aside for the main germination experiment. Once germinated, seedlings were counted to determine the germination rate of each species at each of the sites. When large enough, seedlings for each species, all from the same location, were pricked out and put into the competition experiment.

Germination experiment

Preliminary seed germination trial

Prior to the main germination experiment, a preliminary trial was undertaken to determine seed viability i.e. how many were expected to germinate in the main experiment. One thousand seeds were counted out from three sites for each species, *O. lineata* and *O. bullata*. Mean seed germination was 4.9% ($\pm 8.1\%$) for *O. lineata* and 2.6% ($\pm 3.8\%$) for *O. bullata* (Table A3.1). A binomial general linear model (fitted with quasi likelihood to account for overdispersion) determined that there was no significant difference in the proportion of seeds that germinated between the three sites for each species ($p = 0.259$, $F = 5.4$ for both *O. lineata* and *O. bullata*). Notwithstanding this, seed from just one site for each species was used for the germination experiment to avoid adding uncertainty to results due to possible genetic differences among plants from the differing sites.

Main Germination Experiment

Forty seeds were counted out for *O. lineata* and *O. bullata* for each treatment due to the number of seeds available. These were then sown into one of three *A. capillaris* grass treatments - grass, grass with bare potting mix patches and no grass (Figure 3.1). The grass was sown in the pots prior to the beginning of the experiment. The bare potting mix patches were made in the soil by cutting out the grass to construct four patches of the same size with a diameter of 4cm. The purpose of these patches was to allow belowground root competition but remove above ground competition for space and reduce competition for light (Figure 3.2). There were eight pots per treatment per species resulting in 48 pots altogether. Treatments were randomised within the experimental layout (Figure 3.1). Pots were watered regularly with the same amount of water to the maximum capacity of the potting mix soil.

Three measurements of seedling germination were made at time 1: 4th July 2014, time 2: 9th August 2014 and time 3: 31st October 2014. At each time, all pots were examined for germinating seeds.

Each seedling was counted and seedlings were marked with toothpicks and recorded. Grass was also kept cut and low (5 cm) in this experiment to reduce extra shading of the seeds.

Data analysis

The main germination experiment was analysed with two different objectives. Firstly, data were analysed to investigate the success of germination (i.e. the proportion of seeds that germinated). A binomial generalized linear model was used in R to determine germination success in each of the three grass treatments for each species (including a grass treatment x species interaction term). Secondly, germination rate was investigated over time. A Poisson generalized linear model in R was used to determine if there was a difference in the number of seedlings germinating at each of the three time steps between treatments and species. Neither of these models showed evidence of overdispersion, and the canonical link functions (log for Poisson, logit for binomial) were used in all models.



Figure 3.1: Germination experiment layout showing the randomised grass, grass patch and no grass treatments.

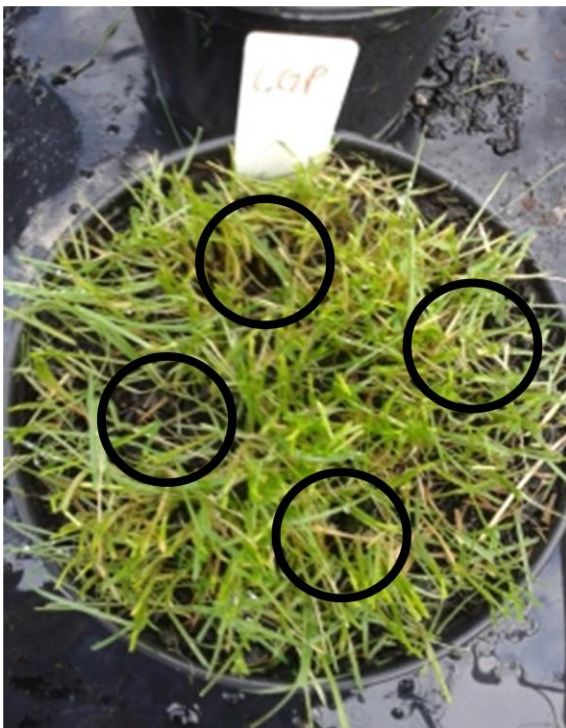


Figure 3.2: Pot from the main germination experiment showing the grass patch treatment. Black circles indicate the bare patches within the grass.

Competition experiment

An experiment was used to test whether the growth of seedlings of the two *Olearia* species was influenced by competition with exotic grasses and to investigate the role of shading (competition for light). The competition experiment was set up with seedlings of *O. lineata* and *O. bullata* and with the exotic grass *Agrostis capillaris* (two levels of grass treatment: present or absent) under three shade treatments (heavy, light and no shade) constructed out of shade cloth. *Agrostis capillaris* was used because it was the most common grass at all the field sites (Chapter 2-Table 2.3) and it was sown in grass-presence pots at a constant density. Each shade treatment produced differing light exposure to the seedlings. On average the heavy shade let through 25.9% of ambient light and the light shade let through 57.6% of ambient light (Table A3.2).

This experiment was set up in a similar manner to an experiment by Gruner (2003). Figure 3.3, 3.4 and 3.5 show the layout of the experiment with an example of one replicate. The whole experimental layout had three replicates including both *O. lineata* and *O. bullata* plus another two replicates with only *O. lineata*, giving five replicates altogether of each grass x shade treatment combination. There were fewer *O. bullata* replicates due to insufficient numbers of seedlings that germinated. Although the number of replicates differed across the two species, the proportion of replicates assigned to different treatments remained constant, so the treatments remained orthogonal despite the unbalanced design. Under each shade treatment there were 16 pots, of which eight contained *A. capillaris* whilst the others lacked grass. Grass was established in the pots prior to the seedlings being planted. Within each of the pots (with and without grass) four seedlings of *O. lineata* or *O. bullata* were planted, with all pots having a similar average seedling starting height. Pots were fully randomised within each shade treatment and were spatially randomised again each time after the seedlings were measured. Altogether 768 seedlings were used in the experiment.

The seedlings were watered to soil capacity regularly, with all pots watered at the same time. The heights of seedlings were measured four times (7th May 2014, 16th June 2014, 22nd July 2014 and 17th October 2014) over the course of the experiment, which ran from 7th May 2014 to 17th October 2014. The same fertilised potting mix was used in all of the pots which consisted of 80% bark and 20% bioblend (blood and bone) with a low levels of sodium, magnesium, calcium, phosphorus and moderate levels of potassium. Seedling height was measured to the same place on the plant for each species with *O. bullata* height measured from the potting mix to the tip of the highest leaf and *O. lineata* measured from the potting mix to the node between the highest leaves. This difference was because of the much larger and longer leaves of *O. lineata*. The grass was kept cut throughout the experiment to reduce the shading effect of the grass itself on the seedlings within the pots while maintaining a dense grass sward over the potting mix. The grass was cut to a height of 5cm which was less than most of the foliage of the *Olearia* seedlings. All plants were sprayed every two weeks with insecticide (Pyrethum or Confidor) after the discovery of caterpillars feeding on *O. lineata*. All other variables (e.g. temperature, relative humidity and soil moisture) were kept as constant as possible across treatments. Data loggers measured the temperature and relative humidity within each shade level treatment (Figure A3.1). To determine whether any shading effects could have been driven by changes in water availability, rather than light, soil moisture was measured with a moisture probe before watering plants (on three days- 12th June 2014 12pm, 13th June 2014 12pm and 16th June 2014 12pm to account for potential daily variability in moisture) (Table A3.3). A binomial generalized linear model was used to test whether there was a change in soil moisture with shading (Table A3.3). There was a significant difference in soil moisture in the no shade compared with the shaded treatments ($p = 0.12$, Table A3.3) such that pots in the no shade treatment dry out faster than the light and heavy shade treatments. There was also a slight (although non-significant) effect of the absence of grass indicating that pots with no grass had a slightly higher soil moisture content ($p = 0.057$, Table A3.3).

Data analysis

Prior to analysis, any dead seedlings and any seedlings in which their final height measurement was less than their initial height measurement (i.e. those that were partially dead), were removed from the final analysed data set. Some seedlings died due to transplant shock or through contracting fungi. This reduced the number of seedlings from 768 to 609. In addition, some seedlings produced multiple stems, which were all measured, though only the tallest stem per plant was used for analysis.

These data were analysed using a Gaussian mixed effects model in R (Team 2012) within the packages lme4 (Bates 2013) for model fitting and lmerTest (Kuznetsova 2013) for hypothesis testing. The lmerTest package uses the Satterthwaite method of denominator synthesis, which can produce non-integer denominator degrees of freedom (Tylianakis *et al.* 2006). Pairwise post-hoc comparisons were made using Tukey tests for mixed effects models, conducted in the multcomp package in R (Hothorn *et al.* 2008). The model tested the effect of shade level and the presence or absence of grass on the growth of seedlings of both *Olearia* species, and included interaction terms to identify any differences of the effect of shade or grass on *O. lineata* vs. *O. bullata*. The initial model violated the assumption of homogeneity of variances, therefore the data were log transformed and the resulting model met all assumptions.

Fixed effects in the model investigated the independent effect and interaction effects of species, shade level and the presence or absence of grass on the growth of the seedlings. A shade x grass interaction was one focus of this study, to determine if the effect of grass on seedling growth changes in the presence of shade. Growth was expressed as a log response ratio, $\log(\text{Initial height} - \text{Final Height} / \text{Initial height})$, with a constant of 1 added to all values before taking the log, to account

for zeroes. Random effects were hierarchically nested within the model. Although seedlings were tested individually within the model, they were grouped by their pots as a random effect, to account for their non-independence. The pots were also grouped within each shade cage as an additional random effect, and the shade treatments were grouped according to their replicate number (the highest level blocking factor). This nested layout for the random effects accounted for random variation due to various different grouping levels within the split-plot design used here.

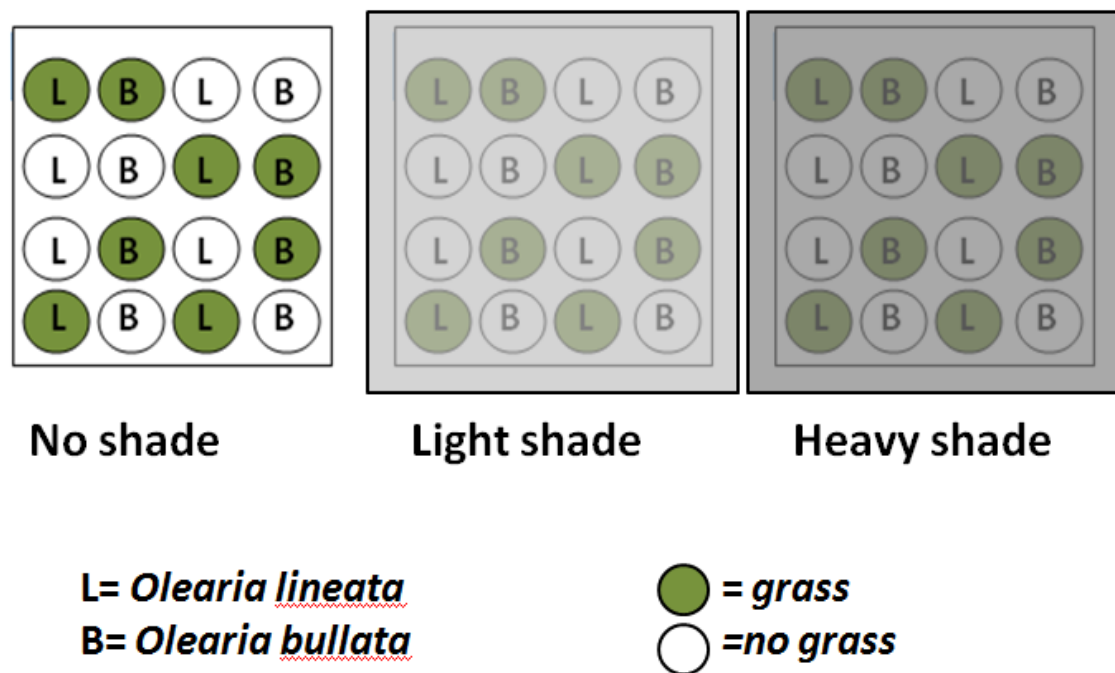


Figure 3.3: Experimental layout for the competition experiment. This is one replicate showing the three shade treatments- heavy, light and no shade, the two *Olearia* species, the presence or absence of grass *Agrostis capillaris* and the randomised layout of the pots within the shade treatment.

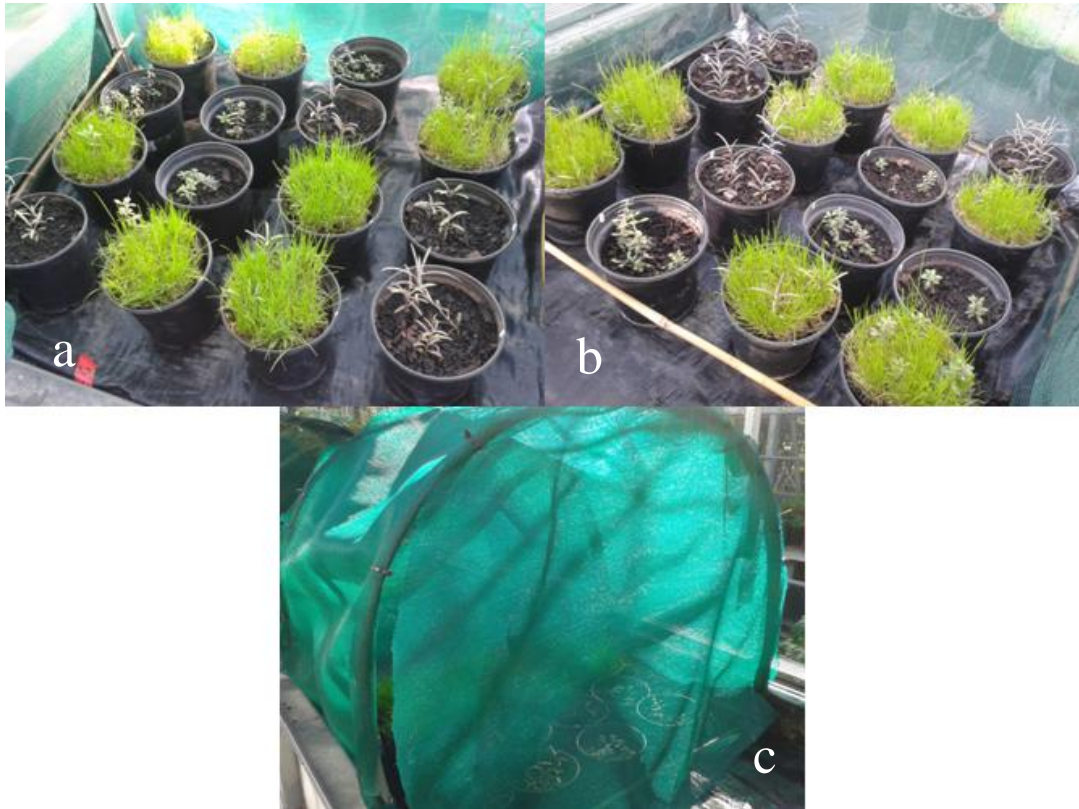


Figure 3.4: (a) Heavy shade cage and (b) light shade cage experimental layout for the competition experiment. The pale green long-leaved species is *O. lineata* and short oval leaved species is *O. bullata*. (c) An example of the heavy shade treatment cage covering the seedlings.



Figure 3.5: Entire experimental set up for the seedling competition experiment.

Results

Germination experiment

Germination success

Overall there was a significant effect of grass treatment on germination success ($p < 0.001$, Table A3.4). There was a significant effect of the presence ($p < 0.001$, $z = -15.04$) or absence ($p < 0.001$, $z = 4.94$) of grass on the germination of seeds but no effect was found from the bare patch grass treatment on germination ($p = 0.35$, $z = 0.93$). More seeds germinated in the no grass treatment compared with either of the other two treatments - grass or grass patch (Figure 3.6). No significant difference was found between the grass and grass patch treatments on the effect of germination ($p = 0.35$, $z = 0.93$).

Although there was no main effect of species, there was a significant treatment by species interaction ($p < 0.001$, Table A3.4), whereby *Olearia lineata* had significantly more seeds germinate in the grass treatment compared with *O. bullata* ($p = 0.003$, $z = 2.93$, Figure 3.6). For both *O. lineata* and *O. bullata*, more seeds germinated in the no grass compared to the grass patch and grass treatments, but due to the significant treatment by species effect more *O. bullata* seeds germinated in the no grass treatment ($p < 0.001$, $z = -3.31$; Figure 3.6), whereas, more *O. lineata* grew in the grass treatment.

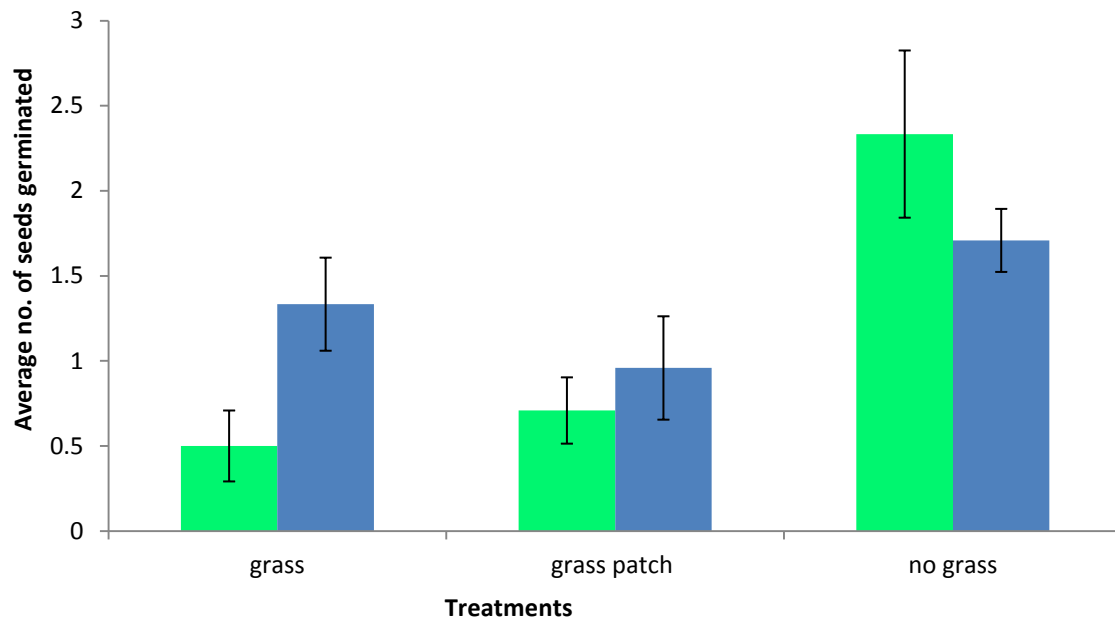


Figure 3.6: Average number of seeds germinated per treatment – (grass, cleared patches in the grass and no grass), for plant species *O. bullata* (green) and *O. lineata* (blue). Error bars are the standard error.

Germination over time

Overall, there was a significant time x grass treatment interaction effect on the germination of seeds ($p < 0.001$, Table A3.5). This is seen clearly when comparing the number of seeds germinated over time for all grass treatments of both species - *O. bullata* and *O. lineata* (Figure 3.7). Germination was earlier in the no grass treatment than the grass treatment for both species.

There was an overall significant species x time interaction effect for the germination of seeds ($p = 0.03$, $z = 10.75$). This indicates that the time taken to germinate differed between the species.

Lastly, there was a three way interaction effect between the treatments, species and time ($p = 0.03$, Table A3.5). Therefore the number of seeds that germinated differed in response to the treatment (grass, grass patch and no grass) over time which then also differed between *Olearia* species. So the delay in germination in the grass treatment relative to the no grass treatment was much greater for *O. bullata* than *O. lineata*. For example, a higher number of seeds germinated in the no grass treatment compared with the grass patch treatment at time 1 for *O. lineata* and this germination

rate differed for *O. bullata* in the same treatments and time (Figure 3.7). There was also significantly lower germination at time three in the no grass treatment for *O. bullata* and *O. lineata* indicating the seed more favourably germinates sooner after being sown in the no grass treatment ($p < 0.001$, $z = -3.306$; Figure 3.10). So it seems that grass had a larger effect on *O. bullata* compared to *O. lineata*.

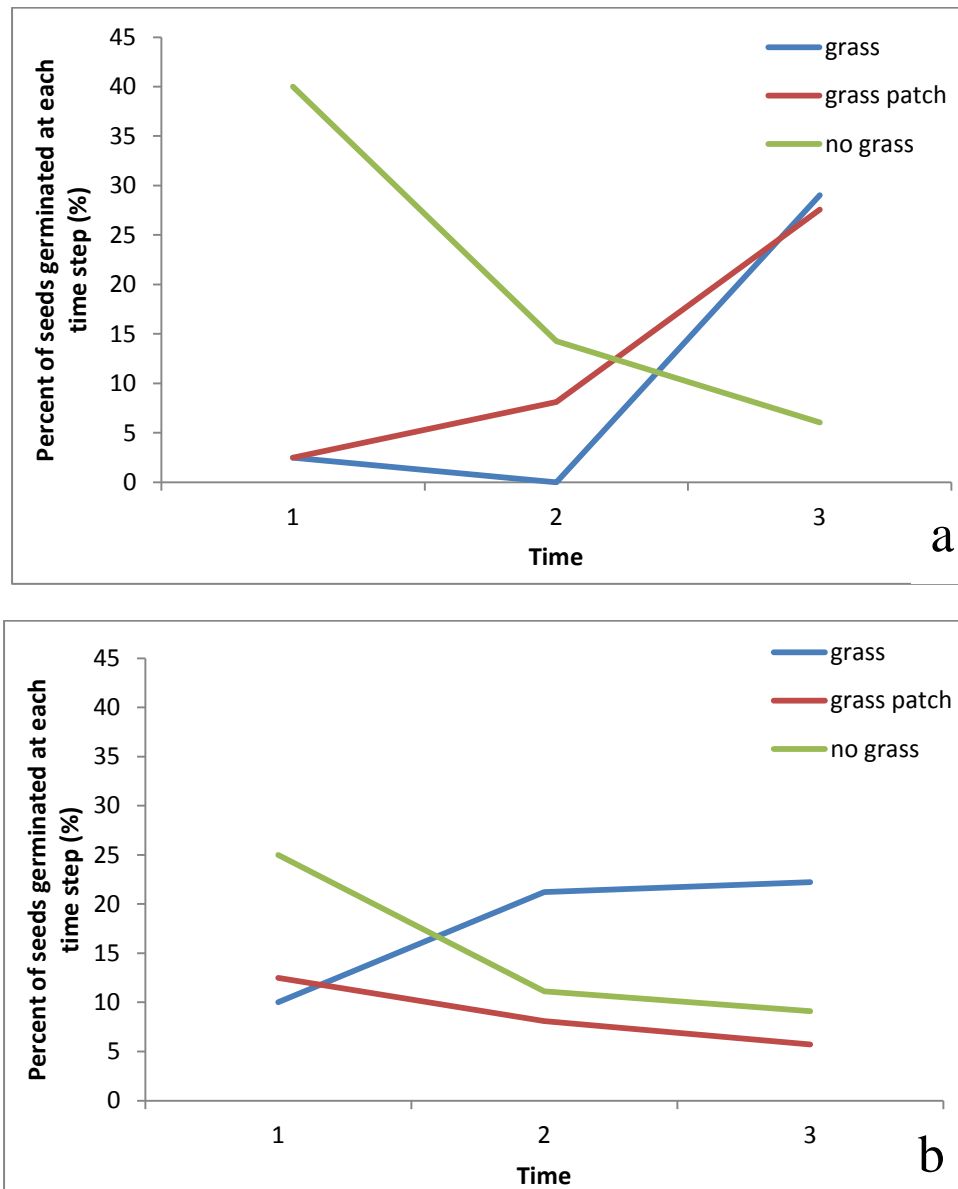


Figure 3.7: (a) *Olearia bullata* germination rate over three time steps in three grass treatments- grass presence, grass with bare patches and grass absence. (b) *Olearia lineata* germination rate over three time steps in three grass treatments- grass presence, grass with bare patches and grass absence. Time 1, 2 and 3 are the same for both species and correspond with 4th July 2014, 9th August 2014 and 31st October 2014 respectively.

Competition Experiment

There was a significant difference in seedling growth between *O. bullata* and *O. lineata* as overall seedling growth was significantly greater in *O. lineata* ($p < 0.001$, $F_{1, 580.13} = 99.9$; Figure 3.8). This effect was significant in the no grass treatment for each of the shade treatments ($p = 0.045$, $F_{2, 579.02} = 3.12$; Figure 3.9). *Olearia lineata* also had significantly higher growth than *O. bullata* in the grass treatments in heavy and light shade treatments but not in the no shade treatment (Figure 3.9). Shade level had a significant effect on seedling growth for both species ($p = 0.0045$, $F_{2, 92.07} = 5.7$). There were differences in seedling growth between the three shade treatments, however, and the significant interaction effect between the grass and shade treatment ($p < 0.001$, $F_{2, 92.14} = 22.1$) indicated that the negative effect of grass on seedling growth was strongest in the absence of shade ($p < 0.001$, $F_{2, 92.14} = 22.1$, Figure 3.8). This grass and shade treatment interaction effect was the same for both species as there was no three-way interaction between grass, shade and species. There was an overall significant interaction effect between shade level and species ($p = 0.04$, $F_{2, 579.02} = 3.12$). Specifically, the effect of heavy shade on seedling growth was significantly greater for *O. lineata* than *O. bullata* ($p = 0.04$, $F_{2, 579.02} = 3.12$; Figure 3.9). Further, there was an overall significant interaction effect between species and the presence or absence of grass ($p < 0.001$, $F_{1, 580.16} = 31.9$). This interaction showed that the difference in seedling growth between the two species was greater in the no grass treatments when compared to the grass treatments (Figure 3.9).

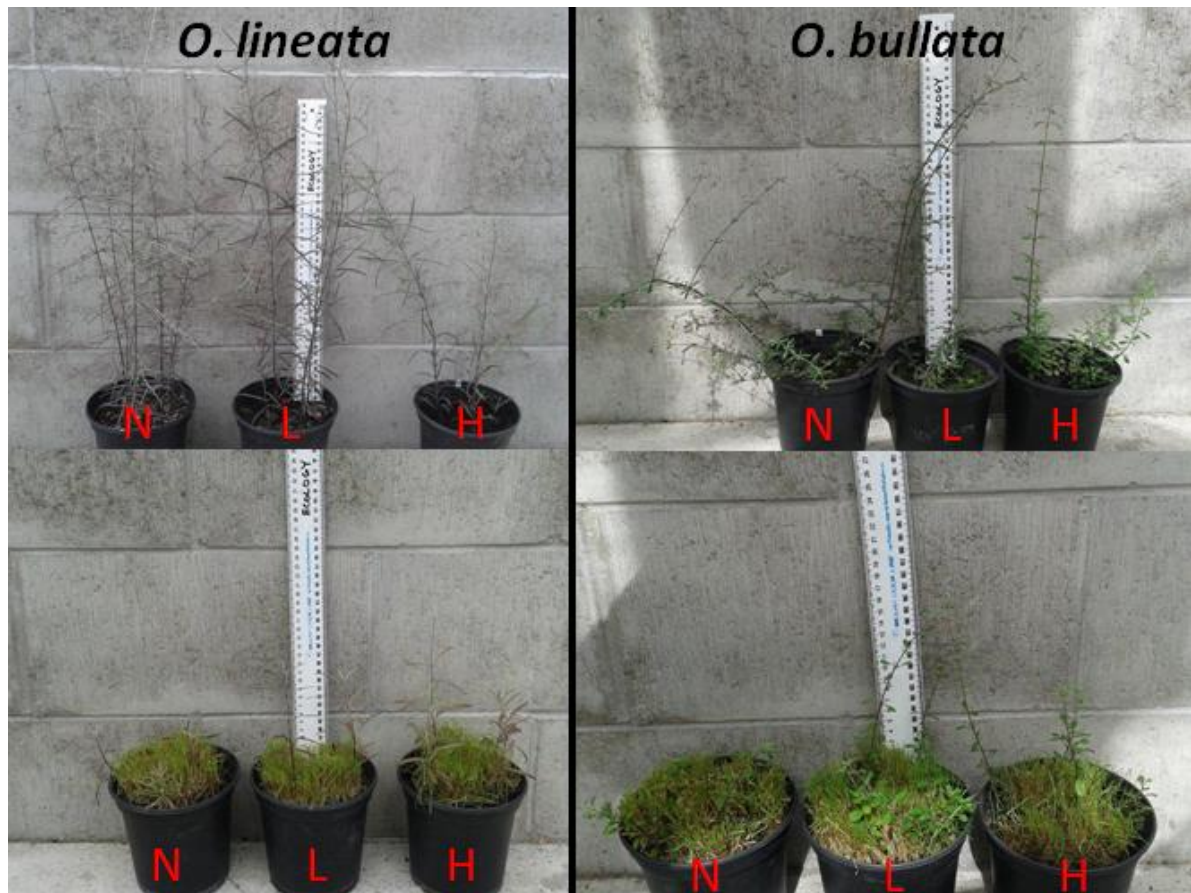


Figure 3.8: Representative pots showing the final heights of the seedlings in the competition experiments. *Olearia lineata* seedlings (left, top and bottom) and *O. bullata* seedlings (right, top and bottom) with a 40cm ruler for scale in all images. Letters represent the shade treatments (N = no shade, L = light shade, H = heavy shade) with no grass treatments top images and grass (*Agrostis capillaris*) treatments bottom images.

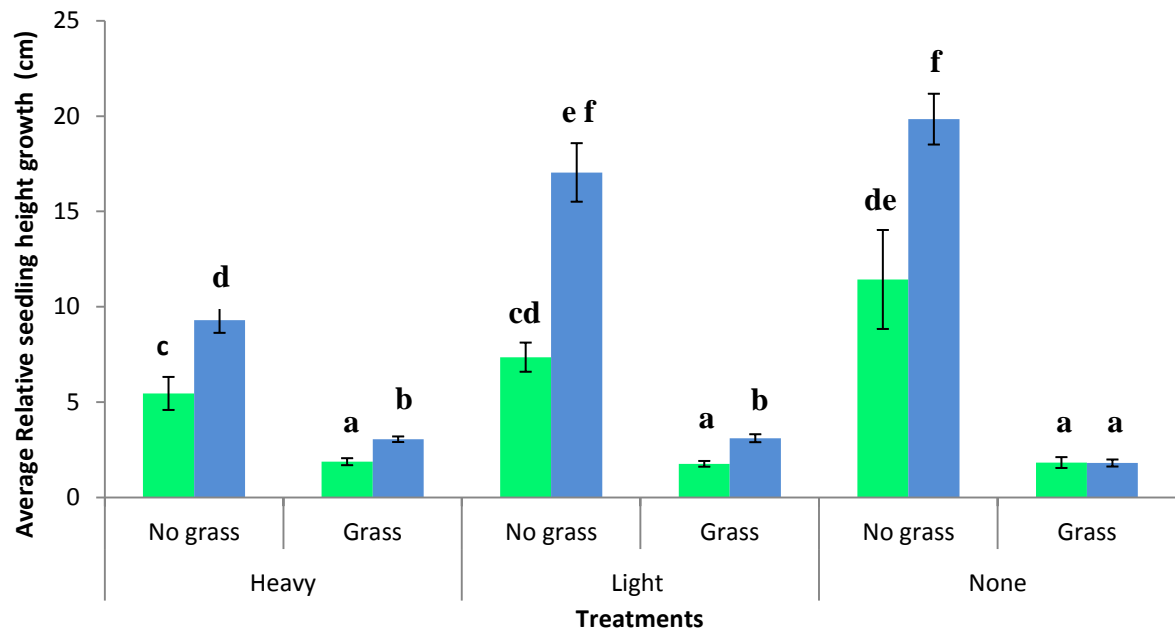


Figure 3.9: Average relative seedling height growth (standard error bars) for *O. lineata* (blue) and *O. bullata* (green) in the three shade treatments- heavy, light and no shade with the presence or absence of grass. The same letters represent treatments that were not significantly different whereas different letters indicate treatments that were significantly different from each other.

Discussion

The experiments presented here demonstrated that an exotic grass can affect *Olearia* species at different stages of their early recruitment. Both species had greatest germination in the absence of grass, with *O. bullata* having a higher germination rate than *O. lineata*. However, the germination patterns through time were different for the two species (Figure 3.7a & b). Both *O. lineata* and *O. bullata* had a decline in germination rate through time in the absence of grass (Figure 3.7a & b). However, *O. bullata* had an increase in germination rate in grass patch and grass treatments, whereas *O. lineata* only had an increase of germination in grass but not grass patch over time (Figure 3.7a & b). This delay in germination rates could possibly be due to the seeds taking longer to gain the required resources (e.g. water and light) for germination due to competition with grass (Bradford 2005). It then has the potential to cause longer exposure of seeds to seed predators or pathogenic fungi, which could negatively affect germination and survival success in the field (Blaney & Kotanen 2002). Surprisingly, *O. lineata* was able to germinate in the grass and grass patch treatment and was to some extent more successful in the grass compared to *O. bullata* at Time 1 and 2 (Figure 3.7). These slight differences may be due to *O. lineata* being able to compete with the below-ground effects from the grass roots such as allelopathy, the harbouring of pathogenic fungi or lack of space better than *O. bullata* (Williams *et al.* 2013). A previous study found that the presence of *A. capillaris* with its denser root system and differing AMF affected the above and below-ground growth of *Podocarpus cunninghamii* (Williams *et al.* 2013). This indicates that possibly below-ground grass effects such as lack of space from the grass roots or the presence of arbuscular mycorrhizal fungi (AMF) from the grass (Williams *et al.* 2013), may play a small role in preventing the germination of *O. bullata* seeds which has less effect on *O. lineata*. *Olearia lineata* was also more successful at germinating in the presence of grass treatments than *O. bullata*, which differs from what was expected and could influence the survival ability of both species.

In comparison, there was a significant effect of the presence of grass on the growth of both *O. lineata* and *O. bullata* seedlings. Both species grew significantly better in the no grass treatments compared with the grass treatments, and grass presence affected both species in the same way (Figure 3.9). There was also an interaction effect such that seedling growth was greater for *O. lineata* than it was for *O. bullata* e.g. *O. lineata* responded better than *O. bullata* with greater growth in all no grass treatments. This difference in seedling growth can be attributed to the difference in ecology of the two species as *O. lineata* is a colonising tree of river terraces therefore it should grow faster than a multi-stemmed shrub which grows in wetland habitats (Heads 1998).

In addition, there was also an effect of shading, which was less important, on the growth of *O. lineata* and *O. bullata* seedlings. Overall, *O. lineata* and *O. bullata* had greater growth in the no shade treatment because these seedlings received the most light likely causing the greatest photosynthesis rate therefore greatest growth. It was also found that the shade affected soil moisture significantly in the no shade treatment, indicating that the pots in the no shade treatment dried out faster than both shaded treatments. This drying out is due to the pots in the no shade treatment having more light exposure and likely greater rates evaporation than the other treatments (Payne & Norton 2011). However, there was an interaction effect between the presence of grass and shade, with seedlings of both species growing only slightly more in the no grass treatments within either shade treatment indicating grass presence had a greater effect on the growth of the *Olearia* seedlings in the absence of shade (Figure 3.9). Grasses are also limited by light and water resources, which are likely to affect their competitive ability with both *Olearia* species resulting in the reduced grass effect seen in the shaded treatments (Payne & Norton 2011).

Interestingly, *O. lineata* seedlings were found to grow significantly less in the no shade and grass treatment than in the heavy shade and grass treatment. This could be possibly due to the greater competitive ability of grass since it is able to outcompete the *O. lineata* seedlings above-ground by photosynthesising faster, and below-ground by utilising a majority of the available water resource.

Olearia bullata, on the other hand, had the same decreased growth rate in all shade levels with grass, indicating that the presence of grass caused a strong negative effect on growth rate for *O. bullata* regardless of the amount of light the seedlings were receiving (Figure 3.9). This shows that although *O. bullata* can germinate in grass it may not be as successful establishing as a seedling in grass, especially when compared to *O. lineata*, resulting in regeneration failure observed in Chapter 2.

Competitive effects of grass

Grass has also been established as an important competitor in other studies involving native plant species in New Zealand and overseas (Widyatmoko & Norton 1997, Gordon & Rice 2000, Miller & Duncan 2004, Thomson 2005). Direct competition for water, nitrogen, light, space and indirect effects such as the harbouring of pathogenic fungi and herbivores, have previously been noted in the literature as the main mechanisms behind the effect of exotic grasses on native species (D'Antonio *et al.* 1998, Gordon & Rice 2000, Sessions & Kelly 2002, Thomson 2005, Williams *et al.* 2013). These mechanisms will now be discussed in relation to *O. lineata* and *O. bullata*.

Water can be a limiting factor for plants due to being essential for all aspects of their growth. This often results in competition for water between plants. Woody species' root systems are usually quite shallow while establishing, and this overlaps the area in which the thick fibrous roots of grasses and other herbaceous species are present (D'Antonio *et al.* 1998, Gordon & Rice 2000). Grasses and other herbaceous species are able to deplete water in the upper soil profile, which can cause a problem for woody species as their roots cannot reach far enough down into the soil profile as seedlings resulting in direct root competition with any grasses and herbs present (D'Antonio *et al.* 1998). For example, in the blue oak (*Quercus douglasii*) water potentials were found to be important in the growth of these seedlings (Gordon & Rice 2000). When grass was present there was less

available water for the blue oak seedlings to grow (Gordon & Rice 2000). In my competition experiment, the pots present in the no shade treatment were significantly different to the shaded pots i.e. the potting mix dried out quicker in the no shade treatment as it had greater light exposure (Table A3.4). There was also a slight positive (though non-significant) effect of grass absence on pots indicating the pots without grasses had slightly greater soil moisture levels (Table A3.3). This slight drying effect may be due to the grasses having denser root systems than the woody *Olearia* seedlings resulting in a faster depletion of water and direct water competition between the grass and *Olearia* affecting the growth rate of the *Olearia* species (Merrett *et al.* 2007). The heavy and light shade treatments had the same soil moisture levels therefore any difference in growth would not be affected by moisture levels in the potting mix.

Grasses can also affect the concentration of nutrients present in the soil especially the availability of nitrogen (D'Antonio *et al.* 1998). Grasses are able to rapidly take up nutrients such as nitrogen and phosphorus, resulting in the depletion of these resources in the soil (D'Antonio *et al.* 1998). In one study the effect of a perennial bunchgrass (*Schizachyrium condensatum*) on the growth and recruitment of native woody species in the Hawaiian woodlands was investigated (D'Antonio *et al.* 1998). Removal of grass resulted in a significant increase in nitrogen present in woody plant tissue and an increase in plant growth (D'Antonio *et al.* 1998). This demonstrates that nutrient availability and competition for those nutrients can be an important growth constraint. In my competition experiment, all pots had the same potting mix soil with fertiliser. However, the grasses, as suggested above, may have been able to uptake these nutrients better than *O. lineata* and *O. bullata* resulting in the reduced growth in both *Olearia* species in the presence of grass. Although, nutrient levels were not measured in the soil as part of this experiment so this nutrient effect can only be speculated.

Light is an important factor that affects species growth especially in the seedling stage (D'Antonio *et al.* 1998). It is especially important for light-demanding species as it drives the increase in height and is crucial for leaf construction (D'Antonio *et al.* 1998, te Beest *et al.* 2015). The heavy shade treatment in the seedling competition experiment seemed to greatly reduce the growth of *Olearia* seedlings, highlighting the need for these species to have reasonable levels of light to ensure greater growth. Even though both species were in full light in the no shade treatment, they grew significantly better in the absence of grass indicating that grass had an effect on seedling growth. Therefore, grass competition via the reduction of light intensity is unlikely to influence seedling growth in these species because grass was kept cut short. It is therefore likely another mechanism of grass such as the alteration of the microbial community or allelopathy that is affecting the growth of these *Olearia* species in this experiment (Williams *et al.* 2013).

The build up of grasses into thick swards directly reduces the space available for seeds to reach suitable areas to germinate (Thomson 2005) and also provides a habitat that favours pathogenic fungi which could indirectly result in pathogen spillover and the possibility of competitive exclusion (Widyatmoko & Norton 1997, Mordecai 2013). The build up of thatch - dry, often dead, thick layers of grass - reduces the space available for seedlings to grow and prevents seeds from reaching the soil surface (Gould & Gorchov 2000, Thomson 2005). *Bromus diandrus*, an invasive grass, was seen to suppress the growth of the Antioch Dunes evening primrose (*Oenothera deltoides* ssp. *howellii*) due to the build up of thatch (Thomson 2005). The thatch layer prevented recruitment in this species as the seeds were not able to reach the soil to germinate (Thomson 2005). Similarly, my germination experiment showed that if the seeds of either *Olearia* species were able to reach the soil the seeds could germinate. The exotic grass thatch layer may also cause an increased density of pathogens possibly resulting in pathogen spillover to native species (Mordecai 2013). In my seedling competition experiment, numerous seedlings died from fungal infection which may have been caused by the presence of *A. capillaris*. Therefore, an important grass effect is the ability to prevent

germination of the *Olearia* seeds through the formation of a physical barrier blocking seeds from reaching the soil as well as indirectly increasing exposure of seedlings to pathogens which reducing native plant survival, through an increase in exotic grass density.

Plants can inhibit germination and growth through other indirect pathways (Sessions & Kelly 2002, Mordecai 2013, Williams *et al.* 2013). Plants have been seen to provide shelter rather than food to some species (Sessions & Kelly 2002) and shift the invertebrate community structure potentially increasing the number and density of herbivores (Pearson 2009). This can create apparent competition where one species has an increase in population causing an indirect negative effect on the population of a second species which is mediated by a third species (Sessions & Kelly 2002). Exotic grass *A. capillaris* has been shown to create habitats for introduced herbivores (e.g. *Deroceras reticulatum*), which have reduced the survival of native fern *Botrychium australe* (Sessions & Kelly 2002). My seedling competition experiment required spraying for caterpillar herbivores, which were only found on *O. lineata* seedlings. These caterpillars were observed to reduce the growth of *O. lineata* seedlings indicating *O. lineata* may be slightly more susceptible to herbivory. Invasion of an exotic species has been shown to increase the density of predators (Sessions & Kelly 2002, Pearson 2009) therefore, the presence of grass could also indirectly affect the survival of seedlings (Sessions & Kelly 2002).

How do exotic grasses invade communities?

Humans have created more pathways for invasive species such as grasses, to spread into new areas (Bellingham & Coomes 2003, Catford *et al.* 2012). The changes in land use interact with the invasion of species allowing further spread and establishment of exotic invasive species into natural ecosystems (Bellingham & Coomes 2003, te Beest *et al.* 2015). The spread of these invasive species often results in the native species being outcompeted (Thomson 2005). This is especially prevalent in

anthropogenically disturbed areas as the invasibility of grassland communities has been found to increase with disturbance (Catford *et al.* 2012, te Beest *et al.* 2015). In addition, alien species are often pre-adapted to anthropogenic environments and anthropogenic disturbance while native species aren't further causing a greater competitive advantage against native species (Bernard-Verdier & Hulme 2015). Anthropogenically disturbed environments, such as the habitats that *O. lineata* and *O. bullata* occupy, consist of a large exotic component (see Chapter 2). This competition with the exotic species has influenced the natural ecosystem reducing the germination of *Olearia* seeds and the growth of seedlings in this community causing regeneration failure in both *O. lineata* and *O. bullata*. However, my germination experiment showed surprisingly that *O. bullata* was more affected by the presence of grass than was to *O. lineata* resulting in the germination of fewer *O. bullata* seeds. *Olearia lineata* and *Olearia bullata* seedlings were negatively affected by grass at the same rate when taking the two species's sizes into consideration. Numerous studies have shown that other native species have become regeneration limited due to competition with alien grasses and other herbaceous species (Gordon & Rice 2000, Thomson 2005, Bernard-Verdier & Hulme 2015). Competition with exotic grasses is especially important at the seedling stage as it can limit survival (DiVittorio *et al.* 2007). Information gained from the germination and competition experiments specifically for *O. lineata* and *O. bullata* as well as other studies, can be used to implement the most beneficial restoration strategies for *O. lineata* and *O. bullata* to be discussed in Chapter 5.

Chapter 4- Lepidoptera and host reliance



Meterana exquisita on host plant *Olearia bullata*

Introduction

New Zealand's invertebrate fauna is unique and highly endemic with 90% of invertebrate species found only in New Zealand (Patrick 1994, Patrick & Dugdale 2000, Derraik *et al.* 2002a). The biggest invertebrate groups in New Zealand are the beetles (Coleoptera), moths (Lepidoptera), flies (Diptera) and true bugs (Hemiptera) (Patrick 1994). Native invertebrates are important as they perform important ecosystem processes such as the breakdown and release of soil nutrients through decomposition, pollination and can maintain community mixtures of species by selectively feeding on plant species (Patrick 1994). Herbivorous native invertebrates tend to depend on common plants rather than rare plants as well as plants that are cold adapted and found in a wide number of habitats (Patrick 2000, Patrick & Dugdale 2000, Derraik *et al.* 2002a). Common host plants in New Zealand for herbivorous invertebrates include members of the genera *Muehlenbeckia*, *Nothofagus*, *Celmisia*, *Hebe* and *Olearia* (Patrick 1994). The ability for these moths to persist is linked to the host plant characteristics (Patrick 2000, Patrick & Dugdale 2000). This means that the future of these native moth species is dependent on the future of the host plant which indicates the importance of conserving the host species in order to conserve plant-insect interactions.

Lepidoptera and other insect groups occur in diverse assemblages on species in *Olearia* section *Divaricaster*, within which *Olearia bullata* and *O. lineata* occur (Hedges 1998, Patrick 2000). Species in *Olearia* section *Divaricaster* also act as hosts to moss, algae and lichen communities providing a habitat and a diversity of resources for invertebrate taxa (Patrick 2000, Patrick & Dugdale 2000). While *Olearia bullata* is known to be an important host for Lepidoptera (Derraik *et al.* 2002a, Derraik *et al.* 2003, Derraik *et al.* 2005) little is known about the Lepidoptera taxa present on *O. lineata*. Host specificity is an interesting issue, therefore, in this chapter; I investigate the importance of *O. bullata* and *O. lineata* as Lepidoptera hosts in comparison with another shrub species - *Coprosma propinqua*, that is commonly found in the same communities as these two *Olearia* species (Chapter 2).

Coprosma propinqua was chosen as it has a similar divaricating habit to *O. bullata*. *Coprosma*

propinqua is also known to be an important invertebrate host (Derraik *et al.* 2001, Derraik *et al.* 2003). *Ozothamnus leptophyllus* was chosen as it is in the same family (Asteraceae) as the two *Olearia* species, but little is known about its role as an invertebrate host. However, it was sampled (n = 19 plants) later than the other species and this timing appeared to be suboptimal as the abundances of invertebrates were low. Therefore, due to these reasons the data on larvae abundance on *O. leptophyllus* is not presented here. The aim of this study was to:

- 1) Investigate the abundance of Lepidoptera species on these four host plants.
- 2) Investigate the host specificity of the Lepidoptera found so as to provide an indication of the importance of non-threatened *O. bullata* and nationally declining *O. lineata* as hosts.

I would expect to find higher larvae abundance per tree on *O. lineata* compared with the other species since it has a greater volume so has the potential to harbour a higher number of larvae (Derraik *et al.* 2002a). I hypothesize that the Lepidoptera community composition of *O. lineata* and *O. bullata* will be very similar (Patrick 2000). *Coprosma propinqua* is seen as an important Lepidoptera host so there is the possibility for some community overlap between *C. propinqua* and the two *Olearias*.

Methods

Field sampling

Moth larvae were collected from three different plant species- *O. lineata* and *O. bullata* (to compare the two *Olearia* species), and *Coprosma propinqua* (Rubiaceae), a shrub commonly found with both *Olearia* species with a similar habit. Moth larvae rather than adult moths are the most suitable to collect as there is a higher probability any larvae collected from the plant feed directly off it (Patrick 2000, Derraik *et al.* 2003, Derraik *et al.* 2002b). Moth larvae were sampled at *O. lineata* and *O. bullata* sites within the Cass Mountain Research Area (*O. lineata* Site 1, *O. bullata* Site 1, 2, 3) and the Poulter River (*O. lineata* Site 2) (Chapter 2- Table A2.1). *Coprosma propinqua* and *O. leptophyllus* were also sampled at these sites (Chapter 2- Table A2.1). These sites were chosen as there is a lack of knowledge of the *Olearia* moths in the Canterbury region (Patrick 2000) and because these sites were close to the University of Canterbury Cass Field Station, so larvae could be quickly processed once caught.

Sixteen to nineteen plants were sampled for each plant species (*O. lineata* n = 19; *O. bullata* n = 16; *C. propinqua* n = 16). Sampling involved laying out a white plain sheet underneath the plant to be sampled and then the branches were hit repeatedly with a plastic tube knocking any larvae off the tree and onto the sheet below. The sheet was then searched for larvae, abundances of all larvae found were recorded and samples were collected. Unknown species were collected, however, to reduce the chance of over-collecting, some of the identified larvae were returned to the plant they were found on, to ensure that there were individuals left to sustain the population (Pyle 1976). The methods used are described further in Derraik *et al.* (2003).

Each larva that was collected was recorded photographically. Species were identified as much as possible at the larval stage and when larvae were reared the identifications were confirmed at the adult moth stage. Photos and specimens were sent to Lepidoptera specialists Brian Patrick and John Dugdale for identification. However, I could only confirm the identity of a few individuals through rearing as only a small proportion of them made it to their adult stage. Identifications of larvae and adult moths are presented in Appendix for Chapter 4 A4.1.

Data analysis

A Poisson generalized linear model, conducted in R (R Core Team 2012), was used to determine if the number of larvae (all Lepidoptera species pooled together) found per plant individual differed with host plant species. This model was overdispersed, so the model was re-fitted using a quasi-likelihood. Lepidoptera often cannot be identified reliably to species level by the larval stage therefore, species richness is not able to be compared between host plant species (Gossner & Hausmann 2009). It is not conservative to compare the richness between the host species, if the ability to rear and identify caterpillars could affect the ability to identify specimens to species level (Gossner & Hausmann 2009). Therefore, larvae abundance was considered instead. Nevertheless, it is still important to have a record of confirmed identifications to indicate which species were present on which plant species.

A network image was produced using the R package Bipartite (Dormann *et al.* 2008), to provide a graphical representation of the herbivore network. The network was then used to further identify which moth species were feeding on which plants and how host specific the moth species were.

Results

Abundance of larvae

There was a significant difference in the abundance of moth individuals per plant species ($p = 0.014$, $F_{2, 302.08} = 4.64$). There was a significantly higher number of moth larvae found on *O. lineata* compared with *O. bullata* and *C. propinqua* ($p = 0.02$, $t = 2.412$). Whereas there was no significant difference in larvae abundance between *C. propinqua* and *O. bullata* ($p = 0.94$, $t = 0.07$).

The higher abundance of larvae found on *O. lineata* compared to *O. bullata* and *C. propinqua* can be readily observed in the box representing *O. lineata*, which is at least twice the size of *O. bullata* and *C. propinqua* boxes (Figure 4.1). The three most abundant Lepidoptera species in this study were *Thiotricha oleariae* (Gelechiidae) (H4) and the *Declana* sp. group (Geometridae) (H5), which was made up of *Declana juncitilinea* and *Declana toreuta* as it was difficult to ascertain the difference between the two species as larvae, and *Meterana equisita* (Noctuidae) (H11) (Figure 4.1).

Community composition

Moth community composition is quite similar for the two *Olearia* species but there is very little overlap with the species found on *C. propinqua*, apart from *Thiotricha oleariae* and the *Declana* sp. group (Table 4.1). One species found on *C. propinqua*, *Pyroderces deamatella* (Cosmopterigidae) (H1) was a new and only breeding record for this species in the Canterbury area (Brian Patrick, pers. comms.). One parasitoid was also reared from larva that was present on *O. bullata*.

Figure 4.1: Moth abundances on host plants *O. lineata*, *O. bullata* and *C. propinqua*. The host plants are represented by the green boxes and the moth species are represented by the orange boxes (H1 = *Pyroderces deamatella*; H2 = *Batrachedra* sp.; H3 = Unknown species 1; H4 = *Thiotricha oleariae*; H5 = *Declana* sp. (*Declana junctilinea* and *Declana toreuta*), H6 = *Austrocidaria* sp.; H7 = *Harmologa oblongana*; H8 = Unknown species 2; H9 = *Pasiphila cotinaea*; H10 = *Planotortrix octo*; H11 = *Meterana exquisita*; H12 = *Pyrgotis plagiatana*; H13 = *Phaeosaces* sp. and H14 = Unknown species 3). The grey/black lines between the moth species and the host plants indicate a feeding interaction between a moth and a plant, and the width of the line shows how abundant that moth species was on that plant (wider line represents greater number of individuals).

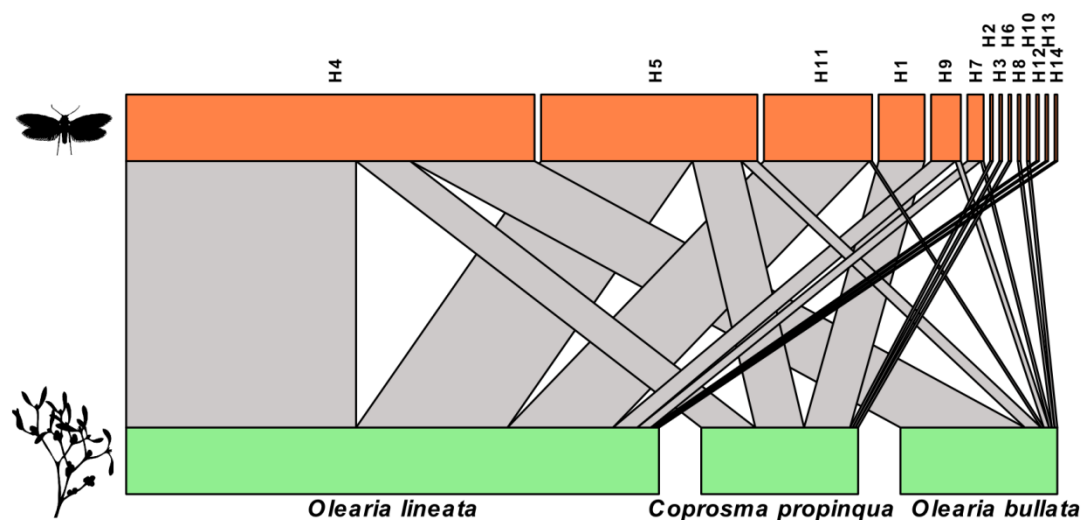


Table 4.1: The presence of identified Lepidoptera on the three host plant species sampled. Empty cells indicate the absence of that moth species on that host plant species. Refer to Appendix A4.1 for species identifications.

Plant species	<i>Olearia bullata</i>	<i>Olearia lineata</i>	<i>Coprosma propinqua</i>	total number of host plants
<i>Thiotricha oleariae</i>	Present	Present	Present	3
<i>Harmologa oblongana</i>	Present	Present		2
<i>Declana</i> spp.	Present	Present	Present	3
<i>Meterana exquisita</i>	Present	Present		2
<i>Planotortrix octo</i>	Present			1
unknown 2	Present			1
<i>Pasiphila cotinaea</i>	Present	Present		2
unknown 3		Present		1
<i>Pyrgotis plagiatana</i>		Present		1
<i>Phaeosaces</i> sp.		Present		1
<i>Pyroderces deamatella</i>			Present	1
unknown 1			Present	1
<i>Austrocidaria</i> sp.			Present	1
<i>Batrachedra</i> sp.			Present	1

Discussion

There was a significantly higher abundance of moth larvae feeding on *O. lineata* compared to *O. bullata* and *C. propinqua*. The greater difference in larvae number for *O. lineata* could be due to the greater volume of the trees (Chapter 2, Derraik *et al.* 2002a), so there is more available area to host larvae than in *O. bullata*. *Olearia bullata* and *C. propinqua* were not significantly different in larvae abundance, which could be due to *C. propinqua* and *O. bullata* having similar volumes, which has been noted in the literature (Derraik *et al.* 2003).

It was evident there was some moth community compositional overlap between the three host species, with the most overlap occurring between *O. lineata* and *O. bullata* (Table 4.1). This is to be expected as it is well known that *Olearia* section *Divaricaster* species are hosts to a specialist group of moths (Patrick 2000, Patrick & Dugdale 2000). *Harmologa oblongana* (Tortricidae), *Pasiphila cotinaea* (Geometridae), *Meterana exquisita* (Noctuidae) are all species that have been recorded as present on *O. lineata* and *O. bullata* before, since they are specialists for the *Olearia* section *Divaricaster* group (Patrick 2000). Other species identified *Pyrgotis plagiatana* (Tortricidae), *Planotortrix octo* (Tortricidae), and *Declana* species (*Declana junctilinea* and *Declana torueta*) are polyphagous so are not restricted to *Olearia* hosts and feed on numerous different trees and shrub species (Patrick 2000). However, I did record larvae of one species (*Thiotricha oleariae*) that is an *Olearia* specialist (Patrick 2000) on *C. propinqua*. There are numerous possible reasons as to why this may have been observed such as *Coprosma* being part of the same habitat matrix as the *Olearia* species enabling *T. oleariae* to switch hosts so this may be an unrecorded host species for *T. oleariae* or the species might not actually be feeding on the *Coprosma* and using it for shelter instead (Sessions & Kelly 2002).

Diversity in Lepidoptera feeding methods

Each of these plant species hosts a diverse invertebrate community, in which one reason they are likely to co-exist is because they feed on different parts of the plant. For example, *Thiotricha oleariae* forms a leaf case and mines leaves, *Harmologa oblongana* feeds on fresh foliage and *Phaeosaces* sp. (Oecophoridae) feeds on lichen present on the plants (Patrick 2000). Other species are known to feed on moss, flowers and dead bark of the plants (Patrick 2000, Patrick & Dugdale 2000). Therefore these moths, some of which are specialists, have developed methods enabling them to efficiently feed on different parts of their *Olearia* hosts plants (Patrick 1994, 2000, Patrick & Dugdale 2000). Similarly, this host specialisation has been seen in other moth-host interactions such as the yucca moth *Prodoxus* species (Prodoxidae) in which up to three species in the *Prodoxus* genus can co-exist on the same Yucca plant (Drummond *et al.* 2010). Additionally, species can be polyphagous and feed on numerous host plants such as *Planotortix octo* and *Pyrgotis plagiatana*, which may cause moth species diversification (Janz *et al.* 2006, Mercader & Scriber 2007).

Olearia as an important Lepidoptera host

Olearia lineata and *Olearia bullata* are important hosts since they harbour a diverse range of native moths (Patrick 2000). Some of these Lepidoptera do feed on multiple plants, however some are more specialised and found exclusively on these *Olearia* species (Patrick 2000). However, the populations of *O. lineata* and *O. bullata* are fragmented, isolated and in decline due to human land-use modification and the invasion of exotic species (Chapter 2 and 3). This results in the Lepidoptera populations also being fragmented and isolated too due to their close association with these host species (Patrick 2000). This is problematic for those specialist Lepidoptera restricted to *Olearia* species, as they may suffer more than the less specialised species, should their *Olearia* hosts go extinct as they will also face a high risk of extinction (Patrick 2000). This has already occurred as the species *Meterana exquisita* has gone extinct from its type locality in Invercargill since the

disappearance of its *Olearia* host plants from that area (Patrick 2000). Therefore, to ensure the future persistence of these endemic Lepidoptera especially the specialist species it is important to ensure the future persistence of host species *O. lineata* and *O. bullata* in the face of global environmental change.

Chapter 5- Synthesis



Olearia lineata population on farmland in Roxburgh Central Otago.

Introduction

This chapter is a synthesis of chapter two, three and four discussing results and stating overall conclusions of what was found in my research. This is then followed by an assessment of the future trajectory of *Olearia lineata* and *O. bullata* populations with recommendations on the most appropriate management practices to restore populations of *O. lineata* and *O. bullata*. Lastly, the chapter will cover limitations of my research and my suggestions for future research.

Why is *Olearia bullata* non-threatened and *Olearia lineata* nationally declining?

Olearia bullata and *Olearia lineata* are closely-related plants in the same genus. However, these species have a different threat status, as *O. bullata* is non-threatened and *O. lineata* is nationally declining. What factors cause the difference of threat status between the two species? Chapter two and Chapter three investigated the similarities and differences in relation to the abiotic and biotic effects of these two closely-related species. It was determined that differences in abiotic factors altitude and drainage, in conjunction with biotic factors such as how these *Olearia* species interact with other species in their communities, can influence the ability to regenerate and hence the threat ranking of each species.

The most significant abiotic factor affecting the current distribution of *O. lineata* and *O. bullata* is the altitude at which populations are found. *Olearia bullata* is present in higher montane habitats compared with lowland river terrace and terrace risers populated by *O. lineata*. In lower altitudes, there is a higher proportion of human-induced land modification (Craig *et al.* 2000, Ewers *et al.*

2006, Brockerhoff *et al.* 2008). There is the conversion of easily accessible land from native ecosystems to farming or forestry, and the development of towns and infrastructure such as roads, thus reducing *O. lineata* populations to small isolated fragments (Craig *et al.* 2000, Ewers *et al.* 2006, Merrett *et al.* 2007, Brockerhoff *et al.* 2008). In addition, lower altitude areas tend to be near large water courses e.g. the Waimakariri River or Clutha River, which the rivers themselves or their tributaries are modified for irrigation or city flood protection by channel straightening, possibly altering natural flooding disturbance regimes. It is known that many New Zealand shrubs and small tree species need some kind of disturbance event to clear a space to regenerate, so the disruption and alteration of the landscape wide disturbance regime can reduce and prevent regeneration in lowland plants (Walker *et al.* 2006b, Merrett *et al.* 2007). Therefore, the increasing development of the lowland areas where *O. lineata* is present is likely to cause its decline. *Olearia bullata*, on the other hand, is present in higher altitude montane areas, which are affected by land-use changes to a lesser degree than the lowland areas of New Zealand (Ewers *et al.* 2006, Walker *et al.* 2006a, Brockerhoff *et al.* 2008). These higher altitude areas are less accessible to farming and forestry and hence are less developed (Ewers *et al.* 2006, Walker *et al.* 2006a, Brockerhoff *et al.* 2008). In addition, *O. bullata* was found to occupy poorly drained wetland seepage area sites, which are less suitable for intensive farming activities as opposed to the flat vast river terraces that *O. lineata* occupies (Walker *et al.* 2006a, Brockerhoff *et al.* 2008). Water is less of a limiting factor in *O. bullata* habitats, which could also affect the growth and regeneration capabilities when compared to *O. lineata* (D'Antonio *et al.* 1998).

Although, both species were found to have the same vegetation community structure, the surrounding community composition and the interaction between those species are potentially important factors that may drive regeneration failure and eventually the decline of a species.

Discaria toumatou, a colonising and nitrogen fixing species, was found at most sites so it is likely to benefit the community as it increases soil nitrogen levels (Widyatmoko 1994), which could aid in the

establishment of species such as *O. lineata* and *O. bullata*. There was also a higher abundance of light demanding vines *Rubus schmidelioides*, *Muehlenbeckia complexa* and *M. australis* at *O. lineata* sites, whereas at *O. bullata* sites they were low in density or absent. They were present all over the canopy of the *O. lineata* trees (pers. obs.). These vines may have a negative effect on the persistence of *O. lineata*, as they have been noted to have a smothering effect on other trees such as *O. hectorii* and reduce the amount of light available to the plant (Rogers 1996a). However, this may only have an adverse effect on small fragmented populations of *O. lineata*.

A group of invasive exotic species including the grasses *Agrostis capillaris*, *Anthoxanthum odoratum*, *Holcus lanatus* and the legume *Trifolium repens* were also found at a majority of sites (Chapter 2- Table 2.3). These species are likely to reduce regeneration of either *Olearia* species due to competitive exclusion resulting in the lack of *O. lineata* seedlings and lack of *O. bullata* seedlings (Chapter 2). At *O. lineata* sites, there was a higher abundance of several exotic invasive species and the presence of a few exotic invasive species that weren't found in the *O. bullata* sites. *Hypochaeris radicata* and *Dactylis glomerata* were both found in higher abundances at *O. lineata* sites compared with *O. bullata* sites (Chapter 2- Table 2.3). *Digitalis purpurea* was observed at half of the *O. lineata* sites but was completely absent from *O. bullata* sites (Chapter 2- Table 2.3). The observed greater number of invasive exotic species at the *O. lineata* sites compared with *O. bullata* sites is likely to have a strong negative effect on regeneration of *O. lineata*. The response of both *Olearia* species to the presence of grass was very similar (Chapter Three). My experiments showed that both *Olearia* species germinated in greater numbers in the absence of grass than in its presence. While surprisingly, both species were found to germinate in the presence of grass over time (Chapter 3). On the other hand, both *O. lineata* and *O. bullata* seedlings demonstrated reduced seedling growth in the presence of invasive grass *Agrostis capillaris*. This negative competitive effect of the grass indicates that *O. lineata* and *O. bullata* are outcompeted or inhibited by *A. capillaris*, which is likely

to be a contributing factor in the absence of seedlings and regeneration failure for both *Olearia* species.

Lastly, *O. bullata* has larger seed and pappus than *O. lineata* (pers. obs.), which may confer a greater dispersal capability in *O. bullata* as both species are wind dispersed (Sheldon & Burrows 1973). The difference in seed size and pappus structure may result in *O. bullata* possibly being dispersed further than *O. lineata* as it has been seen that pappus geometry in Asteraceae can increase dispersal ability of a seed (Sheldon & Burrows 1973).

On the other hand, there are other potential reasons for *O. lineata* to be declining, such as the effect of herbivory from livestock (cattle and sheep) and invasive mammals (deer and hares) (Morta 2004). This has been seen as an important cause of decline in other species, as it affects the survival of recruits- seedlings and saplings (Morta 2004, de Lange *et al.* 2009, de Lange *et al.* 2010). There is also the possibility of pollination limitation, which results in reduced seed set and inbreeding depression (Willi *et al.* 2005, Chi & Molano-Flores 2014, Ison & Wagenius 2014). However, I was unable to investigate these possible causes of decline in relation to *O. lineata* and *O. bullata* in this study, due to time limitation and the failure of the pollination experiment.

Overall, the location of habitats and the competitive effect of grass have likely played the largest role in determining why *O. lineata* is nationally declining and why *O. bullata* is non-threatened. The human development of land and the invasion of exotic species is the greatest in the more accessible lowland areas that *O. lineata* inhabits. The following section describes in greater depth mechanisms of how land use change and invasion of exotic species has resulted in the decline of *O. lineata* and regeneration failure in *O. bullata*.

Effect of land modification and exotic species on *Olearia lineata* and *Olearia bullata*

A significant amount of land conversion from forest and shrubland into productive land (e.g. farming and forestry) has occurred in the eastern lowland areas of New Zealand, affecting many native plants, resulting in the decline of some species (de Lange *et al.* 2010). In addition to land-use change, there has been an increase in the abundance of exotic species as it is easier for exotic species to disperse into more accessible, already modified land, resulting in competition for native plants that are present in these areas (Levine *et al.* 2003). This land-use change in combination with the invasion of exotic species is likely to have had a marked effect on regeneration and persistence of *O. lineata* and *O. bullata*.

Land-use change acts more on a landscape scale causing habitat loss, the fragmentation of populations forming patches, hence restricting populations to less optimal areas (Chapin III *et al.* 2000, Diaz *et al.* 2006, Fischer & Lindenmayer 2007), which is evident in study species *O. lineata*. These small, isolated fragments may not be the most optimal sites for these populations, and are more susceptible to processes such as the allee effect, which can decrease pollinator visitation and the probability of receiving pollen from a suitable donor (Willi *et al.* 2005, Chi & Molano-Flores 2014, Ison & Wagenius 2014). Populations then display inbreeding depression as they are only able to reproduce with individuals within their own population fragment (Willi *et al.* 2005, Chi & Molano-Flores 2014, Ison & Wagenius 2014). This can result in the production of weaker recruits as deleterious genes are more likely to be expressed making the population more susceptible to factors such as disease (Willi *et al.* 2005, Chi & Molano-Flores 2014, Ison & Wagenius 2014). A study on critically endangered *O. gardneri* showed evidence of the allee effect as it was found to have a lack

of viable seeds resulting in regeneration failure (Barnaud & Houliston 2010); this could also potentially occur in *O. lineata*, especially if further habitat fragmentation reduces the number of populations and the size of remnant populations even further. The restriction of fragments to less desirable areas can also cause further risk to the future persistence of the species (Chapin III *et al.* 2000). When a species is restricted to particular locations, through fragmentation or due to habitat specialisation, it puts it at a higher risk of extinction (Fischer & Lindenmayer 2007). This specialisation may be a reason behind why a lack of seedlings was observed for *O. bullata*, due to this species having specific habitat requirements (Wilson & Galloway 1993, Heads 1998).

In contrast to habitat loss, the effect of invasive species, such as exotic grasses, shows the strongest effects at a smaller spatial scale, affecting individual plants within populations (Gaertner *et al.* 2009). This can result in the formation of grass swards and thatch increasing competition with native seedlings and reducing establishment space (Rogers 1996b, Williams *et al.* 1996, Thomson 2005), resulting in the regeneration failure evident in *O. lineata* and *O. bullata* populations. Invasion of exotic grasses and herbs has increased although the effect these plants have on native species varies from species to species (Levine *et al.* 2003). As seen in Chapter three, exotic grasses have a negative competitive effect on seedlings of both *O. lineata* and *O. bullata* causing a reduction in seedling growth. This reduced growth can result in reduced survival of species possibly causing regeneration failure seen in *O. lineata* and *O. bullata*. In New Zealand, other *Olearia* species, *Hebe cupressoides*, *Carmichaelia muritai* and *Muehlenbeckia astonii* all are outcompeted by exotic grasses (Williams *et al.* 1996, Widyatmoko & Norton 1997, Heenan & Molloy 2004, Barnaud & Houliston 2010). Overseas in California, regeneration of *Quercus douglasii* has become threatened due to the same exotic grass competitive processes (Gordon & Rice 2000) which are affecting *O. lineata* and *O. bullata*.

Although seeds of both *Olearia* species were able to germinate in grass, this will only be possible if seed can be dispersed to reach the soil (Thomson 2005). Grasses can form thick dense patches (swards) or in thatch layers resulting in no bare space on the soil and preventing seeds from reaching the ground (Rogers 1996b, Thomson 2005). Seeds of *O. lineata* and *O. bullata* are too light to break

their way through the grass swards and thatch, since they are wind dispersed, resulting in the failure of seeds to germinate. The formation of grass swards means the suitable areas for colonisation and establishment of *O. lineata* and *O. bullata* are reduced, ultimately causing a decline in recruitment of individuals within populations (Rogers 1996b, Williams *et al.* 1996, Thomson 2005). Additionally, if land is suitable for the establishment of both *Olearia* species, it is likely that grasses will disperse and establish in such a site first, outcompeting any dispersal and establishment from *O. lineata* and *O. bullata* (Rogers 1996b, Thomson 2005). This has been seen to occur in other species such as the Antioch Dunes evening primrose, which has become endangered due to the formation of grass thatch layers resulting in regeneration failure (Thomson 2005).

Land-use change and the invasion of exotic species can also interact with the effect of one driver strongly influencing the effect of another (Didham *et al.* 2007). The loss of habitat or degradation of land is usually followed by the invasion of exotic species, often affecting how the exotic species acts or its functional response (Didham *et al.* 2007). The habitat locations of these *Olearia* species, specifically *O. lineata*, are present in areas that are heavily influenced by land-use modification due to intensive development for farming and forestry (Craig *et al.* 2000, Ewers *et al.* 2006, Brockerhoff *et al.* 2008). The development of productive land increased the abundance of exotic herbaceous species, due to direct planting (Grauver *et al.* 2008, Norton & Reid 2013), or through their own dispersal mechanisms as exotic species are often pre-adapted to anthropogenic habitats (Levine *et al.* 2003). The combination of the two drivers, through land degradation and formation of fragments (Fischer & Lindenmayer 2007) in concert with direct and indirect grass effects (Levine *et al.* 2003), resulted in changes to the land making it no longer suitable for *O. lineata* and *O. bullata* to regenerate (Chapter 2 and 3).

Future persistence trajectory of *Olearia lineata* and *Olearia bullata* populations

It has been seen that environmental change due to the human modification of habitats and the spread of invasive species, and the interaction between the two drivers described above, has resulted in the regeneration failure and decline of *O. lineata* as well as regeneration failure of *O. bullata*. However, if land development intensifies in the eastern montane areas of the South Island it is likely that *O. bullata* may also start to decline. These drivers result in the degraded remnants which are likely to become part of an extinction debt. An extinction debt is a process which involves the number of populations that may become extinct after a land-use change event (Kuussaari *et al.* 2009, Gilbert & Levine 2013). Extinction debts may not be paid immediately but over time resulting in populations persisting in the landscape which will not persist in the long term as they are essentially extinct (Kuussaari *et al.* 2009, Gilbert & Levine 2013). There is often a time lag before the impact of the habitat change can be seen in the populations in these modified areas. There is a possibility that *Olearia lineata* may be part of the extinction debt resulting from the land use changes from the colonisation and development of lowland New Zealand. *Olearia bullata* currently appears to have limited regeneration hence is not as far down the pathway towards an extinction debt as *O. lineata*. Species which have a low rate of turnover and are small habitat remnants much like *O. lineata* populations are highly susceptible to be facing an extinction debt (Kuussaari *et al.* 2009).

The future trajectory of *O. lineata* and *O. bullata* makes the outlook for their associated Lepidoptera troubling too. The suite of moths, especially specialists, on these *Olearia* display a patchy and restricted distribution due to their association with *O. lineata* and *O. bullata* (Chapter 4, Patrick 2000). Therefore, any decline in individuals of these two *Olearia* species within populations and over the landscape is detrimental to the future of the specialist moth species, as there are fewer available

patches for them to feed from. Some of the moths feed on multiple hosts, therefore they have a lower chance of decline (Mattila *et al.* 2006). However, the moths that are specialists require these *Olearia* so the restoration of *O. lineata* and *O. bullata* populations will not only provide conservation benefits for themselves but also for the suite of reliant moth species.

Overall, the future outlook for *O. lineata* is worse than for *O. bullata*, especially if *O. lineata* is part of an extinction debt. But since both species are still present there is time to actively manage and reduce the chance of extinction (Kuussaari *et al.* 2009). Possible management methods are outlined in the next section.

Management to aid in future persistence of *O. lineata* and *O. bullata*

Active management is required for *O. lineata* and *O. bullata* populations to reduce the effect of land-use change and the invasion of exotic species, and lower the chances of *O. lineata* and *O. bullata* going extinct. Management strategies work at different scales (local vs. landscape) much like the mechanisms (land-use change and invasion of exotic species) driving the decline of *O. lineata* and *O. bullata*.

Local scale management for O. lineata and O. bullata

Chapter two indicated that there was a lack of recruits in both species of *Olearia*, therefore to increase the long-term persistence of these species there needs to be an increase in the number of recruits and the survival of recruits in populations for both species. Recruits can be added through several methods, such as through direct seeding and the transplanting of seedlings. However, before considering these two strategies the effect of grass needs to be considered. Chapter Three highlighted that competition with exotic grasses plays a vital role in negatively affecting germination

and growth, and hence recruitment of seedlings in *O. lineata* and *O. bullata*. Therefore in direct seeding and transplantation of seedlings it is important to remove or reduce the density of the grass sward within these populations to eliminate the negative competitive effect of the exotic grasses. The removal of grasses could be done by mowing, tilling or with light stock grazing (Miller & Wells 2003, Dodd & Power 2007, Ledgard *et al.* 2008). However, results from my experiments indicate that mowing or cutting of grasses will not be effective enough to reduce the effect of exotic grasses on *Olearia* seedlings. The light grazing from small stock such as sheep would be desirable if population sites are not easily accessible as sheep can graze the grass and other exotic plants to low densities allowing some seedlings to survive, although sheep can also eat seedlings so may be best prior to seed sowing or seedling establishment (Miller & Wells 2003, Dodd & Power 2007). Removal of grass combined with soil disturbance would be the best option (Ledgard *et al.* 2008), with more described on this option below.

Direct seeding would benefit populations of *Olearia*, as it will increase propagule pressure, which can result in higher germination numbers, and therefore higher numbers of recruits (Hooper *et al.* 2005, Ledgard *et al.* 2008). However, direct seeding would only be beneficial in favourable conditions such as adequate soil moisture and the absence of grass (Hooper *et al.* 2005, Dodd & Power 2007, Douglas *et al.* 2007), even though it has been seen that seeds from both *Olearia* species were able to germinate amongst grass (Chapter three). The removal of grasses would not only increase the chance of germination of *O. lineata* and *O. bullata* but increase the growth and chance of survival at later developmental (e.g. seedling and sapling) stages (Dodd & Power 2007, Douglas *et al.* 2007). Removal of grass would need to ensure the roots were not left intact in the soil via soil disturbance methods such as tilling (Ledgard *et al.* 2008), since it was seen *O. lineata* was unable to germinate in bare soil patches with the presence of the grass roots belowground. Ledgard *et al.* (2008), found soil disturbance had the strongest positive effect on seedling numbers especially where grass had been long. Therefore the removal of grass should increase the chance of

germination, and hence survival of the potential recruits (Miller & Duncan 2004, Ledgard *et al.* 2008). Direct seeding is also seen to be a cheap restoration option for restoring large areas of land so is a valuable method to use when money for species management is scarce (Dodd & Power 2007, Douglas *et al.* 2007, Ledgard *et al.* 2008). Additionally, seedlings have been seen to grow successfully from seed, but not from cuttings therefore it is recommended to collect seed to grow seedlings rather than trying to grow from cuttings (Jason Butt, pers. coms.).

Transplantation of seedlings into populations or establishing new populations are options that would increase the chance of persistence of *O. lineata* and *O. bullata* (Williams *et al.* 1996). Transplantation of seedlings is a useful method as plants are prepared in controlled environments ensuring seeds will germinate and seedlings will survive until transplantation (Douglas *et al.* 2007). Utilising the interactions between the effect of shade on grass and the *Olearia* seedlings could benefit this method. Shade was seen to have an effect on the growth of exotic grasses so the implementation of shading could be another possible method to reduce the effect of grass on *O. lineata* and *O. bullata*. Artificial shade structures could be added to sites in which the transplantation of seedlings was to occur, as seen in Chapter three, grasses were unable to cope with reduced light levels. Natural shading could also be used as a strategy where seedlings of *O. bullata* and *O. lineata* are planted in shaded areas within established *O. lineata* or *O. bullata* populations as these areas will contain lower grass density and have a lower chance of exotic grass reinvasion. Although *O. lineata* and *O. bullata* seedlings did not have optimum growth rate under the shade, they still grew significantly better with shade than with the exotic grasses so this method will benefit both species. However, it would be important to avoid heavy shade as this would reduce the growth of the seedlings too.

Landscape scale management for O. lineata and O. bullata

On a larger landscape scale, it is beneficial to ensure the future persistence of species through ensuring the populations we have left are protected and not lost through land development. To ensure these plants are protected, it is important to educate people on what the plants are and why they are important to the environment and how they can benefit the general public (de Lange *et al.* 2010, Norton & Reid 2013). Education of landowners is especially vital, as these often are the people behind the land-use decisions on whether or not to develop land (de Lange *et al.* 2010, Norton & Reid 2013). There are many benefits of *Olearia* for farmers land such as providing shelter for stock, the reduction of soil erosion and promoting an increase in abundance of native invertebrates, which can provide important ecosystem services such as pollination (Norton & Reid 2013). Landowners also often take pride in the presence of rare species once they know that they are present on their land (Norton & Reid 2013). Therefore the education of land owners can help them make more informed decisions on how to use and develop their land in the presence of native declining species (de Lange *et al.* 2010, Norton & Reid 2013).

The protection of *O. lineata* and *O. bullata* on private land is very important as the majority of the populations I sampled (*O. lineata* sites 1-7, *O. bullata* sites 1-3 & 6) were found on land that is not in the public conservation estate. A covenant is one method to protect portions of private land often forest fragments from being developed (Norton & Reid 2013). Covenants provide benefits to conservation through the protection of habitat and individual species and benefits to farmers by gaining financial support to maintain the covenant (Norton & Reid 2013). Additional benefits include gaining environmentally friendly certification standards by sustaining native biodiversity and threatened species, which can provide a market advantage to those farmers (Norton & Reid 2013). Often covenants are fenced off from livestock such as cattle and deer (Norton & Reid 2013), which

has positive benefits to populations of *O. lineata* and *O. bullata* as it reduces the degradation of habitat and ensures the future persistence of these species.

The management and protection of *O. lineata* and *O. bullata* also provides protection to the suite of native Lepidoptera and other invertebrates that rely on these plants as hosts (Patrick 2000). So it is important to protect these *Olearia* species as any protection of these species also provides protection to the endemic native Lepidoptera (Patrick 2000, Patrick & Dugdale 2000).

Limitations and future research

This section outlines some of the limitations to my research and suggestions of interesting future possible studies building from my research.

Limitations of my research

Firstly, demographic measurements in this study used the height and basal diameter of individual plants as a proxy for age to determine the age structure of each individual population. These measurements are sufficient to determine if the populations are suffering from regeneration failure as the presence or absence of small individuals is evident from these measurements. However, these trees were not able to be aged specifically; proper age estimates may have been able to provide more definitive evidence to show if these populations are regeneration limited and therefore declining and estimate when the last phase of recruitment occurred in each population.

A pollination experiment set up to determine if these *Olearia* species may be pollen limited did not work for several reasons. However, there are various uncertainties to take into consideration when undertaking this type of experiment such as flowering time, the production of enough flowers by the individual plants and site access. I would suggest not relying on a single population of both species

for the experiment and would recommend trying to find sites that are reasonably accessible so flower production and the opening of flowers can be closely monitored to ensure the experiment is set up and undertaken at the most optimum time.

Lastly, I would have a better system in place to collect and rear moths. Larvae were only collected during the day from individuals in populations, which restricts the moth larvae found to species active in the day whereas some species are only active at night (Patrick 1994, 2000, Patrick & Dugdale 2000, Derraik *et al.* 2002a, Derraik *et al.* 2002b). Species identity can be determined from the larvae collected, however, a large proportion of moths collected died from desiccation resulting in possible misidentifications. Other measures were undertaken to reduce the chance of misidentification (e.g. through photographs), but some individuals were just too small or were unidentifiable through photos. However, some larvae may not be easily identifiable so rearing of larvae to adult moths was crucial to confirm the identification of some species collected (Patrick 2000, Derraik *et al.* 2002b). Therefore, due to the low success rate of rearing in this study, some moth species were still unable to be identified. The ability to be more accurate with larval species identifications would have allowed moth species richness to be compared between host plant species as more species would have been identified to species level and may reduce the reliance on the rearing of larvae to fully confirm species identities.

Further research

Firstly, more research investigating the population demographic structure of *O. bullata* would be useful to determine if *O. bullata* is actually regeneration limited or if this conclusion was an artefact of the sites that were sampled. *Olearia bullata* is present in communities in which the other species present are long-leaved and have the potential to visually obscure the presence of seedlings (especially the tall growth of sedges such as *Schoenus pauciflorus*). Therefore, more research into *O.*

bullata population demographics would aid in determining if these species are actually regeneration limited and possibly declining.

Further expanding on the population demographic research, investigating how closely related the plants are within each population and between populations, as it would be beneficial to identify how genetically isolated the individuals are within and between populations. It would be interesting to know if most of the individuals in one population are all related as that could influence population recruitment as recruits produced may have low fitness therefore have a lower chance of survival compared with genetically diverse recruits (Willi *et al.* 2005, Ison & Wagenius 2014). It is also known in populations of *O. hectorii* that when branches droop down and touch the ground they are able to reroot and produce surviving offspring (Rogers 1996a). This drooping of branches is also observed in *O. lineata* (pers. obs.), therefore, it could be possible that populations of *O. lineata* may consist of some genetically identical individuals reducing the variation of genes in the gene pool for that population and potentially causing a reduction of successful recruits.

When setting up the pollination limitation experiment, I observed the *O. bullata* population being used had very low flowering capitula numbers per branchlet when compared to plants I had observed the previous year with high capitula numbers per branchlet. This difference in flowering effort could be investigated further to determine if there is a masting effect and the plants had heavily flowered the previous year and this year had a low flowering effort since most resources were used up in the mast flower or if the population was going through the year to year variation in flowering effort. This population was also quite small which has been seen in the literature as a possible explanation for low flowering effort (Chi & Molano-Flores 2014).

Herbivory could be an important factor that may also affect recruitment in these *Olearia* species as most populations of these plants were found on private land with stock present. Other studies have

shown that herbivory is an important factor in regeneration failure in other *Olearia* species and in many other declining species (Morta 2004). It could be useful to further investigate whether herbivory has an effect on survival and regeneration in *O. bullata* and *O. lineata* populations. Lastly, there should be the further collection and identification of moth species and investigations into any moth-parasitoid networks. Two parasitoids were found on two different host plants and caterpillars therefore an investigation into the plant-moth-parasitoid networks in the shrubland and grassland area of the Canterbury high country. This would be interesting to see what networks have formed in the natural shrubland and grasslands, compared with the grazed and human modified grasslands that are present in that area, considering different moth species feed on the differing vegetation in those communities (Chapter 4).

Overall Conclusion

The future persistence of *O. lineata* and *O. bullata* does not look very promising unless there is a reduction of human land-use change and the impacts of invasion of exotic species can be addressed. These species need management with a combination of active restoration involving transplantation and direct seeding and wider landscape scale management such as the implementation of covenants to protect populations, and the education of landowners. An increase in population size of specific sites (Rogers 1996a, Fischer & Lindenmayer 2007) and overall, would aid in ensuring the future persistence of this species by increasing stand numbers, improving floral display and reproductive success (Chi & Molano-Flores 2014, Ison & Wagenius 2014). Additionally, the protection of *O. bullata* and *O. lineata* will also result in conservation benefits for invertebrates providing protection for the suite of Lepidoptera and other invertebrates that utilise these plants as hosts (Patrick 2000, Patrick & Dugdale 2000). This will provide *O. bullata* and *O. lineata* along with their suite of native Lepidoptera, some chance of long term persistence in the face of continual environmental change.

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Appendices:

Appendix to Chapter 2:

Table A2.1: Details of Site locations used in this study. *Olearia lineata* seed from site 3 was collected from Jason Butt from Wai-ora Landscapes Ltd. and was unable to disclose the exact location due to needing landowner permission.

Site	Species	Site number	Latitude	Longitude
Waimakiriri Flats	<i>Olearia lineata</i>	1	-43.036583	171.808167
Poulter River	<i>Olearia lineata</i>	2	-43.045358	171.908911
Rakaia Island	<i>Olearia lineata</i>	3		
HighPeak Station	<i>Olearia lineata</i>	4	-43.42044	171.800777
Craigmore Station	<i>Olearia lineata</i>	5	-44.4335	171.003333
Rugged Ridges	<i>Olearia lineata</i>	6	-44.644247	170.323847
Gorge Creek	<i>Olearia lineata</i>	7	-45.377193	169.272785
Millers Flat	<i>Olearia lineata</i>	8	-45.720101	169.445621
Island Block	<i>Olearia lineata</i>	9	-45.72262	169.46759
Speights Saddle	<i>Olearia bullata</i>	1	-43.046611	171.802361
Middle Bush	<i>Olearia bullata</i>	2	-43.034028	171.761944
Cass Hill	<i>Olearia bullata</i>	3	-43.018517	171.756366
Mt Somers	<i>Olearia bullata</i>	4	-43.631436	171.300301
Mackenzie Pass	<i>Olearia bullata</i>	5	-44.194833	170.594639
Guide Hill	<i>Olearia bullata</i>	6	-43.979497	170.311325
Lees Valley	<i>Olearia bullata</i>	7	-43.188461	172.143439

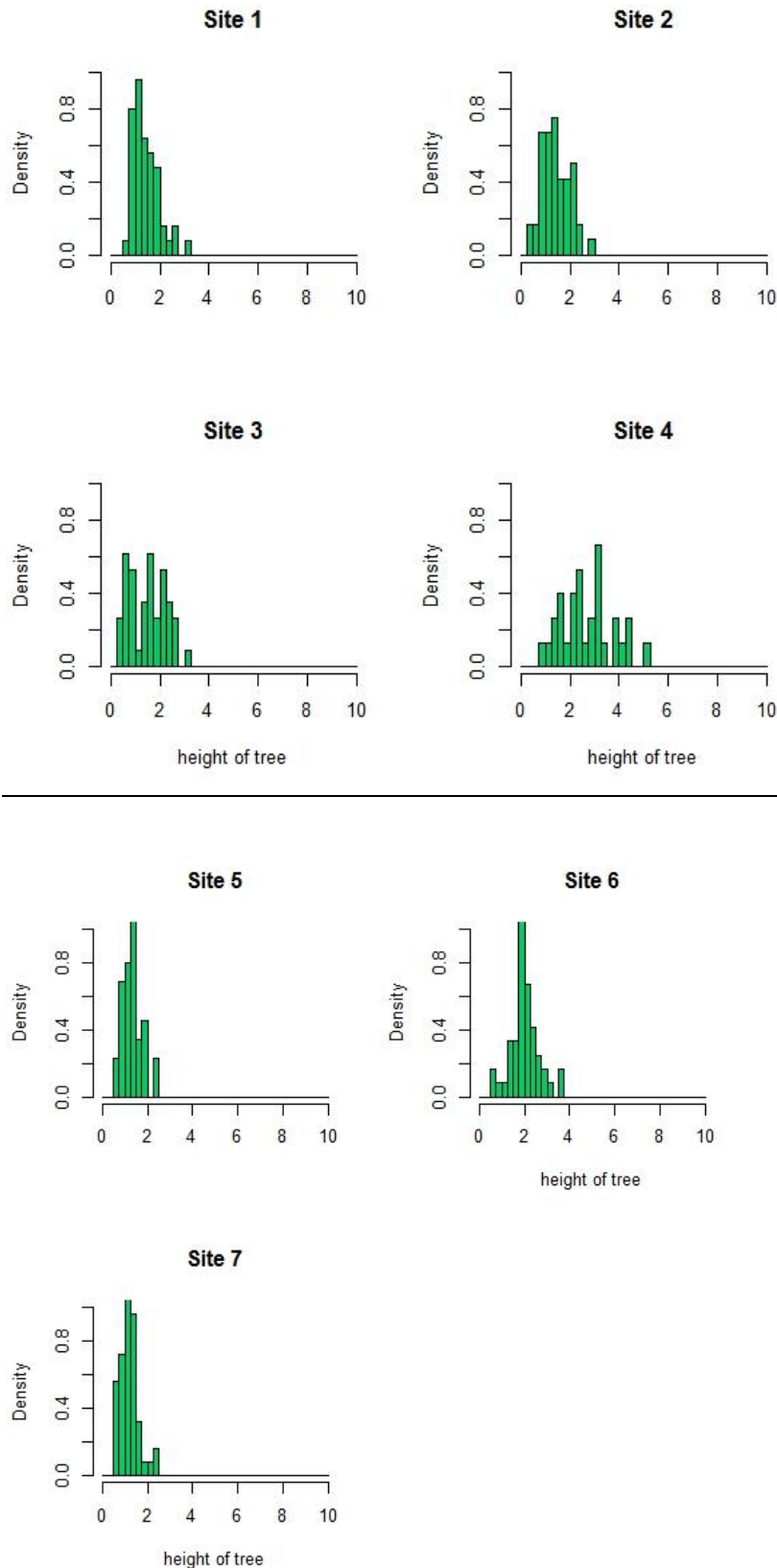


Figure A2.2: *Olearia bullata* (N=7) height of trees at sites Speight's Saddle (n=50), Middle Bush (n=48), Cass Hill (n=45), Mt Somers (n=30), Mackenzie Pass (n=35), Guide Hill (n=48) and Lees Valley (n=50).

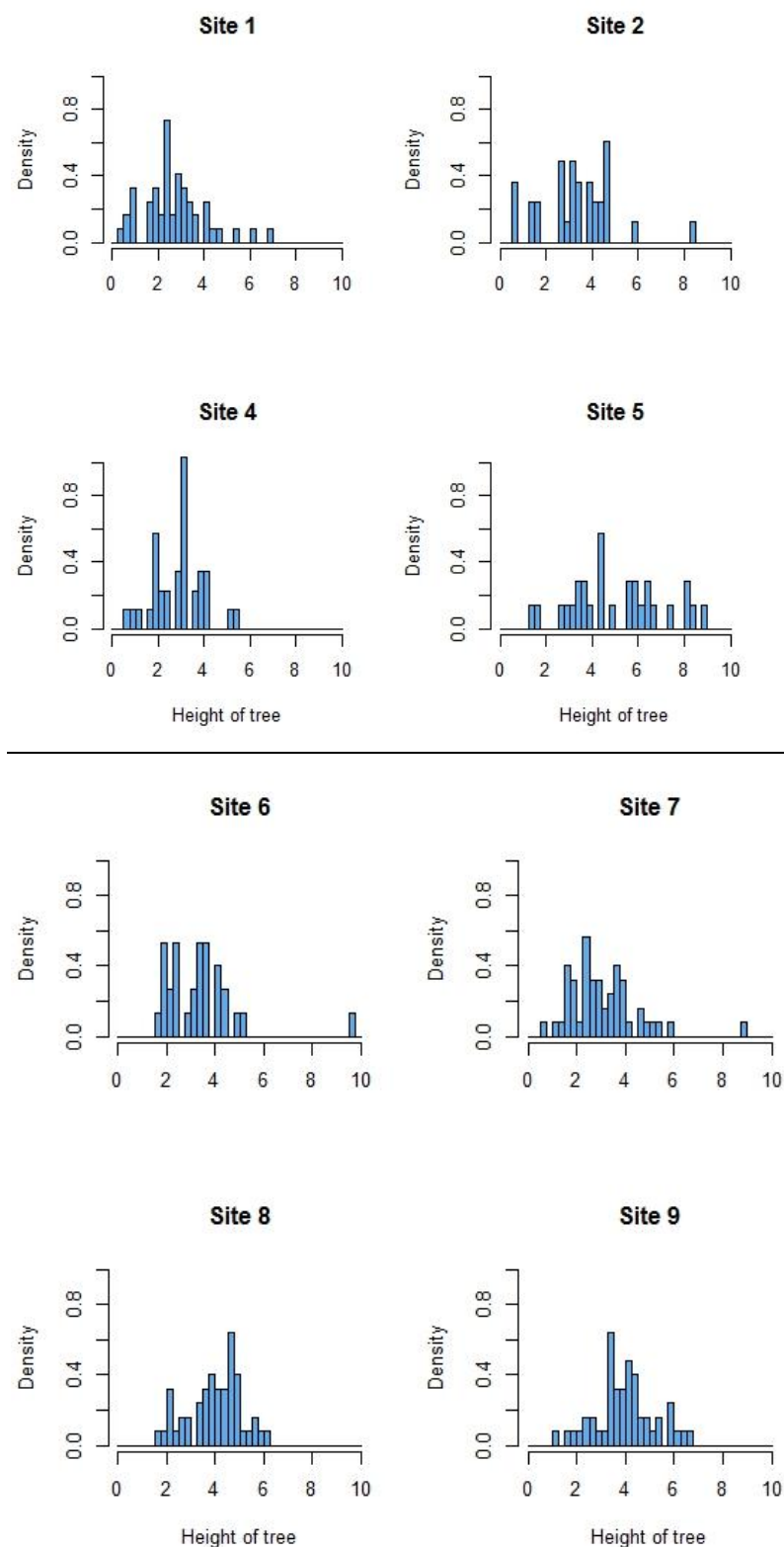


Figure A2.3: *Olearia lineata* (N=8) height of trees at sites Waimakariri Flats (n=50), Poulter River (n=33), High Peak Station (n=35), Craigmore Station (n=25), Rugged Ridges (n=30), Gorge Creek (n=50), Millers Flat (n=50) and Island Block (n=50).

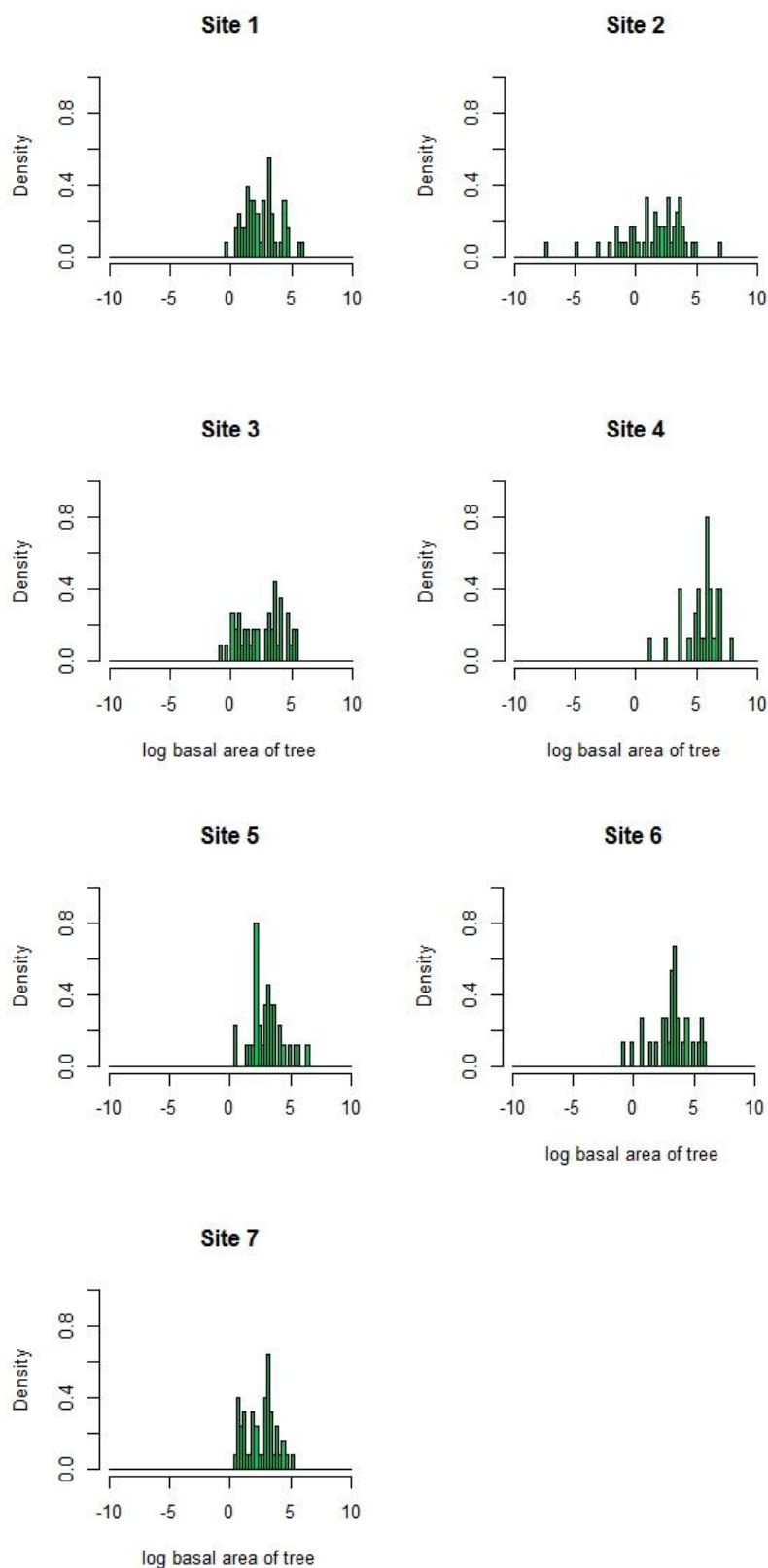


Figure A2.4: *Olearia bullata* (N=7) log basal area of trees at sites Speight's Saddle (n=50), Middle Bush (n=48), Cass Hill (n=45), Mt Somers (n=30), Mackenzie Pass (n=35), Guide Hill (n=48) and Lees Valley (n=50).

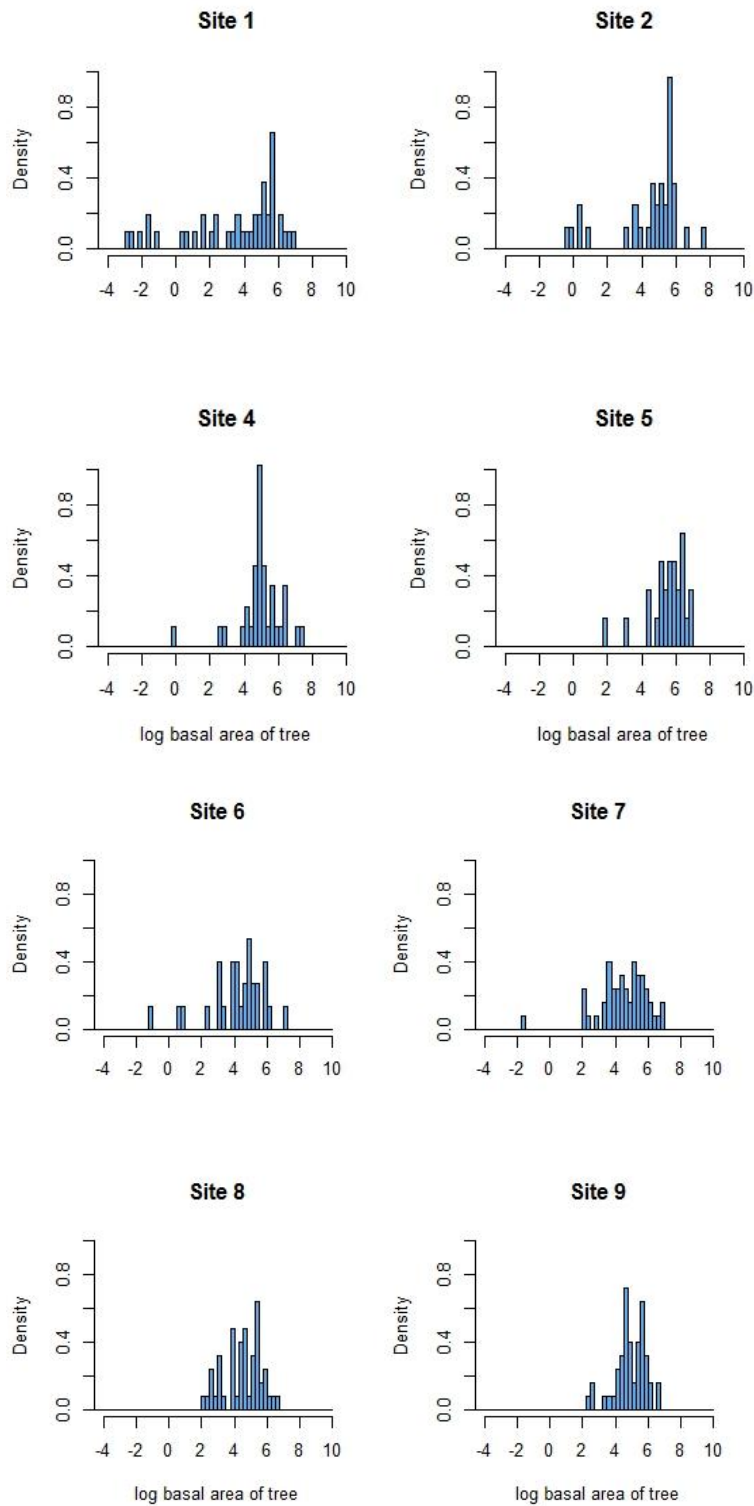


Figure A2.5: *Olearia lineata* (N=8) log basal area of trees at sites Waimakariri Flats (n=50), Poulter River (n=33), High Peak Station (n=35), Craigmore Station (n=25), Rugged Ridges (n=30), Gorge Creek (n=50), Millers Flat (n=50) and Island Block (n=50).

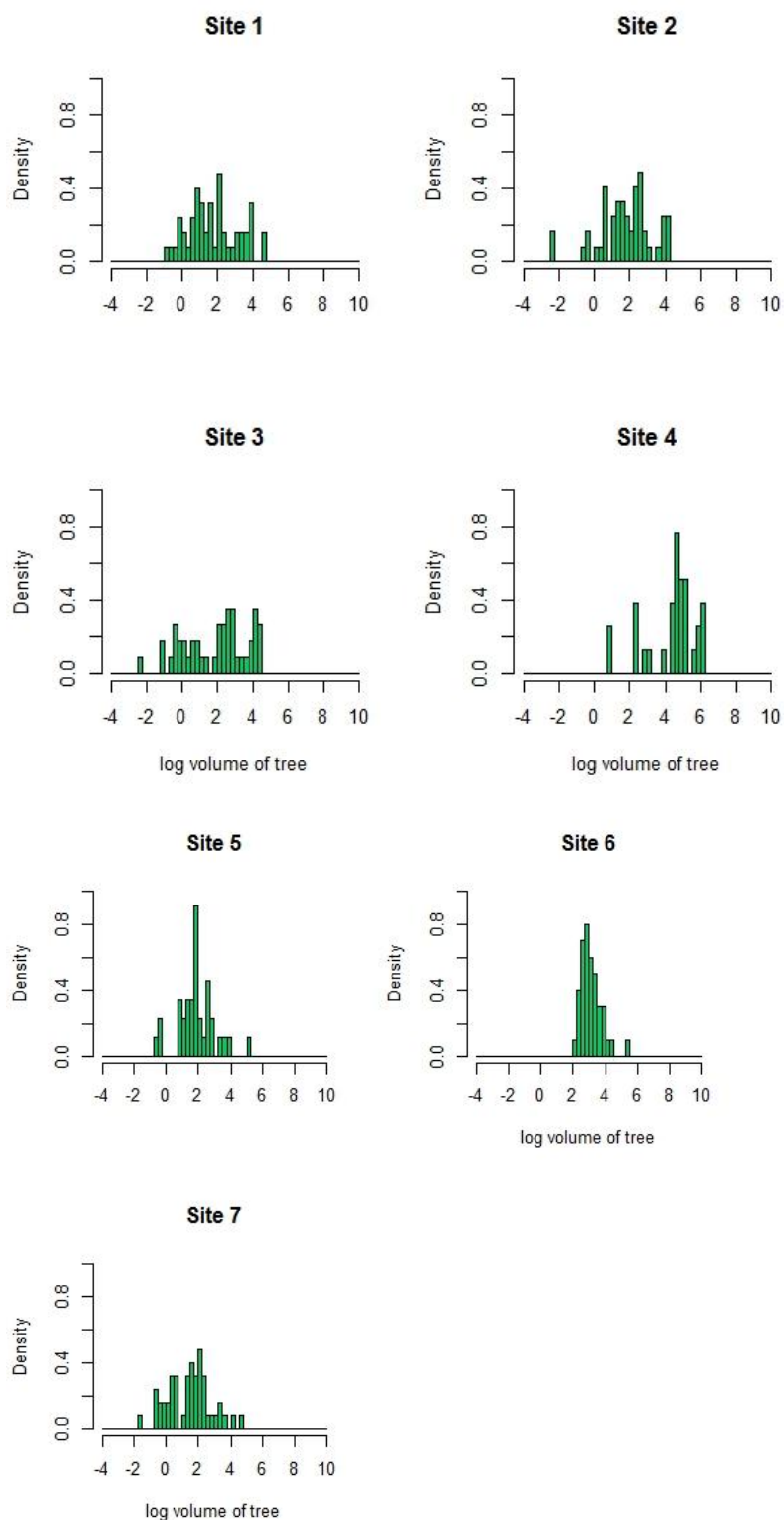


Figure A2.6: *Olearia bullata* (N=7) log volume of trees at sites Speight's Saddle (n=50), Middle Bush (n=48), Cass Hill (n=45), Mt Somers (n=30), Mackenzie Pass (n=35), Guide Hill (n=48) and Lees Valley (n=50).

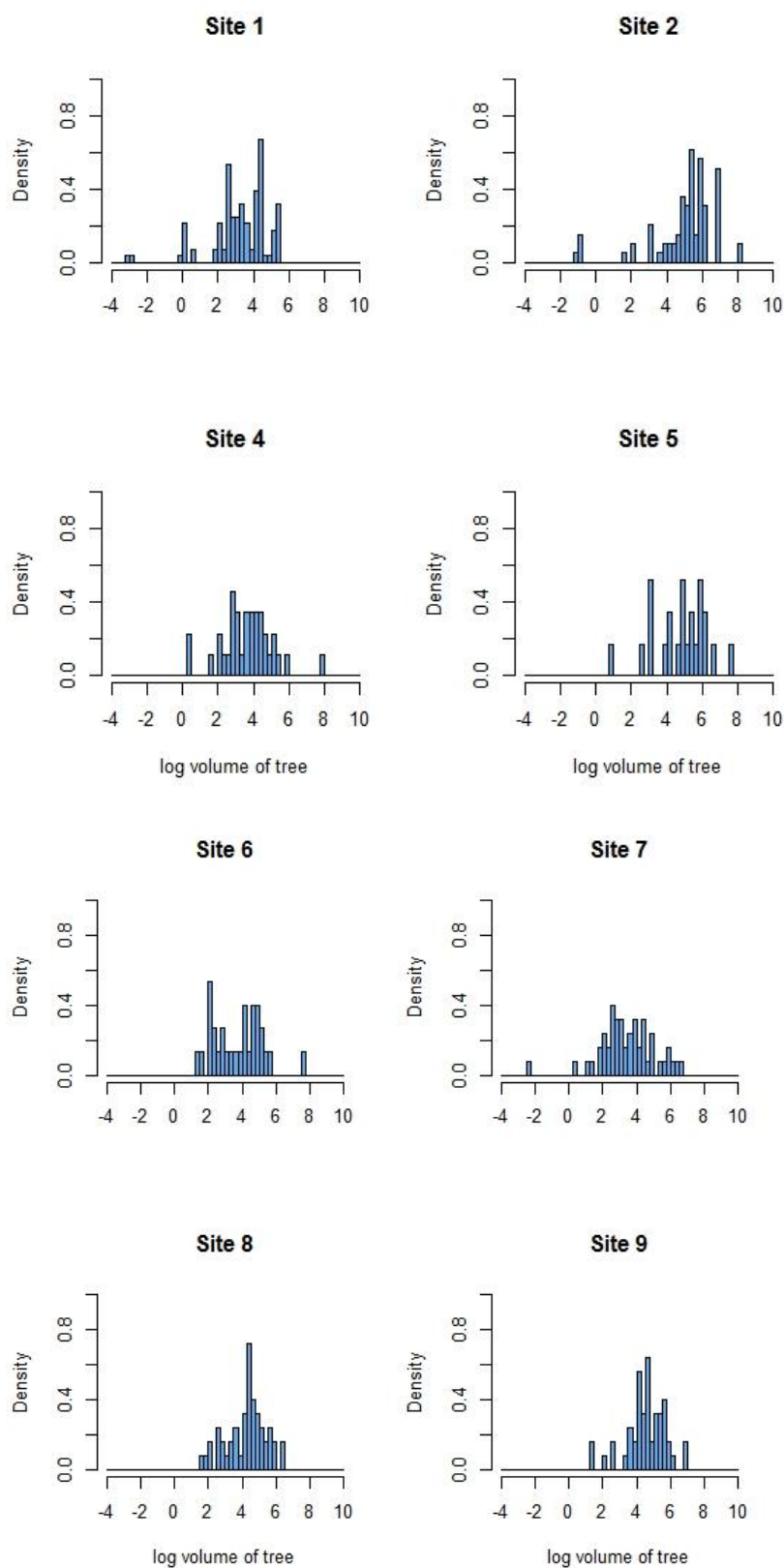


Figure A2.7: *Olearia lineata* (N=8) log volume of trees at sites Waimakariri Flats (n=50), Poulter River (n=33), High Peak Station (n=35), Craigmore Station (n=25), Rugged Ridges (n=30), Gorge Creek (n=50), Millers Flat (n=50) and Island Block (n=50).

Appendix to Chapter 3:

Table A3.1: The total number of seeds (out of 1000) germinated during the preliminary trial from three sites for each species.

Site	Species	total germinated	total not germinated
1	<i>Olearia lineata</i>	142	858
2	<i>Olearia lineata</i>	0	1000
3	<i>Olearia lineata</i>	5	995
4	<i>Olearia bullata</i>	6	994
5	<i>Olearia bullata</i>	70	930
6	<i>Olearia bullata</i>	3	997

Table A3.2: Average and Standard Deviation light level measures for the heavy shade (n=5) and light (n=5) shade treatments as a proportion of the total available ambient light (no shade treatment) in the seedling competition experiment. The light measure was recorded once the meter reached an unchanging number.

Replicate	Treatment	
	Heavy	Light
1	25.8 ± 0.02	37.6 ± 0.08
2	23.2 ± 0.03	68.35 ± 0.3
3	24.8 ± 0.01	58.8 ± 0.06
4	24.9 ± 0.01	71.07 ± 0.13
5	30.8 ± 0.07	52.2 ± 0.13
Average	25.9 ± 2.9	57.6 ± 13.5

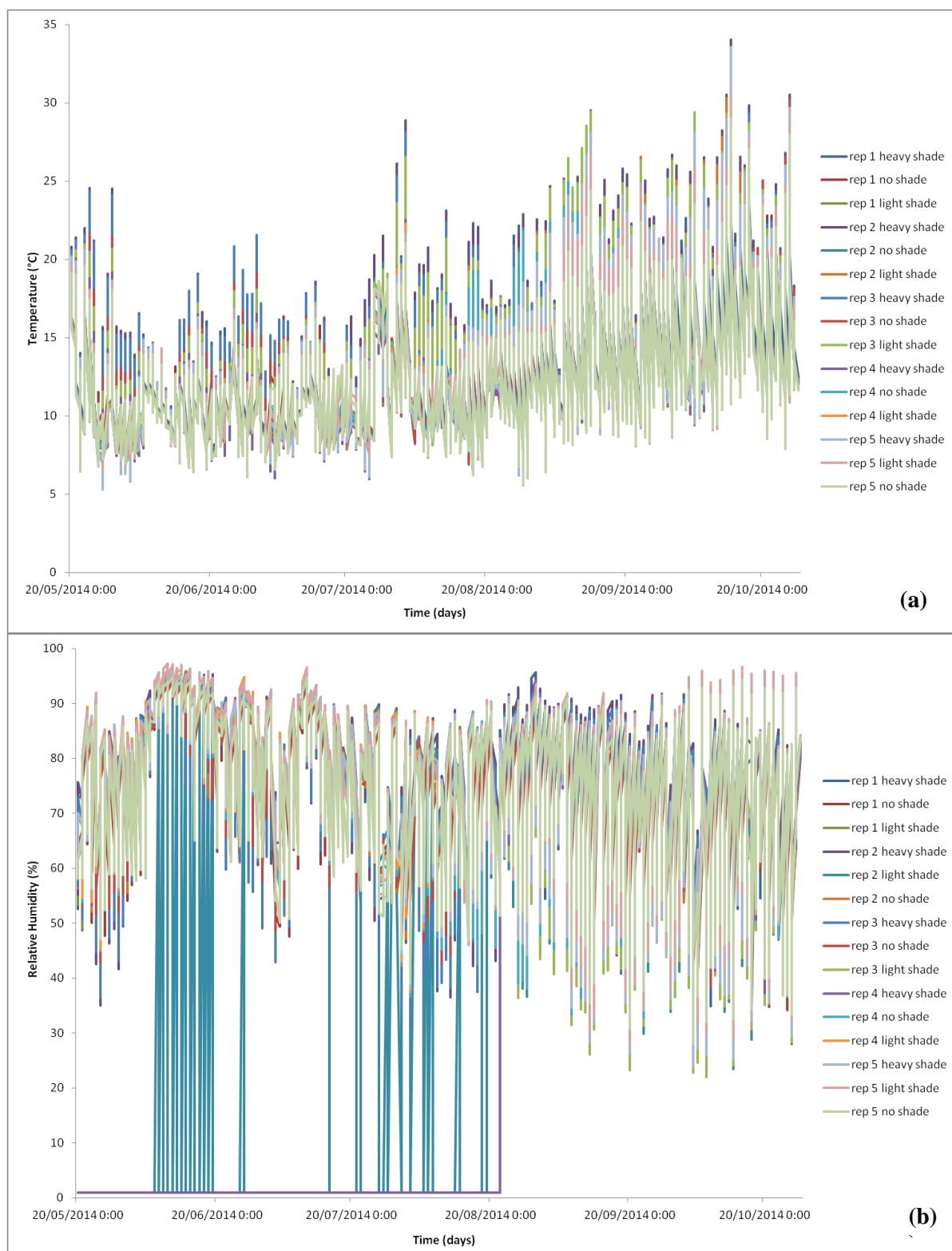


Figure A3.1: The temperature and relative humidity for the duration of the glasshouse competition experiment from data loggers with each line representing measurements from inside one of the shade level treatments within each replicate ($n=15$). (a) Temperature for May – October 2014. (b) Relative humidity for May – October 2014. Graphs indicate all treatments were experiencing the same temperature and relative humidity fluctuations. However, the lines not fitting the trend were malfunctioning data readers.

Table A3.3: Coefficients table for fixed effects from binomial generalized linear model testing how soil moisture responded to the three shade level treatments (heavy, light, and no shade) and the presence or absence of grass treatments for two species: *O. lineata* and *O. bullata*. Soil moisture was measured over three days, at the same time each day and in the same pots, so pots were included as random effects to control for the non-independence of these multiple measures.

Fixed effects:

	Estimate	Std. Error	t value	Pr(> t)
Grass presence: Heavy Shade	42.095	4.702	8.953	1.87e-05 ***
Grass absence	5.958	3.012	1.978	0.0573 .
Light Shade	-1.900	3.573	-0.532	0.6016
No shade	-10.013	3.573	-2.803	0.0120 *
Olearia lineata	3.192	1.993	1.602	0.1195
Grass absence: light shade	3.125	4.260	0.734	0.4690
Grass absence: no shade	6.833	4.260	1.604	0.1193

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table A3.4: Analysis of Deviance table for the binomial generalized linear model testing the success of germination in treatments – grass presence, grass absence and bare soil patch, for two species *O. lineata* and *O. bullata*.

	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)
NULL				143	271.84
Treatment	2	32.547	141	239.29	8.561e-08 ***
species	1	0.695	140	238.60	0.404541
treatment: species	2	12.326	138	226.27	0.002105 **

Significance. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table A3.5: Analysis of Deviance Table for the Poisson generalized linear model testing the germination rate of two species - *Olearia lineata* and *O. bullata* within three grass treatments – grass presence, grass absence and bare soil patch, at three time steps.

Model: poisson, link: log

	Df	Deviance	Resid.	Df	Resid. Dev	Pr(>Chi)
NULL				17	51.538	
treatment	2	5.6671		15	45.871	0.0588029 .
species	1	0.0112		14	45.860	0.9155816
time	2	3.8613		12	41.998	0.1450503
treatment: species	2	2.9100		10	39.088	0.2334060
treatment: time	4	21.2982		6	17.790	0.0002763 ***
species: time	2	7.0445		4	10.746	0.0295333 *
treatment : species: time	4	10.7457		0	0.000	0.0295756 *

Significance. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

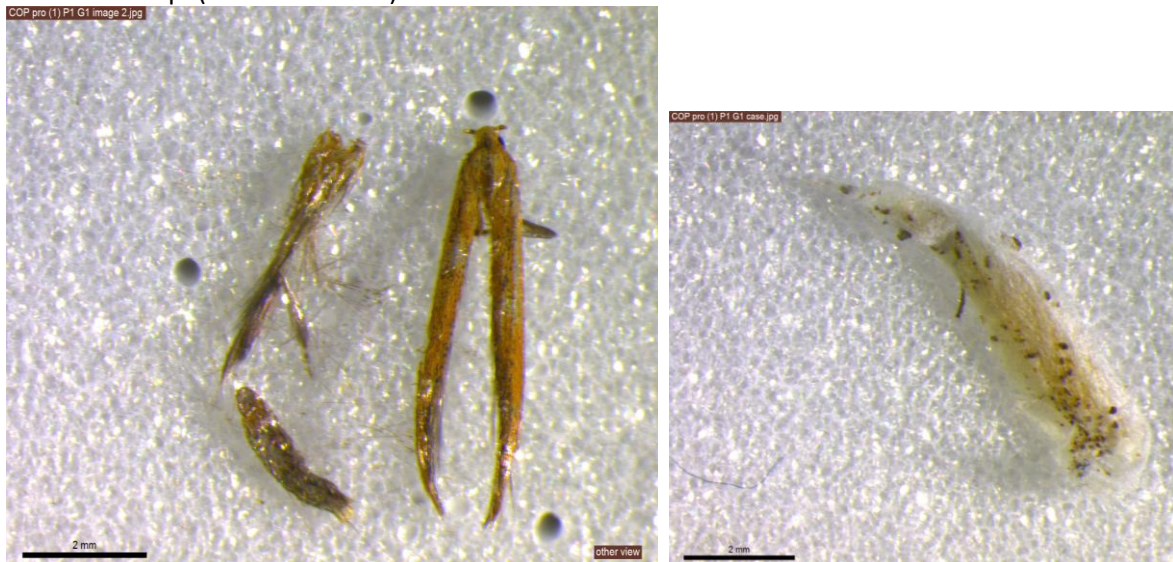
Appendix to Chapter 4:

Figure A4.1: Examples of each of the moth (Lepidoptera) species identified in this Chapter.

Pyroderces deamatella (Cosmopterigidae)



Batrachedra sp. (Batrachedridae)



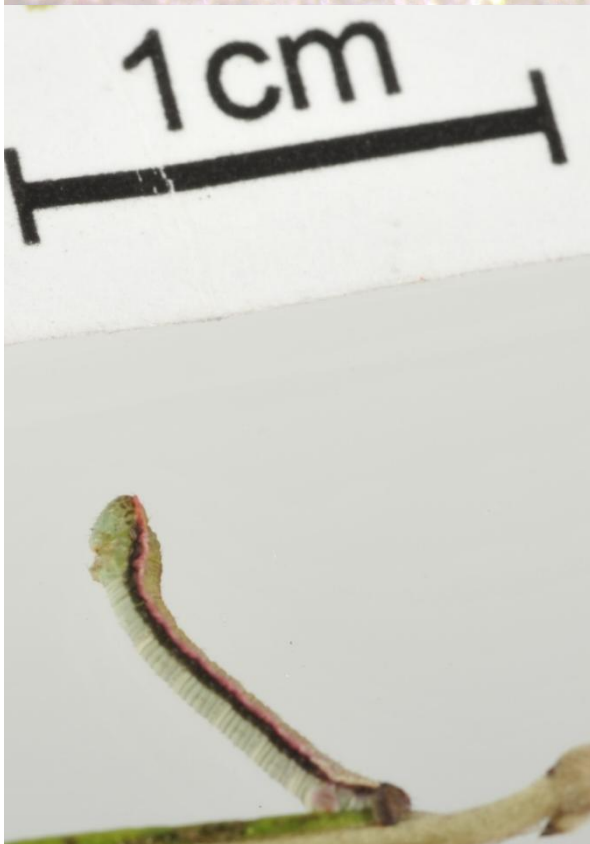
Unknown 2

OLEbul (3) moth 3.jpg



Pasiphila continua (Geometridae)

OLEbul (3) moth 4.jpg



Planotortrix octo (Tortricidae)



Pyrgotis plagiatana (Tortricidae)



Thiotricha oleariae (Gelechiidae)



Meterana equisita (Noctuidae)



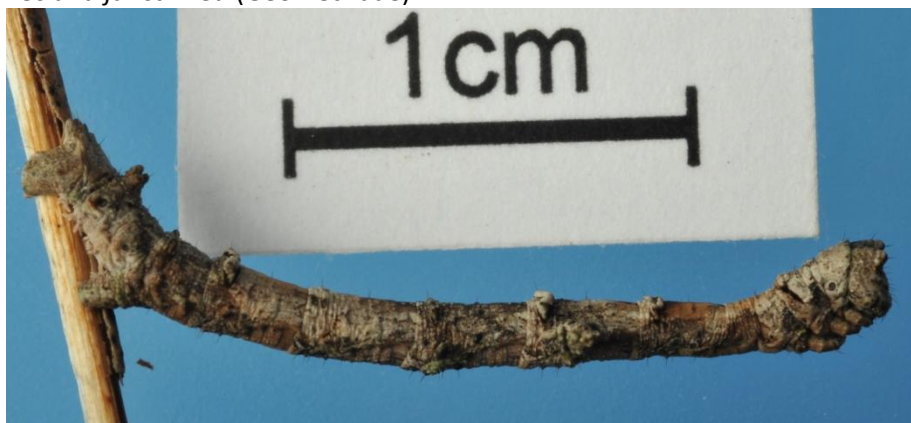
Harmologa oblogana (Tortricidae)



Phaeosaces sp. (Oecophoridae)



Declana junctilinea (Geometridae)



Declana toreuta (Geometridae)



Austrocidaria sp. (Geometridae)

