Publishing conventions follow *Austral Ecology*

Looks can be deceiving: *Leucanthemum vulgare* Lam. (Asteraceae) appears be a benign invader in the sub-alpine region of Victoria.

BREANNA TURNER

A thesis submitted in partial requirement for the Degree, Bachelor of Wildlife and Conservation Biology with Honours

Department of Botany
School of Life Sciences

Faculty of Science, Technology & Engineering
La Trobe University
Bundoora, Victoria 3086
Australia

19th May, 2014
Approximately 19,800 words

Declaration

I certify that the attached document is my original work. No other person's work has been used without due acknowledgement. Except where I have clearly stated I have used some of this material elsewhere, it has not been presented to me for examination in this or any other institution. I understand that the work submitted may be reproduced and/or communicated for the purposes of detecting plagiarism.

None of the research undertaken in connection with this thesis required approval by a University Ethics Committee.

Name: Breanna Turner

Subject: Botany 4HONS

Document: Thesis

Signature:

Student Number: 16125910

Date: 19.5.2014

ACKNOWLEDGEMENTS

I would firstly like to give the biggest thank-you to my supervisors Dr. Peter Green and Dr. John Morgan for their time, effort, guidance and ongoing support throughout the duration of this project. Both have persisted and remained calm with me through my many learning curves, and taken far too much time explaining things I just didn't get. I would like to thank Zach Walker for spending six weeks in the mountains with me and everything he has done for me since, my data would not have been collected without you, what a trooper. Max Bartley for his ongoing work in the glasshouses that provides all equipment and assistance for experiments to run smoothly. A special thanks to Kelsey James and Misty Walton for their ongoing support, financially and emotionally, throughout the entirety of this project, I wouldn't have made it without you two! To my fellow honours students Rohan Ball, Karina Salmon and Natalie Zrimsek, for making this year all the more enjoyable. Lastly I would like to thank the Research Centre for Applied Alpine Ecology at La Trobe University for their funding support.

TABLE OF CONTENTS

ABSTRACT

Invasive species are spreading into new habitats in ecosystems throughout the world. In many cases the impact of these invaders on native communities is unknown, so the primary means of management prioritisation for these species is the ‘precautionary principle’. Under this principle, alien species are prioritised for management if they spread rapidly and reach high population densities, or if they are considered problematic in other parts of their invaded range. However, the impacts of invasive species vary, and determining which alien invasive species have the greatest impacts on their recipient communities should be at the forefront of invasion science. Much of the research to date either fails to decouple a species’ ‘invasiveness’ from its realised ‘impact’, or tests too few impact variables.

The Ox-eye daisy (*Leucanthemum vulgare* Lam., Asteraceae) is widely considered as a problematic invader, because of its ability to form dense stands which are thought to have large, negative impacts on native communities. However there is little empirical data supporting these claims. This study used multiple metrics to assess the impact of *L. vulgare* in subalpine vegetation at Mt Hotham in the Australian Alps. Species diversity, richness, composition, structure and traits were all compared between paired transects in which ox-eye was rare or absent on one, but abundant on the other. A pot trial was also conducted to assess the competitive ability of *L. vulgare* relative to other native and invasive daisy species, and the CSR strategy scheme was used to compare the traits of *L. vulgare* against those of other invasive and native daisies from the area.

Although *L. vulgare* has the ability to form dense, visually displeasing stands, this study found no consistent evidence for high negative impacts due to its invasion. The disproportionate contribution of other exotic species to differences between High and Low *L. vulgare* transects suggests that this species may be a passenger responding to alterations in these communities as a result of invasion by other exotic species. Although found to be highly competitive when compared to other daisy species based on its functional type, growth of *L. vulgare* was found to be significantly affected when grown with *Poa sieberiana.*

These findings highlight the benefits of testing multiple metrics for impact assessment, and suggest that future research over longer time spans is needed in order to confirm that this highly invasive weed has no measurable impact.

INTRODUCTION

Native species are declining throughout the world and one of the key drivers for this loss is the invasion of plant and animal species that have been introduced to areas far from their native range (Didham *et al.* 2005; Lonsdale 1999; Mack & Lonsdale 2001; Vitousek *et al.* 1997). Many species dominate natural and disturbed ecosystems in their new range, negatively impacting their new ecosystems (Mack & Lonsdale 2001; Ravi *et al.* 2009). However, many of these invading species do not spread widely and have little to no consequence for the native biota (Barney *et al.* 2013; Parker *et al.* 1999; Ricciardi & Cohen 2007). Understanding which species have the highest impact on natural ecosystems is arguably one of the most important needs of invasion science (Barney *et al.* 2013). Research on exotic species impacts on natural systems is used to inform management decisions on priorities for control and ecological restoration (Parker *et al.* 1999; Thiele *et al.* 2010). However, there is a general lack of conclusive data for species impacts on natural systems to support management actions (Barney *et al.* 2013; Hejda & Pysek 2006).

Decoupling invasiveness and impact

Invasion biology research has two core objectives: to understand which species may become invasive in new ranges, and to determine what ecological impacts such species might have on natural ecosystems. It is often suggested that the impact of a species increases with its perceived invasiveness (Kolar & Lodge 2001; Magee *et al.* 2010; Rejmanek & Richardson 1996); this has resulted in the terms 'invasive' and 'impact' being used interchangeably and has lead to miscommunication between management and research (Ricciardi & Cohen 2007). The term invasive is often used by policy makers and land managers to describe a species that is non-native to the ecosystem being considered and has the ability to cause environmental and economic damage (Ricciardi & Cohen 2007; Richardson *et al.* 2000). However, when Ricciardi & Cohen (2007) tested the relationship between invasiveness and impact they found that the two are not strongly linked. Many ecologists believe that the impact of a species should not be linked to its perceived 'invasiveness' and that the term invasive should be used strictly to describe a species that has spread outside its native range (Colautti & MacIsaac 2004; Falk-Peterson *et al.* 2006; Ricciardi & Cohen 2007; Richardson *et al.* 2000).

Correlation vs causation

Declines in native species or ecosystem changes in the presence of invasive species are often documented (Khuroo *et al.* 2010; Pysek *et al.* 2012), but this does not mean that the invasive species have caused the changes (Gurevitch & Padilla 2004). Distinguishing correlation from causation has long been a problem in invasion ecology where control and impacted sites are assumed to have been similar prior to invasion (Barney *et al.* 2013; Parker *et al.* 1999). MacDougall & Turkington (2005) suggested the passenger-driver theory as a way of explaining this phenomenon. Here, a 'driver' is an invader that has the ability to enter a community and cause changes in species diversity and ecosystem function (usually negative). 'Passengers', on the other hand, are species that have little to no impact on the systems they invade; their ability to enter and succeed in native systems is not because they are good at altering the diversity and ecosystem function but rather, they invade because there has already been a previous environmental change that releases resources (MacDougall & Turkington 2005). Examples of these changes may be loss of diversity, fire suppression, disturbance or reduced dispersal due to fragmentation that add nutrients and provide available niches for invading species (Didham *et al.* 2005; Gurevitch & Padilla 2004; MacDougall & Turkington 2005).

This theory attempts to use the method of invasion as a predictor of impact, with drivers being labelled as species likely to have a high impact. Passengers, however, have also been found to have impacts on natural systems, despite them being considered less likely to demonstrate negative changes (Bauer 2012; Bulleri *et al.* 2010). These secondary invaders have been named the 'back-seat drivers' of ecological change as they enter as passengers, but persist as drivers (Bulleri *et al.* 2010). Using these methods of invasion to assess impact can also be risky because invaders can change their status throughout the stages of invasion (Dietz & Edwards 2006).

Impact frameworks

Several studies have attempted to develop frameworks that can reliably quantify the impacts that invasive species can have on native ecosystems and hence, attempt to inform management decisions (Levine *et al.* 2003; Thiele *et al.* 2010; Vila *et al.* 2011). Many frameworks rely on invasion impact metrics such as a) effects on species diversity, b) effects on geochemical cycles and c) effects on disturbance regimes. Documenting more than one metric type is generally difficult (time-consuming and costly), so many studies rely on determining impacts based on one or few metrics (Barney *et al.* 2013). The use of few response variables, however, has led to outputs from these frameworks giving misleading information on the magnitude and direction of impact. (Parker *et al.* 1999; Ricciardi 2003; Ricciardi & Cohen 2007; Thiele *et al.* 2010; Thomsen *et al.* 2011). It is not just the number of metrics used that can affect these results, but also the type of metric used (Hulme *et al.* 2013a; Pysek *et al.* 2012).

Parker *et al.* (1999) suggest a mathematical framework that gives a quantative measure of impact by encompassing the range, invader abundance and per capita or per biomass effect of the invasive species. However, as in other models, this model encompasses only one response variable and has not been widely accepted. To date, 75% of studies have examined fewer than three impact metrics when quantifying invasion, and less than 1% have used more than five (Hulme *et al.* 2014). This lack of a solid and applicable framework that encompasses multiple impact metrics has led to many management decisions being based on observational and anecdotal data (Byers *et al.* 2002). An example of this is Kudzu (*Pueraria Montana*) described by Barney *et al.* (2013) as ‘the poster child for invasive species’; however, even for this well-known and widespread invader, there is a lack of quantitative ecological impact data (Barney *et al.* 2013).

Of the existing frameworks, the most common factors incorporated are range, abundance, per capita effect and recipient community composition (Parker *et al.* 1999; Ricciardi 2003; Thiele *et al.* 2010). Traits of species are often used to infer a species functional role in a system (Rejmanek & Richardson 1996). Much of the research on species traits has been focused on characters that determine invasiveness rather than impact (Pysek *et al.* 2012). Thomsen *et al.* (2011) suggest that it is better to include attributes of the invader and resident biota with resource levels and abiotic conditions in order to establish invasive species impacts. Using species traits to predict potential for invasion and impact has become a popular way of informing management (Goodwin *et al.* 1999; Rejmanek & Richardson 1996).

In order to reduce uncertainty response variables should be chosen to suit the hypothesis being tested and should encompass multiple metrics (Barney *et al.* 2013). Barney *et al.* (2013) suggest a quantitative mathematical framework that encompasses multiple impact metrics into a single element. These different levels of metrics include individual (trait), community (existing), structure (tree or herb), biogeochemical (nutrients), and ecosystem (disturbance etc.). Within each of these levels, multiple impact metrics exist that can be quantified in this framework. Although Barney *et al.* (2013) have been criticised for their framework not being realistic or applicable in the field (Hulme *et al.* 2014), the benefits of using multiple metrics in analysis of impacts are echoed through multiple studies (Hulme *et al.* 2013a; Magee *et al.* 2010; Thomsen *et al.* 2011).

Impact assessment for management prioritisation

Large amounts of time, money and resources are put in to the eradication and control of exotic plant species (Hulme 2012). In Australia, $4 billion is spent annually on the control of weeds, with the annual cost for controlling a single species being as much as $500K (Martin 2003). Without reliable impact assessments being undertaken that encompass multiple response variables, conservation and land managers are at risk of targeting species or ecosystems of low risk rather than those of highest concern (Davis *et al.* 2011; Hulme *et al.* 2013a). Weed risk assessments for many introduced species are undertaken and used to inform management; however, these risk assessments often do no incorporate impacts, and focus on traits of the invader to determine 'invasiveness' (Pheloung *et al.* 1999). The NSW weed impact assessment does incorporate impact, but the measures do not necessarily use quantifiable data, and many of the questions are subjective and based on visual information that can often be misleading.

In the past, managers have targeted species of low environmental concern due to a lack of reliable information on species impacts (Hejda & Pysek 2006; Meffin *et al.* 2010). This inefficient use of time and resources emphasizes the need for impact assessments to be undertaken in a way that can inform management decisions (Hulme *et al.* 2013b). In order to move the focus of research to invasive impacts that inform management, Hulme *et al.* (2013b) suggest a) focusing on quantifying the distribution and local abundance of alien species, b) quantitative assessments of impacts should target the most widespread and abundant taxa and studies should be representative samples of a species' wider distribution and c) studies should examine biodiversity and ecosystem impacts that are of greatest concern to the integrity and value of the area in question.

Current Study – Alpine ecosystems

The Australian Alps cover an area of 5,200km^2, from Victoria to New South Wales, covering just 0.15% of Australia's mainland (Costin *et al.* 1979). The Australian Alps are a multi-use landscape of cultural, biological and hydrological significance (Murphy & Timbal 2008). The heritage-listed region is one of 11 Australian centres of plant diversity and one of the world's 187 biodiversity hotspots (Thorsell 2003). Further, the water flowing from the Alpine region is of national economic importance throughout southeast Australia (Murphy & Timbal 2008). Already experiencing reduced snow cover, increased temperatures and elevated CO2, the Australian Alps have been identified by the IPCC as critically vulnerable to climate change (IPCC 2007; Murphy & Timbal 2008).

Alpine ecosystems have been rated the least threatened by invasive species in Australia (Humphries *et al.* 1991). Compared to lowland, high-elevation ecosystems are thought to be more resilient to plant invasion, most likely due to the climatic conditions and low human populations (Pauchard *et al.* 2009). However, there has been an increase in the number of exotic species invading the Australian Alps since land use by non-indigenous people began 170years ago (Johnstone & Pickering 2001). In a review of the invasive species in he Australian Alps, McDougall *et al.* (2005) found there to be 128 established invasive species in the treeless areas alone. Many of these invading species are associated with disturbance, with roadside habitats and resort surroundings being particularly susceptible to invasion (Johnstone & Johnstone 2004; Johnstone & Pickering 2001; McDougall *et al.* 2005). Roads and road maintenance are the most common ways in which exotic species spread and succeed as the roadside soil composition is altered (Johnstone & Johnstone 2004). With an increase in disturbance to many areas through tourism, there is thought to be an inevitable increase in the spread and occurrence of exotic species into the future (Godfree *et al.* 2004; Johnstone & Johnstone 2004; Johnstone & Pickering 2001; Pauchard *et al.* 2009).

Studies undertaken on invasive species in the Australian Alps has been limited (Pauchard *et al.* 2009). There is little knowledge of the impacts many of these invasives have, or may have in the future, on the recipient alpine and subalpine communities (Johnstone & Pickering 2001; Pauchard *et al.* 2009). Due to this lack of knowledge, management often resort to speculation when making decisions (Johnstone & Pickering 2001). Various Hawkweed species (*Hieracium* spp.*)* are an example of this management. Hawkweed is found as a weed in New Zealand and causes native species decline and total ecosystem changes to the native communities it resides (Makepeace 1985; Makepeace *et al.* 1985; McIntosh *et al.* 1995; McIntosh & Allen 1993). In the 1990s hawkweed was found in the Australian Alps; the presence of this species has lead managers to expend considerable time and resources on seasonal surveys, mapping and herbicide spraying in an attempt to eradicate this species from the Australian Alps without any evidence of impact (Hauser & McCarthy 2009; WIlliams & Holland 2007). Researchers are continuing to develop new methods of surveillance (Hauser & McCarthy 2009), when perhaps this time would be better spent testing for an impact, or eradicating more serious threats to the alpine flora.

Current study - Leucanthemum vulgare

One potentially damaging invader in the Australian Alps is the introduced daisy *Leucanthemum vulgare.* Lam*,* commonly known as the Ox-eye daisy. *Leucanthemum vulgare* is a species of European and Asian origin that has spread from its native range to many parts of the world including India, Canada, America and Australia (Khuroo *et al.* 2010). Originally introduced as an ornamental species for its attractive white flowers, *L. vulgare* has escaped cultivation and now creates dense patches in many natural ecosystems (Clements *et al.* 2004). It is most often seen in disturbed habitats such as roadsides, agricultural fields and abandoned farms, but has been documented quickly encroaching into wild habitats (Clements *et al.* 2004).

Leucanthemum vulgare is a perennial herb from the Asteraceae that develops white ray florets and yellow disc florets. It is known to reach heights of nearly 2 m, however it is more commonly found between 30-90 cm (Clements *et al.* 2004; Khuroo *et al.* 2010) and is known to successfully reproduce by prolific seed production, in which seeds are nearly all viable and reach reproductive age after one year (Clements *et al.* 2004). Spreading by rhizomes is also very common; this can be a more successful method of invasion as rhizomes coming from the adult plant can creep into intact systems avoiding reliance on successful seed germination. *Leucanthemum vulgare* is highly variable throughout different ecosystems and has been split into many different subspecies in different parts of the world based on variations in chromosome number, heads, leaves, stems and pollen size (Clements *et al.* 2004).

The suggested cycle of establishment for *L. vulgare* by Clements *et al.* (2004) begins with disturbance, allowing establishment of seedlings, the plants then mature, produce large amounts of seed and develop large dense stands. If the disturbance stops then these populations can be subdued by the proliferation of grasses. In populations where grazing by cattle occurs, *L. vulgare* can form homogeneous stands as they are actively avoided by grazers (Mitch 2000).

Leucanthemum vulgare has the ability to survive under a variety of climatic conditions, and although it is most abundant in moist climates, it has been found to be drought-tolerant and can survive the harsh conditions of alpine and subalpine terrain (Olson & Wallander 1999). It is also tolerant of light frosts during its growing season (Olson *et al.* 1997). Its high tolerance to a variety of conditions has been attributed to its success, it has been found to be most prolific on poorer soils, suggesting it has a competitive disadvantage on soils of high quality (Olson & Wallander 1999).

Impacts of *L. vulgare* are not well documented. It is thought to be highly detrimental to native species diversity due to its life history traits and its ability to form dense stands (Clements *et al.* 2004). In the Kashmir valley, India, these dense patches of *L. vulgare* (>70% cover) were found to be associated with a significant decrease in species diversity and evenness (Khuroo *et al.* 2010). In this field example it was found to increase the homogeneity of a site and potentially inhibit natural regeneration at the edge of the forest (Khuroo *et al.* 2010). In Montana, USA, it was found that roadsides were having the largest impact on the spread of invasive species such as *L. vulgare* (Birdsall *et al.* 2012). In an experiment done in it native range, *L. vulgare* was found to be highly resistant to invading species, and plots without *L. vulgare* had a significant increase in invasive species (Ruijven *et al.* 2003). This data suggests that *L. vulgare* is a strong competitor against invasives in its natives range, and may help explain why it is such a successful invader.

Aims of the study

The invasive daisy *Leucanthemum vulgare* is a relatively new species to the Australian highlands and its mode of invasion and impacts on Australian flora have not been assessed. Very little is known about this species in all of its invading ranges, with only one published study attempting to assess its impacts with the use of one impact metric (Khuroo *et al.*). Many fact sheets and studies allude to this daisy being of high impact in its recipient range, however this assumption is based on life history traits and visual assessment with no empirical evidence (Birdsall *et al.* 2012; Clements *et al.* 2004; Lass & Callihan 1997; Mitch 2000; Olson & Wallander 1999; Olson *et al.* 1997). This daisy occurs in dense stands throughout the highland of Victoria and New South Wales. In the subalpine zone of Mt Hotham, Victoria large patches are obvious when flowering begins as it blankets fields and forest openings with carpets of white (Figure 1). Eradication programs have been put in place to try and stop the spread of this species but as yet an impact assessment has not been done. With so few resources and funding for conservation available, focus should be set on species causing the most damage to natural systems.

Using these densely invaded sites of *L. vulgare*, the current study aims to survey areas of high and low density, and determine whether this exotic species is associated with a lowering in native species diversity, or is simply an addition to an already diverse community. These aims were tested in three ways:

1. A comparative field study that considered several measures of impact (species density, species richness, community composition and community structure) between patches where *L. vulgare* was very common, compared to similar patches where it was much less common. This included a trait-based analysis that compared trait composition and diversity between these patches using Grime's CSR plant strategy scheme.
2. A glasshouse pot experiment to determine if invasive daisy species, including *L. vulgare*, were less affected by root competition with the dominant grass *Poa sieberiana* than were native daisy species.
3. A trait based analysis that compared function types of native and invasive daisy species from Mt Hotham, including *L. vulgare*, using Grime's CSR plant strategy scheme.

Figure 1. (a) Close up of *L. vulgare* flower head. (b) Dense patch of *L. vulgare* at the grassland site. (c) Grassland site invaded by *L. vulgare*. (d) Open woodland site invaded by *L. vulgare*

METHODS

METHODS – Comparative field study

Study Area

This study was located at Mt Hotham in the Australian Alps region in North Eastern Victoria, approximately 320 km from Melbourne. Most of the Mt Hotham area is covered and protected by the Alpine National Park. The Victorian part of the Australian Alps is a wide spread mountain range covering nearly 520,000 hectares that reaches elevations of nearly 2,000 meters. Mt Hotham itself reaches to 1,862m; the National Park encompasses both alpine and subalpine ecosystems and receives heavy snowfall throughout the winter months. This region's climate is specific to elevations above 1750m, with low mean monthly maximum temperatures (<18°) and high annual precipitation ranging from 1600-1800mm, depending on elevation (Bureau of Meteorology, unpubl. Data). Alpine humus soils are usually associated with this kind of climate at well-drained sites. This soil type is rich in organic matter in the deep top layer, high in porosity and low in nutrients (Rowe 1967).

The Victorian highlands have a long history of grazing by sheep and cattle, and most areas have been grazed since the mid1800s (Lawrence 1999). Feral animals such as Rabbits, Foxes, Dingoes, Deer and Horses have also populated the high lands since the 1800's and are equally as damaging to native populations (Parks Vic 2010). These kinds of populations and actions have been found to significantly alter native species composition (Wearne & Morgan 2001).

The sites surveyed were located below the tree line in the subalpine zone (Figure 2). The first site was a grassland on the road to the Mt Hotham airport, at an elevation of 1300m. Dense patches of *L. vulgare* were found on hillsides approaching the airport, particularly in the grassland site chosen. At this altitude air temperatures are warmer and precipitation is lower than higher up the mountain. These subalpine grasslands persist at elevations between 1200-1600m, in areas subject to high frost due to topographic depressions that hold cold air from the night (Moore & William 1976). This site is thought to have been subject to grazing in the recent past and would be considered highly disturbed due to the high number of exotic species present. The second site surveyed was higher up the mountain at an elevation of 1460 m near the old Brandy Creek Mine. Approximately 300 m down the track and 50 m into the woodland dense patches of *L. vulgare* were found on a plateau and sampled. This site is open woodland on the edge of the national park, and also considered highly disturbed with a large number of exotic species sampled. The close proximity to the pre-existing mine suggests potential past disturbance from mining and grazing, as well as likely disturbance from feral samba deer that were seen during sampling.

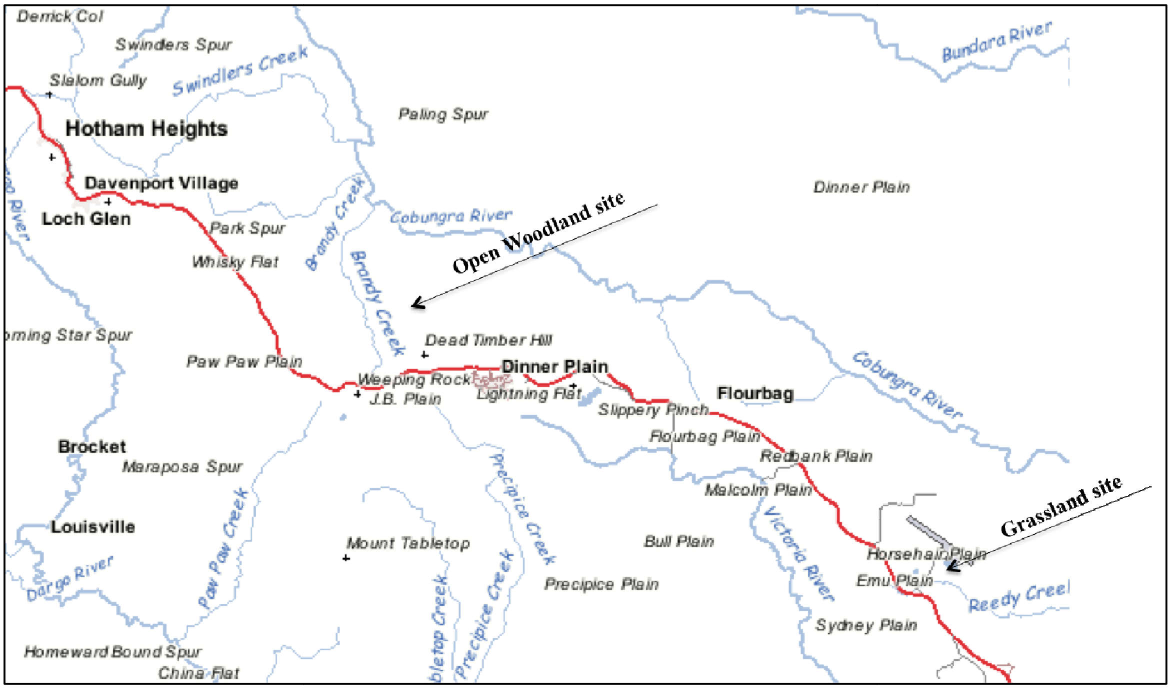


Figure 2. Map of Mt Hotham showing the two study sites. The Grassland (G) site on the road to the Hotham airport, and the Open Woodland (W) site off the track to the Brandy Creek Mine between Dinner Plain and Hotham Heights. Maps taken from Biodiversity Interactive Maps v3.2 (Department of Environment and Primary Industries, 2014).

Approach to sampling

The vegetation at each site was heterogeneous and varied over the scale of tens of meters. For example, areas of the grassland at the Airport turnoff were variously dominated by the grasses *Poa costiniana*, *Poa sieberiana* and *Themeda triandra*, while at the open woodland site *Poa hothamensis, Poa helmsii* and *Poa costiniana* dominated in separate areas. Within these patches, there was wide variation in the local density of *L. vulgare*. A stratified sampling design was used, in which areas of otherwise homogeneous vegetation were first located within each site, and within these areas, adjacent patches of high and low density *L. vulgare* could be sampled. Six High/Low pairs were sampled, three at each of the grassland and open woodland sites. A pair consisted of two parallel transects, each 15 m long and several meters apart. Along each transect there were 100 contiguous 15 cm x 15 cm quadrats. The 'High' *L. vulgare* transects had significantly greater incidence and stem density than did their 'Low' transect pair for the three grassland (G1: $t = 2.874$, $p<0.05$, G2: $t = -3.379$, $p<0.001$, G3: $t = 10.134$, $p<0.001$) and open woodland (W1: $t = -9.152$, $p<0.001$, W2: $t = -7.724$, $p<0.001$, W3: $t = -6.852$, $p<0.001$) pairs (Table 1). Sampling was completed over a four-week period in January 2014. Species occurrence (native and invasive) was recorded in each 15 cm x15 cm quadrat on every transect (n=1200 quadrats). Soil depth in each quadrat was measured with a steel rod, and soil moisture was measured in the grassland quadrats only.

Table 1. Differences in the incidence and stem numbers of *Leucanthemum vulgare* between transect pairs, between High and Low density transects. Incidence is the percentage of 100 15 cm x 15 cm contiguous quadrats in which *L. vulgare* was recorded. Density is the mean number (n=100) of flowering stems per 15 cm x 15 cm quadrat with standard errors.

	HIGH		**LOW**	
Transect Pair	**Incidence (%)**	**Density (#/quadrat)**	**Incidence (%)**	**Density (#/quadrat)**
Grassland (G1)	71	2.38 ± 0.313	58	1.33 ± 0.184
Grassland (G2)	71	1.03 ± 0.187	11	.26 ± 0.131
Grassland (G3)	81	4.00 ± 0.371	16	.18 ± 0.069
Open Woodland (W1)	96	2.46 ± 0.225	62	.26 ± 0.084
Open Woodland (W2)	99	2.89 ± 0.316	54	.38 ± 0.078
Open Woodland (W3)	90	1.64 ± 0.222	17	.10 ± 0.036

Approach to analysis - replicates

Because of the obvious differences in vegetation within and between the grassland and woodland sites, transects were not used as replicates in analyses. Instead, quadrats within transects were replicates and consistent differences in a range of response variables between the High and Low transects within pairs were considered in order to assess potential impact. Thus, the data for each pair of transects is represented separately.

Response Variables

Data derived from the quadrats arranged along transects were used to produce several response variables that could be compared between High and Low *L. vulgare* patches, using both univariate and multivariate analyses. In univariate tests, one-tailed tests were used because of the prior expectation that *L. vulgare* should lower species density. As the supposed driver of any differences between High/Low pairs, *L. vulgare* was omitted from the datasets for each pair.

Species density is the number of species per unit area (15 cm x 15 cm quadrat). Mean species density was compared between paired High and Low *L. vulgare* transects using t-tests.

Species richness is different to species density, in that it is a measure of the total number of species at a site (Gotelli & Colwell 2001). Producing rarefaction curves develops species richness estimates. This method accounts for the under sampling bias that many studies face, as well as estimating asymptotic species richness (Gotelli & Colwell 2011). Rarefaction curves were produced using the S(est) mean, upper 95% confidence interval and lower 95% confidence interval data produced from the EstimateS program (Colwell 2013) for each transect. This data was then plotted in a line graph for each pair. Species richness is judged to differ significantly between transects if the accumulation 'envelopes' do not overlap – that is, if the lower 95% CI of one transect does not overlap the upper 95% CI of the other transect.

Species composition is tested using Bray-Curtis dissimilarity matrices with incidence data, which were then used to construct ordinations and perform ANOSIMs. Environmental vectors were added to determine if soil depth was important in explaining any differences between the vegetation communities on High and Low transects. They were not, and are not reported on further in the analyses. These analyses were all performed using PRIMER 6.1.6.

Following significant ANOSIM analyses, SIMPER analyses were performed for each High/Low pair to determine which species contributed the most to observed community differences. Information from the Simper outputs was used to determine whether the most highly contributing species were invasive or native. This was done by classifying each species as invasive or native and developing a scatter plot with the percent contribution to the difference of these categories plotted against the percent of the total species that category contributed to. In each of the six pairs native and invasive species were plotted. A one to one line was inserted and any points lying on the line will contribute evenly to the x and y-axis, points above the line contribute more than expected to the difference, points below the line contribute less than expected. Simper analysis was performed in PRIMER 6.1.6., with all following analysis performed in excel.

The data using the individual transects from the simper output was then used to develop scatter plots of invasive and native incidence for each pair. These compared the contribution of natives and invasives in High and Low *L. vulgare* transects. The data points are represented by % abundance of each species in the High and Low transects of each pair and are categorised as invasive or native.

Community structure was examined within each pair by using checkerboard distributions developed by Diamond (1975). The C-score statistic uses the average number of checkerboard units found for each species pair in a presence-absence matrix and provides a measure of community organization by testing distributions for non-randomness (Stone & Roberts 1990). Null distributions were developed from 3000 shuffled matrices using EcoSim to develop the C-scores. If the resulting score is higher than expected by the null distribution, this is used as evidence for lowering of species co-occurrence and vice-versa (Sanders *et al.* 2003; Stone & Roberts 1990). To allow for comparisons across sites the standardized effect size (SES) was used (Sanders *et al.* 2003). The SES measures the number of standard deviations that the observed index is above or below the mean index of the simulated communities. Community organization was measured (SES of co-occurrence tests) across each pair to examine differences in structure with respect to co-occurrence in transects of High or Low *L. vulgare* density.

Plant functional types. All species recorded in the 12 transects were scored for their functional traits according to the CSR scheme developed by Grime (Grime 1974; Hodgson *et al.* 1999). Each species was collected and their traits measured. This data was then used to establish a CSR score for each species (Grime 1974; Hodgson *et al.* 1999). Traits were collected for all herbaceous species, as woody species have not yet been tested in the CSR scheme.

Selection of traits was done following the guidelines from the Hodgson *et al.* (1999) paper outlining the CSR point allocations, and collection of traits according to Cornelissen *et al.* (2003). Approximately ten mature, fully-grown individuals of each species were collected to allow for individual variation. Plant height was recorded in the field for each species by measuring height to majority of the leaves. These individuals were then removed from the soil, preserving enough of the roots to measure the root type or lateral spread (if applicable).

To collect leaf traits, these plants were rehydrated overnight in bags or cups filled with water, resulting in full leaf hydration by morning. A number of the largest and healthiest leaves were removed from each plant depending on average plant leaf size, (i.e. more small leaves, less larger leaves). Wet mass was recorded for these leaves on a four point balance; the leaves were then scanned and leaf area measured using software available on the website of the Unit of Comparative Plant Ecology, University of Sheffield U.K. (http://www.shef.ac.uk/%7Enuocpe/ucpe/leafarea. Html). The leaves were then dried for approximately 48 hours at 80°C and weighed to a precision of four decimal places. Leaf area, wet mass and dry mass were used to derive Dry Matter Content, Leaf Dry Weight and Specific Leaf Area.

Flowering period and flowering start were collected from herbarium records from around Mt Hotham that were found on the Australian Virtual Herbarium (http://avh.chah.org.au/). Only records from above 1000 m that were recorded at Mt Hotham, Falls Creek, Mt Bogong or Mt Buffalo were used to eliminate variation in flowering time due to elevation or location differences.

Trait Analysis

Allocating CSR Functional Types

Before any analysis of traits was done, each species was allocated a C, S and R score based on the seven traits outlined in Hodgson *et al.* (1999). This data was entered into the two (graminoid and non-graminoid) customized spreadsheets developed by Hodgson *et al.* (1999) to derive individual C, S and R scores for each species.

Trait diversity Inverse Simpson diversity index was used to determine the diversity of CSR functional types in each transect (${}^2D = 1/ \Sigma^{R}_{i=1} p^2_i$). In each quadrat, each species was assigned its CSR functional type, and the number of functional types present per quadrat was calculated. Average Inverse Simpson Diversity of the traits was computed for each transect by dividing incidence of each CSR type by the total number of types per quadrat squared.

Trait composition Bray-Curtis similarity coefficient was used to produce resemblance matrices for each pair. Non-metric multidimensional scaling (NMDS) ordinations were produced with these matrices to visualize any split in the composition of traits between the High and Low *L. vulgare* transect pairs. A subsequent ANOSIM was then produced to test whether there were significant differences in trait assemblage between High and Low *L. vulgare* pairs. Global R-values were used to accept or reject differences.

Mean CSR scores of High and Low density *L. vulgare* transects for each of the grassland and open woodland sites were developed using the same mean scores, but comparing High and Low transects of a site, rather than between pairs.

Ternary plots were developed using functional type means of each individual transect to visualize the position of each transect in CSR space. A ternary plot has three axes in the shape of a triangle, each axes runs from 0-1 so percentages need to be used. This allows data points to be plotted where the contribution of each axes meets. Each individual transect was plotted into this triangle with points marking the contribution of C, S and R values. This was then used to interpret differences in transect functional type means of High and Low transects in CSR space.

METHODS – Glasshouse pot experiment

The potential competitive ability of four alpine species was investigated in a glass house experiment in which the two invasive species, *Leucanthemum vulgare* and *Taraxacum officinale,* and the two native species *Craspedia aurantia and Senecio gunnii* were grown in competition with *Poa sieberiana*. These four daisy species were chosen because they are all found at Mt Hotham and seeds sourced from the Victorian alpine region were easy to acquire. *Poa sieberiana* was used as the standard competitor as it is the dominant grass species at the grassland site.

Seeds of *Taraxacum officinale, Craspedia aurantia* and *Senecio gunnii* were sown into germination trays using a seed raising mix to promote germination. *Leucanthemum vulgare* seedlings were transplanted from the grassland site because seeds did not successfully germinate. *Poa sieberiana* tussocks were collected from the grassland site and taken back to the University glasshouses where they were split and three small divisions were planted around the perimeter of each pot. The grasses were transplanted early to ensure a root mat had formed before the daisies were transplanted in to the pots. For each species, one seedling was transplanted into each of ten pots with competitive grass tussocks, and a further 10 pots were set up with single seedlings but without grass tussocks as the controls. Shoots of the *P. sieberiana* were tied back to minimize above ground competition (for light) so that root competition was the main factor.

Sacrificial plants of each species were used to estimate the initial biomass of each individual daisy that was used in the experiment, based on total leaf length at the time of transplant. Between 30 and 50 individuals per species were harvested, and total leaf length and number was recorded. The plants were then dried, and their shoots and roots weighed. This data yielded a relationship for each of the four species that could be used to determine initial biomass based on total leaf length.

When all the target species had been transplanted into the pots, they were left for a week to adjust to their new conditions. Initial total leaf length was measured after the first week, which was then used to estimate initial biomass. This experiment was run for eight weeks, at which time they were removed from the pots and separated from the grasses. Target shoots and roots were separated and a final measurement of the leaves was done before being dried and weighed for biomass.

Competition analysis

In analysing the data from this experiment two methods were used. T-tests were used to compare the total biomass differences between the competition and control. These were then separated into the contribution of root and shoot biomass changes to the total biomass differences for each species. In cases where variances were not equal, log10 transformations were calculated and reversed to ensure equal variance between all pairs.

METHODS – Plant functional types of native and invasive daisies

As well as traits being collected for all species recorded in the transects, 34 daisy species (including *L. vulgare*) were sampled from the Mt Hotham region between the altitudes of 1300m and 1862m. This data was used to compare the traits of *L. vulgare* to other daisies in the system. Traits of each species were collected as outlined above.

These 34 daisy species were scored for their CSR plant functional types, using the methods outlines above. These CSR scores were then transformed to percentage contribution of C S and R to each daisy species. This data was then plotted in CSR space using a ternary plot. This was used to test the difference in the functional types of *L. vulgare* compared to other daisies in the Mt Hotham area.

RESULTS

RESULTS - Comparative field study

Species Density

Species density differed significantly between the High and Low *L. vulgare* transects in four of the pairs, but there was no consistent direction of change. At the grassland site, species density was significantly lower on transects with high *L. vulgare* biomass in both pairs G1 (6.12 vs 8.79 species/225 cm^2, t= -8.5, p<0.001), and G2 (6.97 vs 9.31 species/225 cm2 (t = -8.4, p<0.001) (Figs. 3a & 3b, respectively). Conversely, species density was significantly higher with high *L. vulgare* biomass in both pairs W1 (7.32 vs 6.17 species/225 cm^2, t = 3.9, p<0.001) and W3 (7.16 vs 6.02 species/225 cm^2, t = 4.04, p<0.001) at the woodland site (Figs. 3d & 3f, respectively). Species density did not differ between the High and Low *L. vulgare* transects in pairs G3 (6.54 vs 6.14 species/225 cm^2 (t = 1.3, p = 0.104) and W2 (7.55 vs 7.32 species/225 cm^2, t = 0.8, p = 0.212)(Figs. 3c & 3e, respectively).

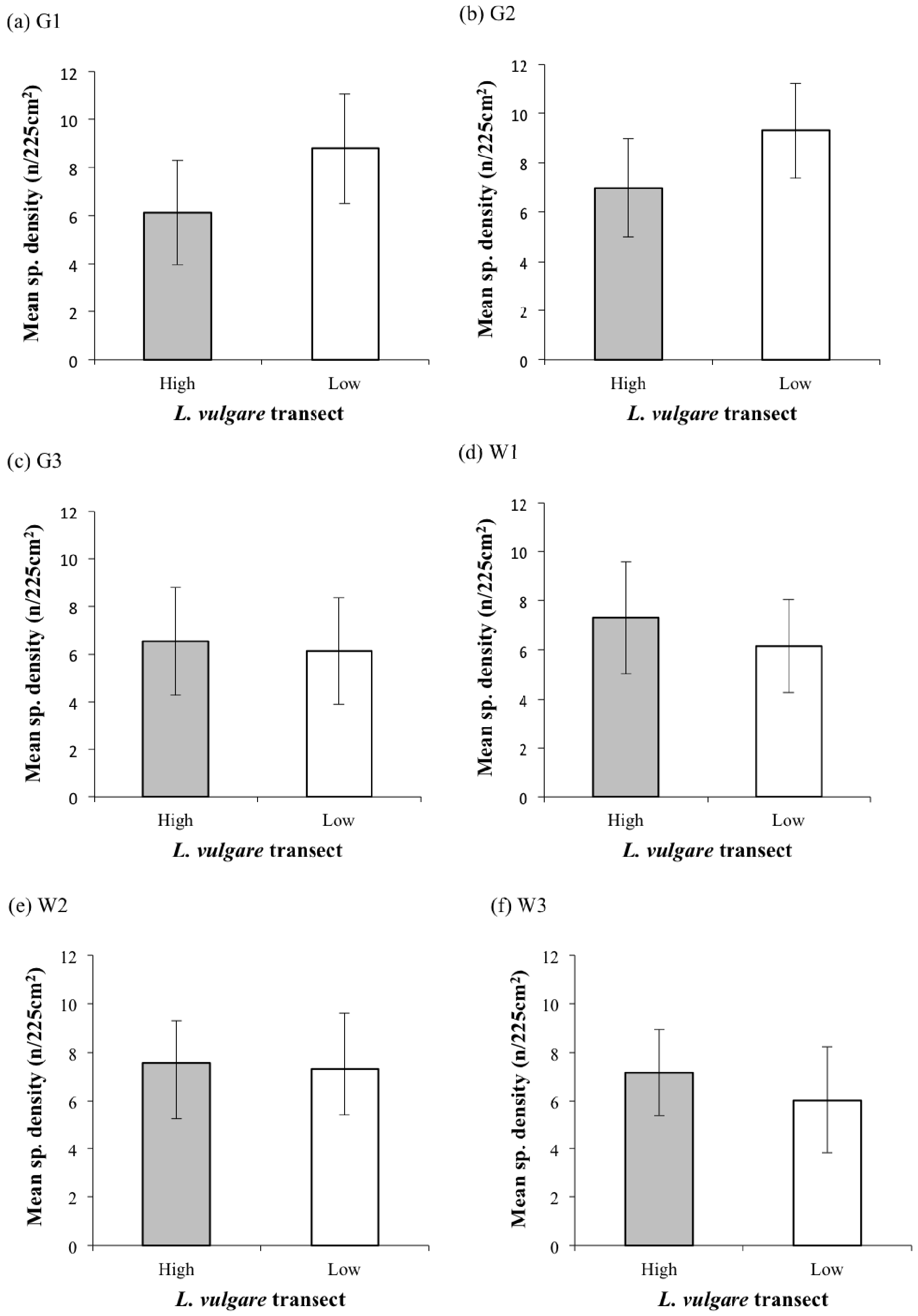
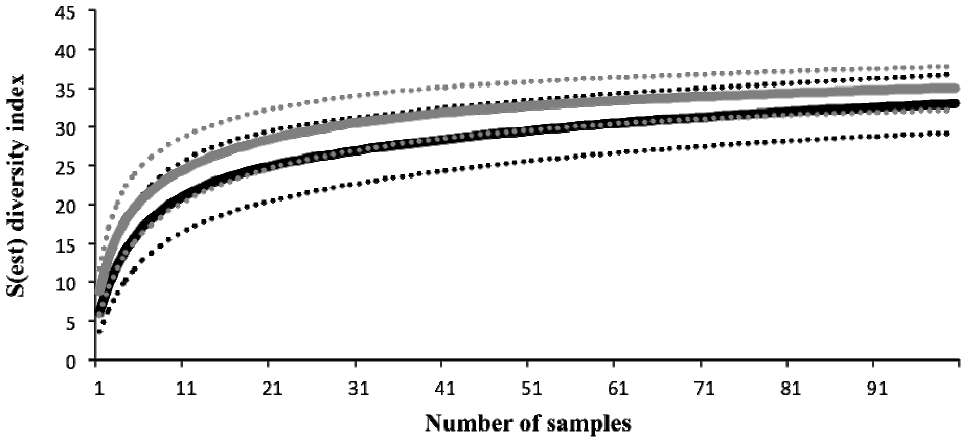


Figure 3. Difference in mean species density on High and Low biomass *L. vulgare* within paired transects. Density is the mean number (*n*=100) of species recorded per 15x15 cm quadrat. (a) G1, (b) G2, (c) G3, (d) W1, (e) W2 (f) W3. Error bars in this and all figures following are standard deviations.

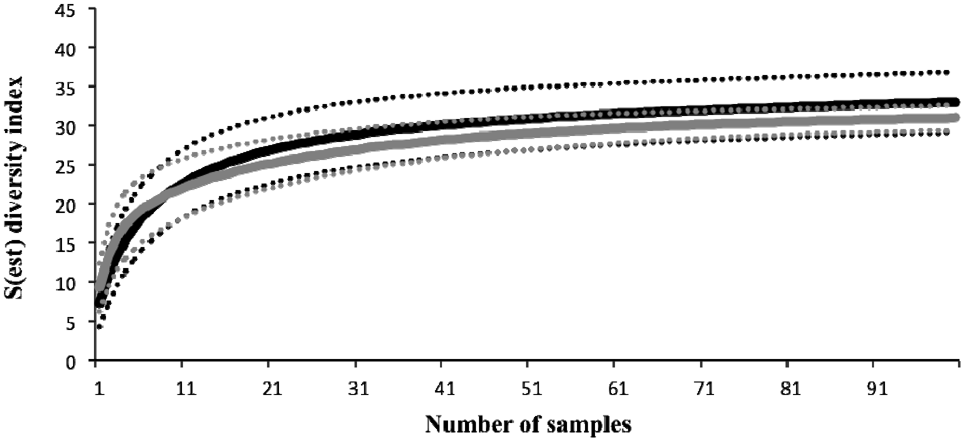
Species richness

In five of six transect pairs, the sample-based rarefaction curves overlapped for the High and Low biomass *L. vulgare* transects, indicating no difference in species richness between them (Figs. 4a-e). Species richness differed significantly on just one transect, W3, where richness was greatest on the Low *L. vulgare* transect (Fig. 4f).

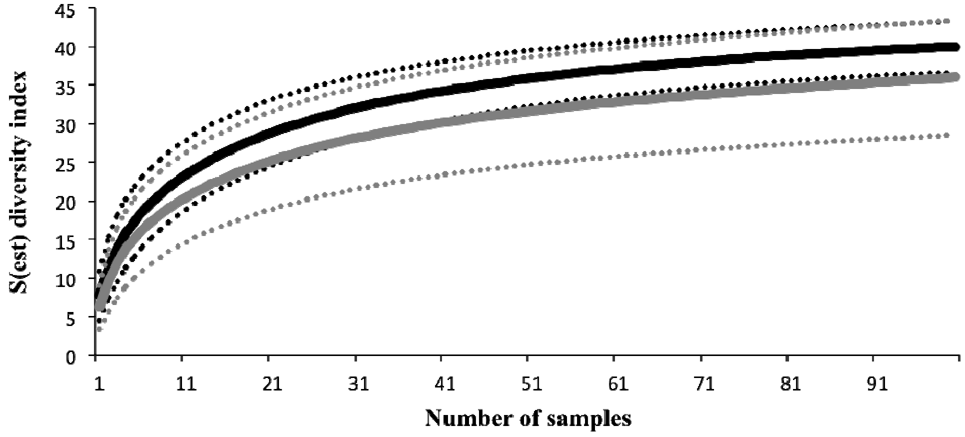
(a) G1


S(est) diversity index
45
40
35
30
25
20
15
10
5
0
1
11
21
31
41
51
61
71
81
91
Number of samples

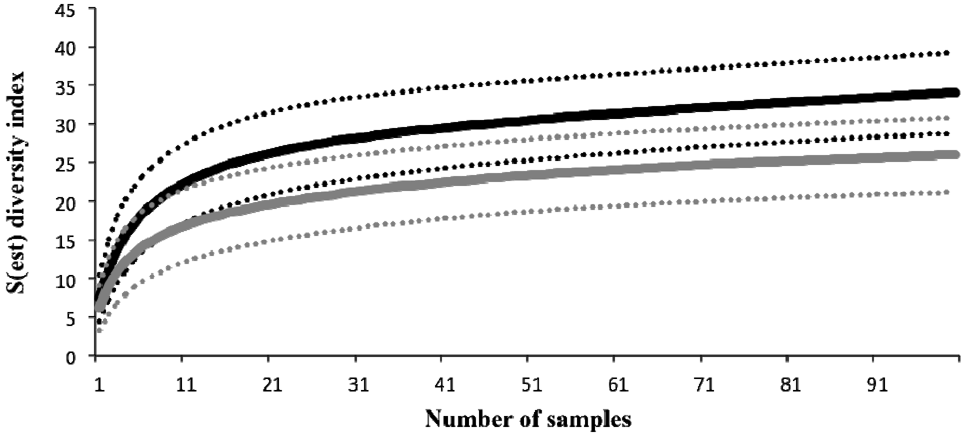
(b) G2


S(est) diversity index
45
40
35
30
25
20
15
10
5
0
1
11
21
31
41
51
61
71
81
91
Number of samples

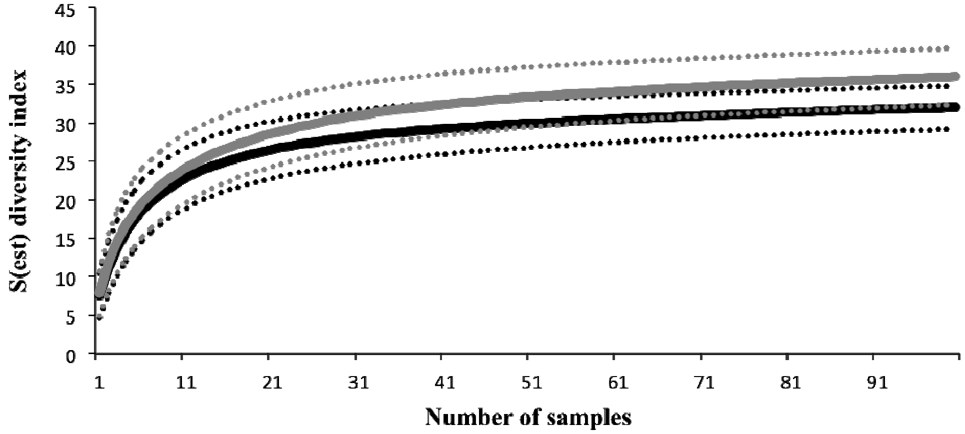
(c) G3


S(est) diversity index
45
40
35
30
25
20
15
10
5
0
1
11
21
31
41
51
61
71
81
91
Number of samples

(d) W1



(e) W2



(f) W3

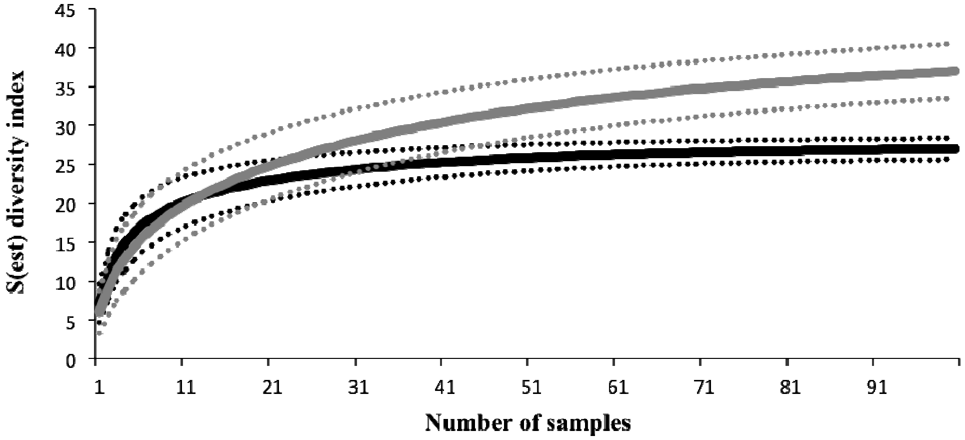


Figure 4. Rarefaction curves depicting species richness of (a) G1 (b) G2 (c) G3 (d) W1 (e) W2 (f) W3. In all six figures the black solid line represents the High biomass *L. vulgare* transect and the grey solid lines represents Low biomass transect. Broken lines indicate upper and lower 95% confidence intervals.

Species Composition

A comparison of the compositional differences between the High and Low *L. vulgare* transects using ANOSIM found each pair to be significantly different in both grassland and open woodland habitats (Global R for G1 = 0.481, $p<0.001$; G2 = 0.377, $p<0.001$; G3 = 0.379, $p<0.001$; W1 = 0.489, $p<0.001$; W2 = 0.299, $p<0.001$; W3 = 0.228, $p<0.001$). Non-metric multidimensional scaling (NMDS) ordinations were then produced and visual assessment of the ordinations found clustering of transects for all pairs (Fig. 5).

Invasive species were found to be contributing disproportionality to the difference in composition found in the NMDS ordinations (Fig. 6). The SIMPER analysis determined that although fewer invasive species were found in transects than natives, they contributed more to the difference due to the lower incidence of natives (Appendix III).

When each pair was tested individually for invasive and native abundance in High versus Low *L. vulgare* pairs, no consistent relationship was found (Fig. 7). G1 and G2 show invasives to be more highly abundant in the Low *L. vulgare* transects (Fig. 7a, b), while G3 and W1 suggest the exact opposite (Fig. 7c, d). W2 and W3 show no relationship linking High or Low *L. vulgare* transects with invasive or native species (Fig. 7e, f).

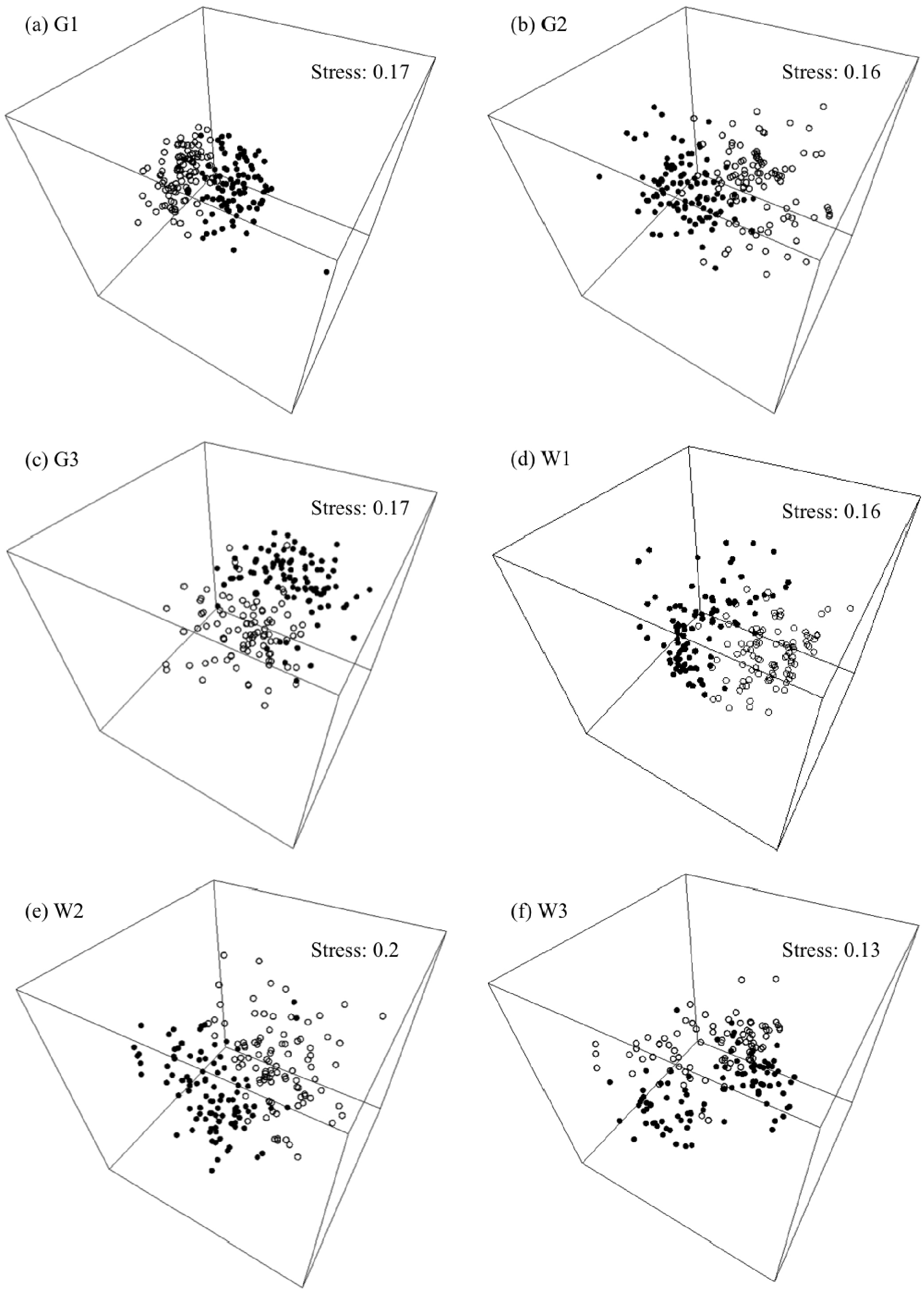


Figure 5. Three-dimensional NMDS Ordinations comparing composition within each pair using species incidence data. (a) G1 (b) G2 (c) G3 (d) W1 (e) W2 (f) W3. For figures (a-f) closed circles = High *L. vulgare* biomass transect, open circles = Low *L. vulgare* biomass transect.

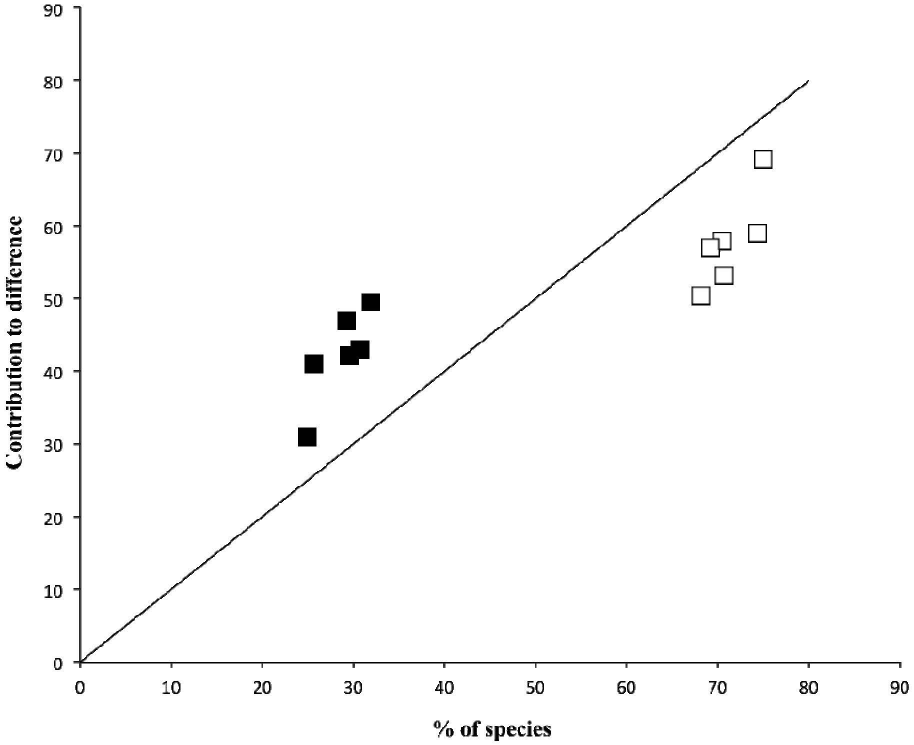


Figure 6. Contribution of invasives (closed squares) and natives (open squares) to the difference in composition found for each pair. Each data point represents the total contribution of native and invasive species to the difference for each pair. All six pairs of transects are plotted. The one to one line is placed through the center as a reference point for equal contribution.

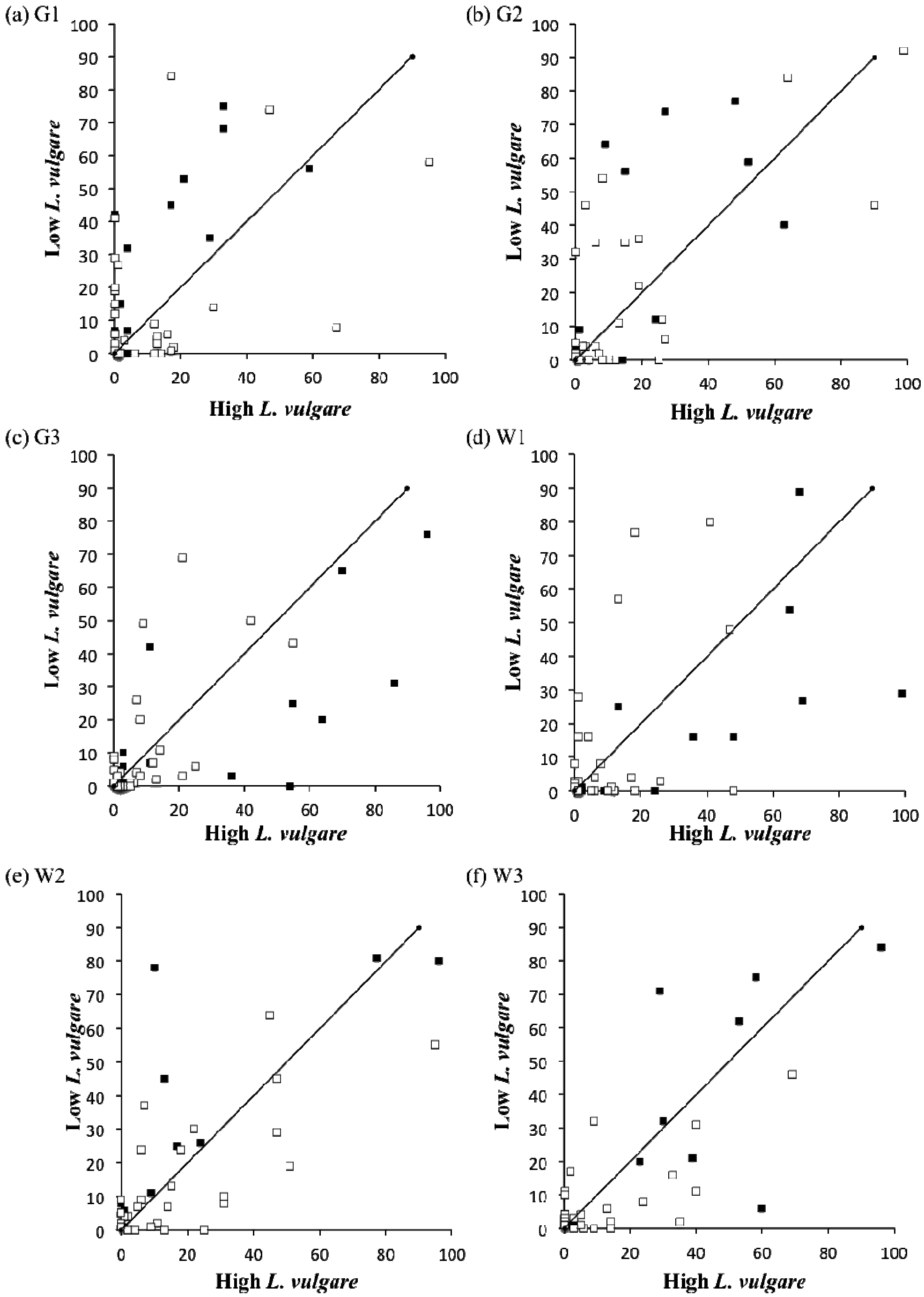


Figure 7. Comparisons of invasive (closed squares) and native (open squares) species in high and low *L. vulgare* transects. Each data point represents % incidence of each species in both High and Low *L. vulgare* transects for each pair. (a) G1 (b) G2 (c) G3 (d) W1 (e) W2 (f) W3.

Community structure

No consistent differences in community assembly were found across the high and low *L. vulgare* pairs in either the grassland or open woodland (Fig. 8). G1 and G2 were found to have relatively large shifts in SES to a more random community. G3 and W1 also shifted to a more random community however the change was smaller than G1 and G2. W2 and W3 have no notable shift in community structure from Low to High *L. vulgare* transects.

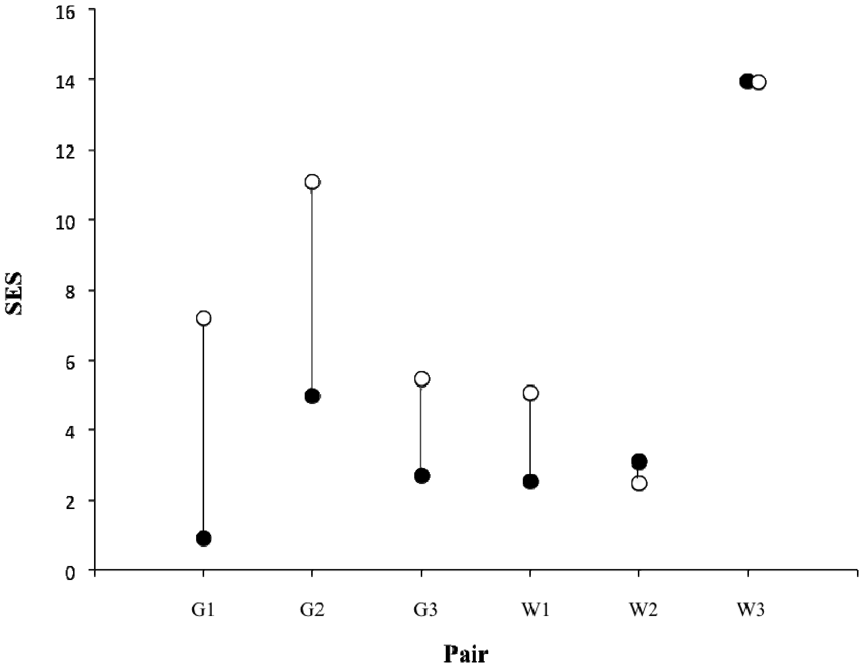


Figure 8. Standard effect size (SES) of co-occurrence patterns for each individual High *L. vulgare* transect (closed circles) and Low *L. vulgare* transect (open circles), linked to its pair for G1, G2, G3, W1, W2 and W3.

Functional type diversity

Functional trait diversity differed significantly between all of the High and low *L. vulgare* biomass transects, but there was no consistent direction of change. At the Grassland site, functional type diversity was higher for the Low *L. vulgare* transects in both pairs G1 (3.32 vs 5.51 traits/225 cm^2, t = -13.29, p<0.001), and G2 (3.8 vs 4.84 traits/225 cm^2, t = 7.15, p<0.001) (Fig. 9a). Conversely, functional type diversity was found to be higher for the High *L. vulgare* in pairs G3 (4.33 vs 3.88 traits/225 cm^2, t = 2.13, p<0.001) (Fig 9a), W1 (4.34 vs 3.15 traits/225 cm^2, t = -7.48, p<0.001), W2 (5.09 vs 3.92 traits/225 cm^2, t = -8.44, p<0.001) and W3 (5.04 vs 3.59 traits/225 cm^2, t = -8.14, p<0.001) (Fig 9b).

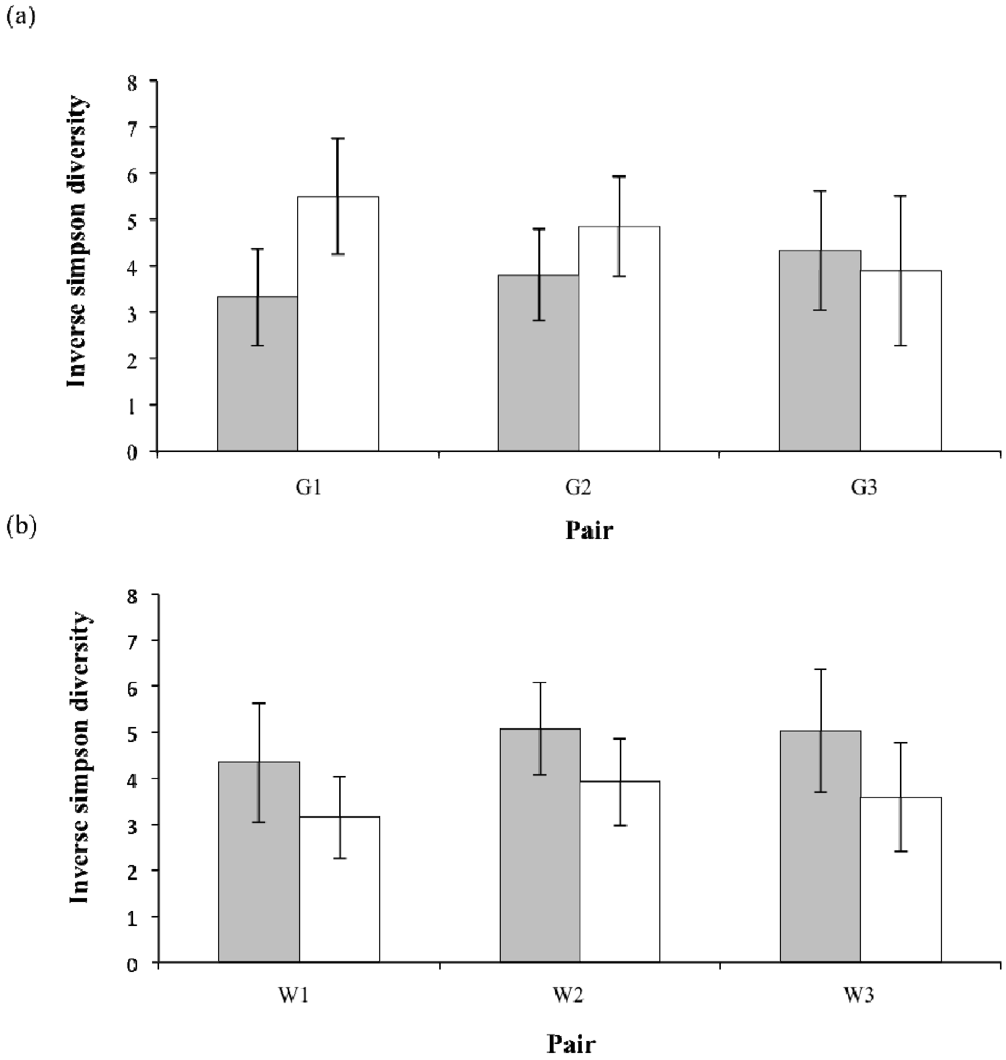


Figure 9. Trait diversity for pairs of each high (full column) and low (open column) *L. vulgare* transect for all six pairs. (a) Grassland site and (b) open woodland site. Error bars are standard deviations.

Functional type composition

A comparison of the compositional differences between the traits of the high and low *L. vulgare* transects using ANOSIM found each pair to be significantly different (Global R for G1 = 0.422, p<0.001; G2 = 0.251, p<0.001; G3 = 0.175, p<0.001; W1 = 0.194, p<0.001; W2 = 0.515, p<0.001; W3 = 0.283, p<0.001). Non-metric multidimensional scaling (NMDS) ordinations were then produced, visual assessment of ordinations found clustering of transects for all pairs, however not total separation of the transects as some overlapping occurs (Fig. 10).

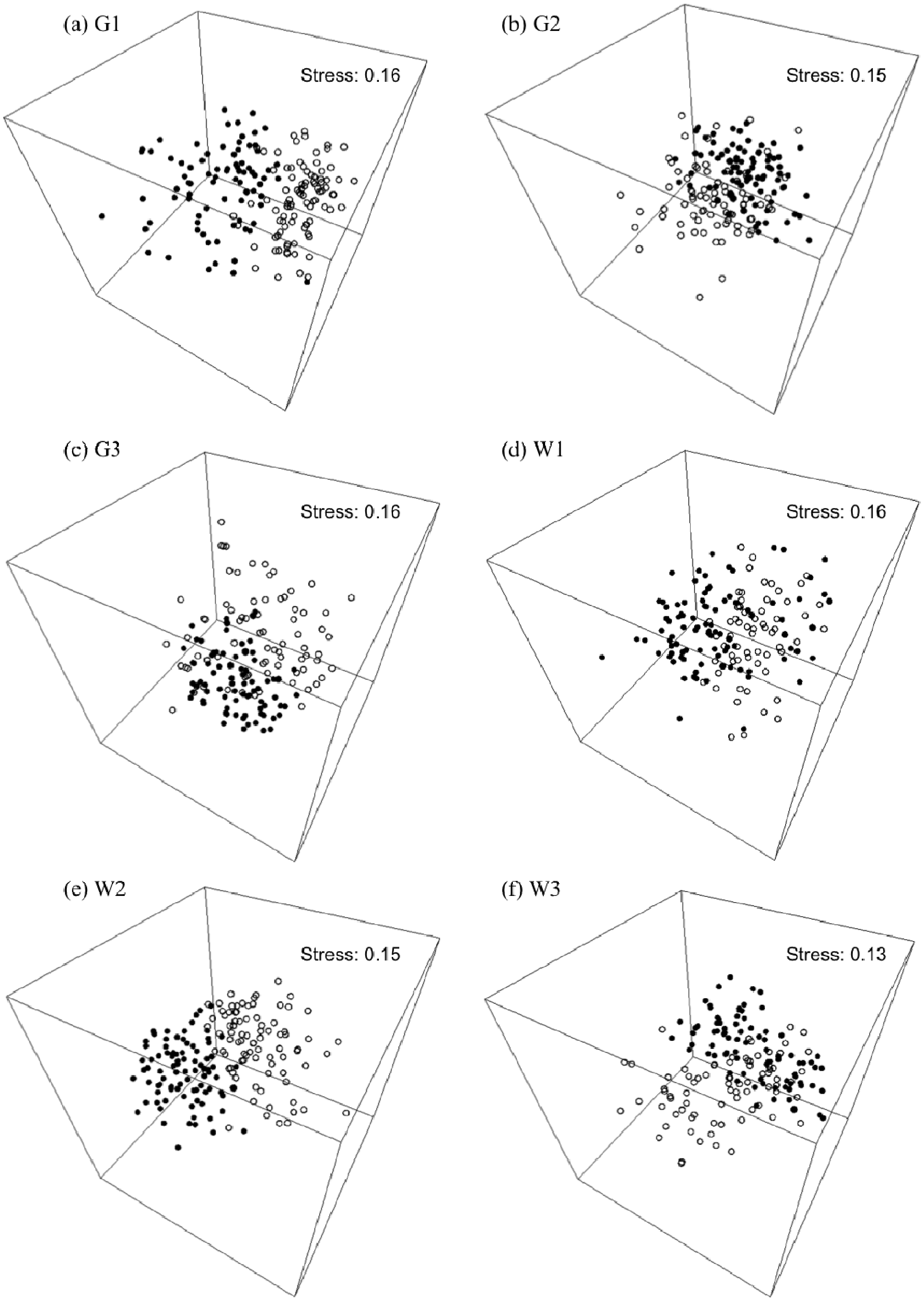


Figure 10. Three-dimensional NMDS ordinations of CSR composition based on incidence of traits in High (closed circle) and Low (open) *L. vulgare* transects. (a) G1 (b) G2 (c) G3 (d) W1 (e) W2 (f) W3.

Mean CSR

Differences between the mean C, S and R scores for high and low transects between the two sites found no consistent patterns of change (Fig. 11). For the grassland site, the C score was found to be higher in the high *L. vulgare* transect, the R score was found to be lower and S scores had no difference (Fig. 11a). In the open woodland site C scores were also found to be higher, S scores were lower and R scores higher in the high *L. vulgare* density transects (Fig. 11b).

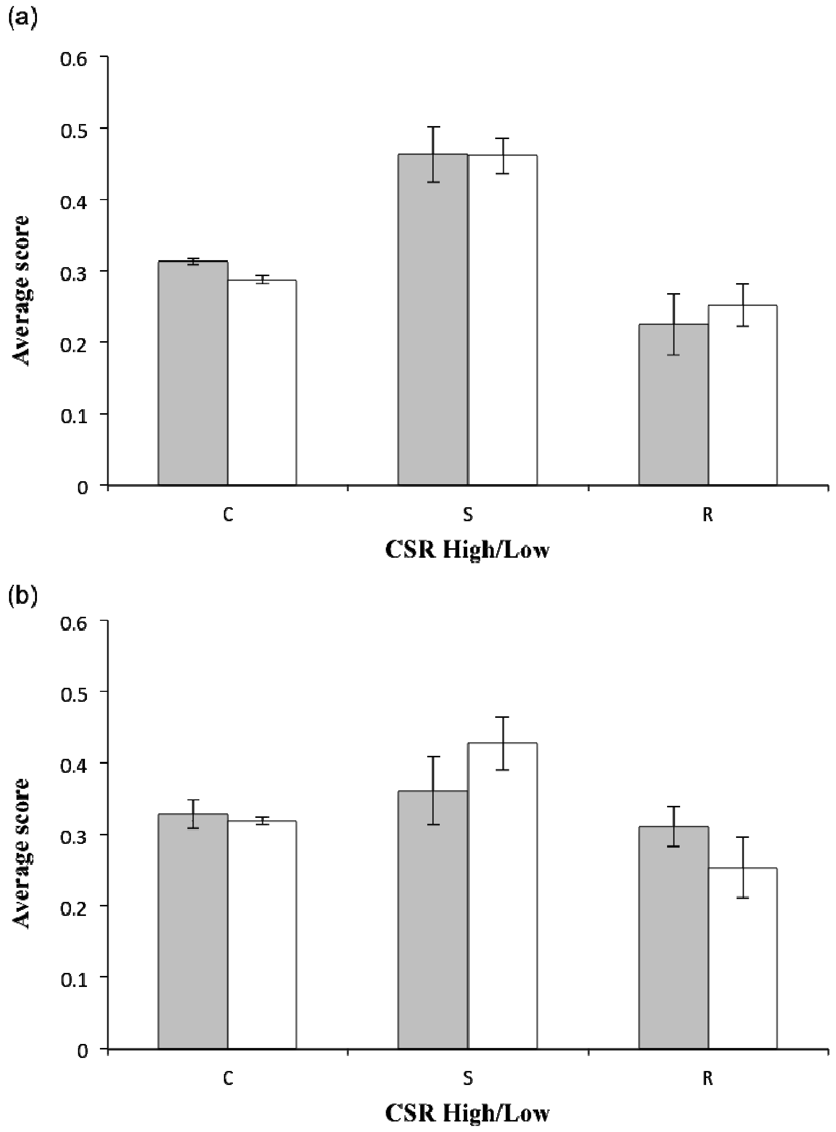


Figure 11. Mean C, S and R scores, for the High (closed column) and Low (open column) *L. vulgare* transects. (a) Grassland and (b) open woodland. Error bars are standard deviations.

Ternary diagrams

When the mean CSR scores for each transect was plotted in CSR space, the High and Low density *L. vulgare* transects show separation (Fig. 12). When looking at the distribution of mean transect CSR scores in the grassland, a separation of the High density *L. vulgare* transects can be seen as being higher in the C score and lower in the R score, with no separation of the S scores for high versus Low (Fig. 12). Separation of the High and Low *L. vulgare* density transects can also be seen for the open woodland site, showing high density transects to have lower S scores, and two of the three high transects to have higher C scores and lower R scores (Fig. 12).

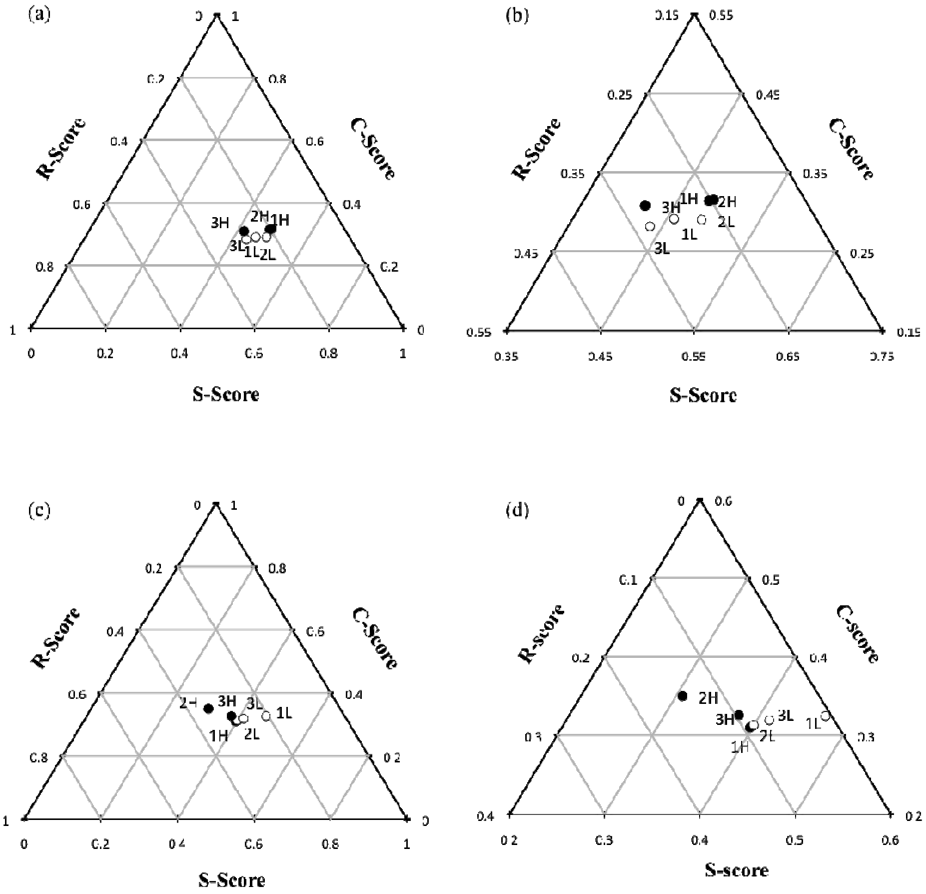


Figure 12. Ternary plots with the percentages of CS & R for each of the high (closed circles) and low (open circles) transects. (a) Grassland site transects with 0-100% contribution of each score on each axis, (b) grassland site zoomed in showing 40% of each axis. (c) Open woodland site transects with 0-100% contribution of each score on each axis, (d) open woodland site zoomed in showing 40% of each axis.

RESULTS – Glasshouse pot experiment

Total biomass

For all species, there was difference in estimated biomass between the treatments at the start of the experiment (Table 2), so all data was analysed using final, measured biomass data. All species experienced a significant decrease in total plant biomass (root and shoots) when grown with competition, *Leucanthemum vulgare* (1.97 vs 7.03, t = -7.6, p<0.001), *Taraxacum officinale* (1.9 vs 7.53, t = -10.3, p<0.001)*, Senecio gunnii* (4.2 vs 7.84, t = -2.6, p<0.001) and *Craspedia aurantia* (0.2 vs 0.85, t = -5.0, p<0.001) (Fig.14). The magnitude of the reduction in growth due to competition was similar for native species *Craspedia aurantia* (76% of control biomass), and the invasive species *Taraxacum officinale* (75%) and *L. vulgare* (72%). The negative effect due to competition was least for the other native species in the experiment, *Senecio gunnii* (47%). Allocation of biomass to shoots and roots was equally effected by competition, except for *T. officinale* where root biomass was more highly affected by the presence of *Poa sieberiana* (Fig. 15).

Table 2. Competition and control mean initial biomass (grams) ±SD for the four daisy species *Leucanthemum vulgare, Taraxacum officinale, Senecio gunnii* and *Craspedia aurantia.* P-value and t-stat show no significant difference in the means for each treatment (degrees of freedom = 18).

	Control	**Competition**	**t**	**P**
Leucanthemum vulgare	0.143 ± 0.104	0.133 ± 0.111	-0.193	0.424
Taraxacum officinale	0.085 ± 0.033	0.093 ± 0.035	0.494	0.313
Senecio gunnii	0.057 ± 0.058	0.046 ± 0.053	-0.438	0.333
Craspedia aurantia	0.019 ± 0.012	0.013 ± 0.005	-1.642	0.059

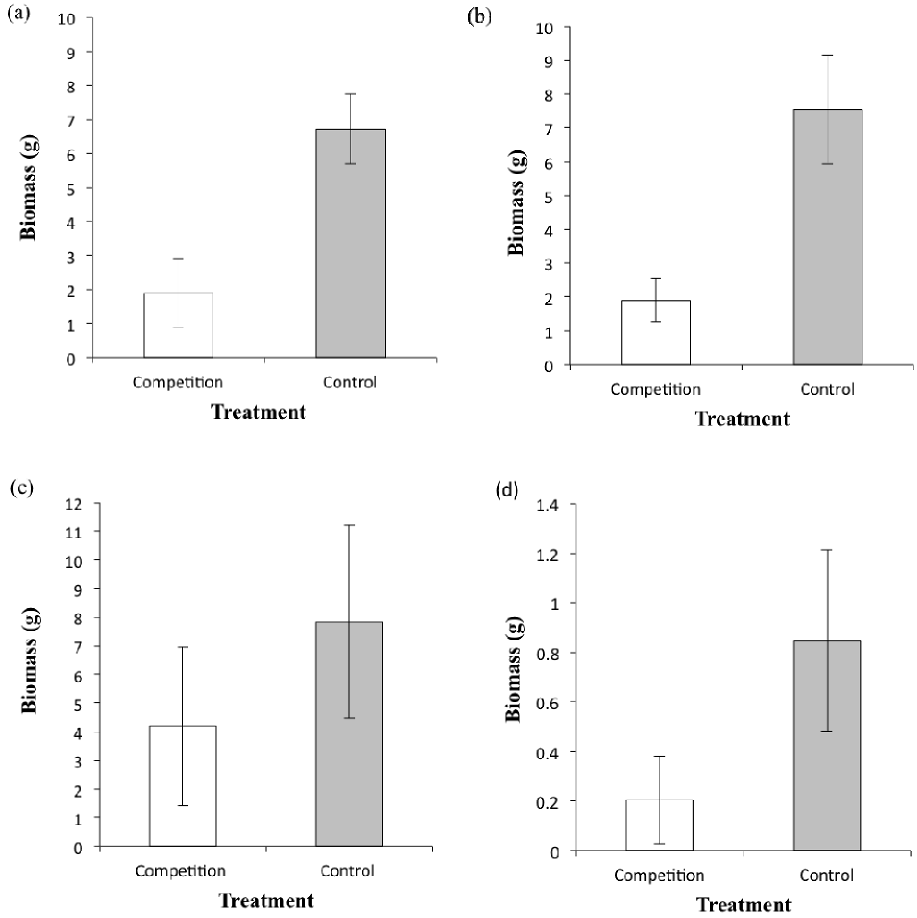


Figure 14. Total final biomass of the competition and control treatments for the four daisy species (a) *Leucanthemum vulgare*, (b) *Taraxacum officinale*, (c) *Senecio gunnii* and (d) *Craspedia aurantia*. Error bars as standard deviations.

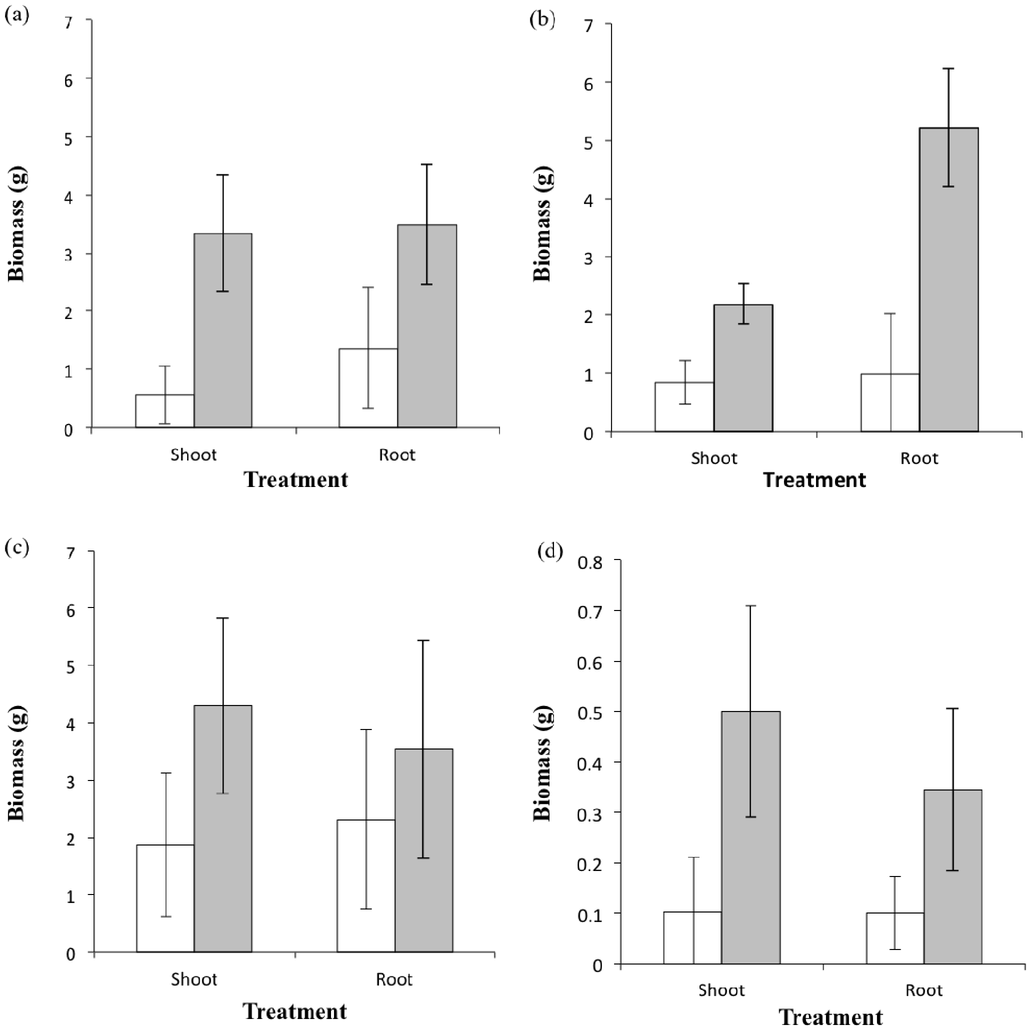


Figure 15. Final biomass of roots and shoots for the competition (open column) and control (closed column) treatments. (a) *Leucanthemum vulgare*, (b) *Taraxacum officinale*, (c) *Senecio gunnii* and (d) *Craspedia aurantia*. Error bars are standard deviations.

RESULTS – Plant functional types of native and invasive daisies

Ternary diagram

A wide spread of scores was found for the 34 alpine daisies in CSR space (Fig. 13). *Leucanthemum vulgare* placed as highly competitive in the C corner of the triangle along with the other well known invasives, *Achillea millefolium* and *Cirsium vulgare* (Fig. 13). The spread of exotic species vary in C and R scores, however all are found with a score of 0 for stress tolerance (S). This result is quite different to the spread of natives that are found to vary on all three axes, only being absent in extremities of C and R. A Cluster of native and invasive species with high R and low C and S scores is found. The opposite is seen with a cluster of native species found to be of high C and low R scores when S is higher.

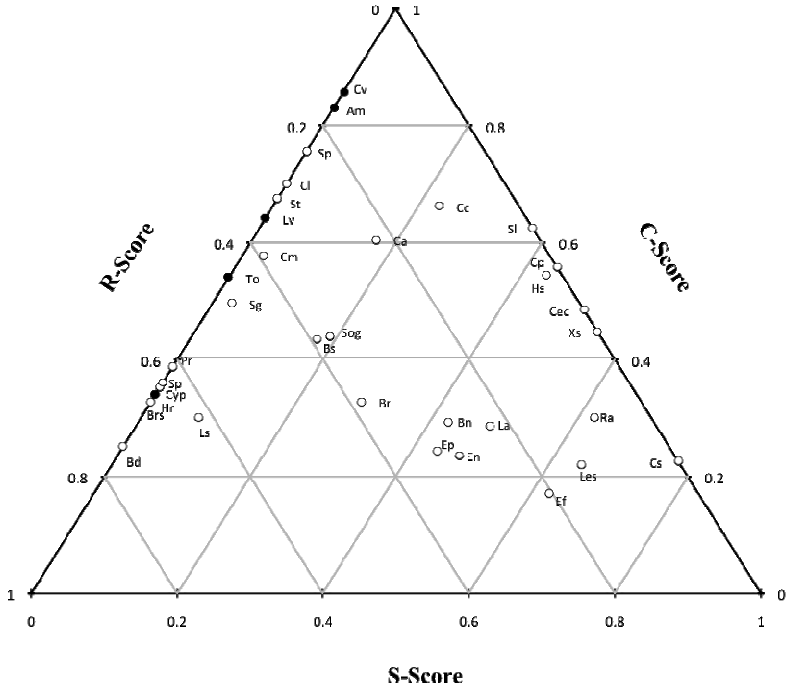


Figure 13. Ternary diagram with the CSR scores of 34 daisy species plotted. Coded as native species (open circles) and invasive species (closed circles). Abbreviations of each species are as follows, Cv = *Cirsium vulgare,* Am = *Achillea millefolium,* Sp = *Senecio pinnatifolius,* Cl = *Craspedia lamicola,* St = *Senecio tenuiflorus,* Cc = *Craspedia coolaminica*, Lv = *Leucanthemum vulgare,* Ca = *Craspedia aurantia.* Sl = *Senecio linearifolius,* Cm = *Craspedia maxgrayii,* To = *Taraxacum officinale*, Sg = *Senecio gunnii,* Sog = *Solenogyne gunnii*, Bs = *Bracteantha subundulata*, Cp = *Celmisia pugioniformis,* Hs = *Helichrysum scorpioides,* Cec = *Celmisia costiniana,* Xs = *Xerochrysum subundulatum,* Pr = *Podolepis robusta,* Sp = *Senecio pectinatus,* Cyp = *Cymbonotus preissianus,* Hr = *Hypochaeris radicata,* Brs = *Brachyscome spathulata,* Br = *Brachyscome rigidula,* Ls = *Lagenophora stipitata,* Bd = *Brachyscome decipiens,* Bn = *Brachyscome nivalis,* Ra = *Rhodanthe anthemoides,* La = *Leucochrysum albicans,* Ep = *Erigeron paludicola*, En = *Erigeron nitidus,* Cs = *Chrysocephalum semipapposum,* Les = *Leptorhynchos squamatus,* Ef = *Euchiton fordianus.*

DISCUSSION

Until relatively recently, the precautionary principle has been the primary tool for prioritizing weeds for management in protected areas – if a non-native species has spread well away from roadsides and other access points, and forms visually impressive populations, assume the worst in terms of impact and prioritise it for control. However, scarce resources demand evidenced-based decision making and resource allocation, and increasingly, there are calls to decouple the terms 'invasive' and 'impact' in favour of considering them independently (Davis *et al.* 2011; Ricciardi & Cohen 2007). Further, there is a need for a more sophisticated approach to quantifying impact, based on multiple measures that go beyond simple comparisons of variables like species density (Barney *et al.* 2013). This study used a comparative approach to investigate if *L. vulgare* is associated with altered species density, richness, composition and organization. Additionally, this study investigated changes to trait diversity and composition that may be associated with *L. vulgare*. Competitive ability was also tested experimentally, comparing native and invasive species to determine whether *L. vulgare* is a better competitor than other native and invasive daisy species found in the area. A trait comparison of other daisies existing at Mt Hotham was also completed looking for trait similarities between *L. vulgare* and the other daisies it may be co-existing with at a larger scale.

Comparative field study

Density vs richness

No consistent differences were found between species density and richness of species when comparing the High and Low *L. vulgare* transects. Significant differences in species density were found between some pairs of quadrats, but the highest densities were found on both High and Low transects. Further, when these data were rarefied, most of the differences disappeared and there was significant difference in species richness between the High and Low transect in just one pair, where richness was highest in the Low transect consistent with predictions for a high impact invader. Differences found in species density therefore do not always translate to differences in species richness.

In the cases where species density was found to be greater in the Low transects, *L. vulgare* may preempt space at the quadrat scale and drive down species density, but when this data is extrapolated to the transect scale all species can still co-exist. This explanation does not hold through the results as in some cases the Low transects were found to have lower species density than the High. This suggests that there must be other local drivers of species distribution and incidence unrelated to *L. vulgare* causing these differences.

The only transect pair that was found to have a significant difference using the rarefaction curves was W3. This pair was located close to a walking track which could have effected the results as walking tracks have been found to contribute to the spread of exotic species in natural areas (Pickering *et al.* 2003). As the High *L. vulgare* transect was slightly closer to the path, and a highly defined patch, these differences could be due to an increased exposure to disturbance and exotic species. Both transects in this pair were found to have high densities of invasive species in both the High and Low *L. vulgare* transects. The presence of tussock grasses in pair W1 could explain the lower species density in the Low *L. vulgare* transect. Much like the presence of dense stands of *L. vulgare,* the tussock grasses *Poa costiniana* and *Poa hothamensis* have the potential to take up the entire space of a quadrat, eliminating the chance for multiple species to exist together at that spatial scale.

Using rarefaction curves for species richness estimates is a more reliable measure of differences in biodiversity than estimates of species density when considering invasive weeds (Gotelli & Colwell 2001). Many weed impact assessments and studies of invasion use species density estimates as their measure of change due to exotic species invasion (Khuroo *et al.* 2010), however this method often results in an underestimation of the true richness of that area (Gotelli & Colwell 2001). McCabe & Gotelli (2000) tested this theory by looking at the density and richness of macroinvertebrates after disturbance compared to a control. They found a significant decline in the density of species after disturbance, however the reverse was found when looking at species richness with rarefaction.

Changes in composition

In every pair, there was a clear difference in species composition between the High and Low transects. In isolation of the other data on species density and richness, these differences *per se* could be interpreted as a consistent impact associated with L. vulgare. However, the SIMPER analyses suggest a more parsimonious explanation – with a few exceptions the other alien species at the sites contributed more to the overall dissimilarity between the High and Low transects than did the native species. It is likely that these species, including *Cerastium glomeratum*, *Holcus lanatus*, *Trifolium repens*, and *Anthoxanthum odoratum,* invaded the sites long before *L. vulgare* arrived, in which case it is possible that *L. vulgare* is simply a passenger (MacDougall & Turkington 2005) who's probability of invasion may be determined, among other things, by the presence of other alien species. Exactly how these other alien species may affect the establishment of *L. vulgare* is likely to be complex, because within transect pairs *L. vulgare* was most dense under conditions of both high and low invasion by other species.

Both the grassland and open woodland sites were highly invaded by multiple invasive species and showed signs of previous disturbance from grazing and close proximity to roads and tracks. Pair level analysis found invasives were not consistently contributing more than natives. Therefore invasives are contributing to compositional differences in both the High and Low *L. vulgare* transects, suggesting the presence of *L. vulgare* may not be the cause. These sites may contain exotic species that have been altering these communities for many years before the arrival of *L. vulgare*. The current spread of *L. vulgare* is thought to be from its ability to exclude other species; data from this study suggests its current spread has more to do with limitations of these clearly exotic-driven sites. *Leucanthemum vulgare* could be responding to other components of the environment that were not tested in this study such as nutrient availability, or lack of a competitively dominant species.

Although not a strict test of the passenger/driver theory, this data does give some insight into mechanisms that may be taking place at this site. MacDougall & Turkington (2005) reasoned that if a species is a driver than its removal would increase the native species diversity. If this removal did not increase diversity given a significant amount of time than other factors must be in play, such as fire suppression or disturbance, that lead to the decrease in diversity. HilleRisLambers *et al.* (2010) used a similar method, however instead of removal, they excluded disturbance and quantified the biomass of an exotic species with and without disturbance. These two methods provide a much more conclusive test of how exotic species are entering and surviving in their resident communities (HilleRisLambers *et al.* 2010; MacDougall & Turkington 2005; White *et al.* 2013). Results of testing this theory do not provide evidence for impact as passengers have the potential to become drivers at stages throughout the invasion process (Dietz & Edwards 2006).

Community association

Changes in community organization have been found after invasion by exotic species that alter systems and displace native species (Sanders *et al.* 2003). Invasives can shift a community from being highly structured – species segregation due to competition, or aggregation due to facilitation - to a more randomly structured community with natural patterns of species co-occurrence broken (Sanders *et al.* 2003). This idea follows the initial theory of Diamond (1975) who suggested that community assembly i.e. species co-existence, is determined by interspecific competition.

The current study tested this concept and found that in four of the six pairs community assembly moved from a highly organised community, potentially structured by competition, to a more random structure in the presence of *L. vulgare* (Standard Effect Size closer to zero). When considered in isolation, these results suggest that *L. vulgare* is changing the dynamics and organization of these communities due to its competitiveness. However the body of evidence seen in previous analyses indicates *L. vulgare* could be a passenger, considering this, these findings may be showing the legacy of other invasives that have previously altered the community structure and allowed for the entrance of *L. vulgare.*

The greatest shift to a randomised community was seen in the first two grassland pairs, (G1 and G2), and they also had the greatest incidence of invasive species in the High transects as shown in the Simper graphs. The two pairs that were found to have less of a change in community structure with *L. vulgare* (G3 and W1) were found to have a lower incidence of invasives. The last two of the six pairs showed little or no difference in community assembly between the High and Low *L. vulgare* transects, these two pairs were found to have a more even spread of invasives across both High and Low transects.

These results show that with an increase in invasive species contributing to the High *L. vulgare* transects, there is shift away from a highly structured community towards one with few positive or negative species associations. Given that differences in community structure between the High and Low transects are more consistent with differences in the incidence and influence of other exotic species than they are with *L. vulgare*, this data again suggests that this species is a passenger, responding to the previous impacts of other invading species.

Traits

A reduction in diversity or a change in composition of traits associated with the introduction of an exotic species can change the resource use within that site, and increase the potential for future invasions (Levine & D'Antonio 1999). Resource availability can increase in a system after a disturbance or the invasion of competitively dominant exotic species; this can increase the invasibility potential for exotics with low competitive ability (Levine & D'Antonio 1999; Shea & Chesson 2002).

The current study found that the diversity of functional types between High and Low *L. vulgare* transects was not consistently different, although a reduction was seen in the High *L. vulgare* transect of G1 and G2 which were the most highly invaded plots. This may also be due to the small size of the quadrats, as when *L. vulgare* is dense the quadrats are preempted. This lowers the possibility of other species existing at the quadrat scale, therefore the possibility of a high diversity of functional types. Quadrats with low densities of *L. vulgare* can still be taken up by high densities of other species, such as tussock grasses and other common invasives for example *Anthoxanthum odoratum* that was found to be common at both sites. These species can lower the potential for multiple species and therefore traits to be captured at the quadrat scale.

A change in composition of functional types was found to be significant for all six pairs, suggesting a correlation between *L. vulgare* and a shift in traits. This functional type change in the presence of *L. vulgare* may have more to do with the legacy of past invasions than the possibility of this species altering the trait composition. If *L. vulgare* is a passenger it may be responding to availability of resources necessary for its survival, brought about by the absence of species possessing particular traits. The absence of particular species and traits in specific locations within a site may be the driving factor of the current distribution of *L. vulgare.*

Comparison of the mean CSR scores for each of the sites between High and Low densities of *L. vulgare* found that at the grassland site there was an increase in C scores and a decrease in R scores for the High *L. vulgare* transects. At the open woodland site there was an increase in C scores and R scores and a decrease in S scores for the High *L. vulgare* transects. When the mean CSR scores of individual transects were plotted in CSR space these patterns were found to persist.

If *L. vulgare* was a passenger to disturbed ecosystems, and not highly competitive, we may expect to find it in areas with a low representation of C scores. However at both sites a higher mean C score was found for the High *L. vulgare* transects. Unexpectedly a decrease in disturbance tolerance (R) was found at the grassland site. If *L. vulgare* is a passenger as species composition results suggest, than we would expect there to be an increase in disturbance tolerance (R) of the high density transects as more disturbance tolerant species can be used as indicators of disturbance. This pattern was found in the open woodland site with an increase in the R score, following the predicted passenger method of invasion.

Although many studies have used traits to test for a species' invasiveness, these results do not always coincide with impact. Testing traits may assist in the understanding of which species are drivers, as a driving species will be able to make necessary resources available, but the spread of a passenger may be limited by the current availability of resources, with an inability to change composition of traits.

Conclusions of comparative field study

Considered together, these results provide no evidence that *L. vulgare* is having an impact on the recipient community. Results could be the outcome of *L. vulgare* being a relatively new species to the area whose impacts are yet to be quantifiable. Sites sampled were both highly invaded by other exotics making it difficult to determine whether *L. vulgare* is the cause of these effects, or if the sites high portion of exotics had altered these communities prior to invasion by *L. vulgare*, allowing the invasion. These results do give an indication that *L. vulgare* may be a passenger in an already highly disturbed and exotic system, however this does not necessarily translate to a lack of impact. Invasive species have been found to enter a new community as passengers, and persist as drivers once they have a foothold in the system (Bauer 2012; Berman *et al.* 2013; Bulleri *et al.* 2010).

Barney *et al.* (2013) suggest the use of multiple impact metrics in determining the true impact of exotic species. Their suggestions have been seen as unrealistic and impractical in the field (Hulme *et al.* 2014), however the benefits of using multiple metrics must not be overlooked. This study uses a single data set, analysed multiple ways in order to determine whether changes in the recipient community are seen to be consistent throughout the sites. Results show that this isn't the case, and that other ecological factors could be in play, determining the current spread of *L. vulgare.* While this approach is not as ambitious as the one advocated by Barney *et al.* (2013), it is a broader approach to testing impacts than the use of a single metric, such as species density.

Glasshouse pot experiment

Competitive ability

The competitive ability of an alien species is considered a key indicator of its potential to invade a recipient community, and has also been linked to the species being a driver in lowering biodiversity (Godoy *et al.* 2011; Grime 1974; Ordonez 2014; Rejmanek 2000; Rejmanek & Richardson 1996). Elevated canopy height, large lateral spread above and below ground, and accumulation of a litter layer were found to be the most important traits of a competitive species (Grime 1974; 1977; Grime *et al.* 1997). When found in its native range in the Netherlands, *L. vulgare* is a strong competitor and when grown in experimental monocultures, it is highly resistant to invasion by exotics (Ruijven *et al.* 2003). These results indicate that *L. vulgare* would be a strong competitor in its introduced range.

The glasshouse pot experiment found evidence for increased competitive ability of *L. vulgare* compared to other daisies grown in the area, however competition still caused a large reduction in growth. The native daisy *Senecio gunnii* was found to have the strongest competitive ability with a reduction in growth of 47% when grown with competition, this species is found in much lower densities throughout the landscape at Mt Hotham. *Leucanthemum vulgare* was found to be the second strongest competitor, however a drastic reduction in growth of 72% was found when grown with competition. Something that wasn't considered at the beginning of this experiment was the time to first flowering. *S. gunnii* had reached flowering at just four weeks after the beginning of the experiment, this fast maturity time is typical of annual species that flower quickly drop seeds and dye back over winter. It is possible that this lead to the increased competitive ability of *S. gunnii* against the native grass. *L. vulgare* does not reach reproductive age until it's second spring (Clements *et al.* 2004).

Taraxacum officinale is another widespread invader in the subalpine landscape and is considered a highly competitive species (Johnstone and Pickering 2001; Stewart-Wade *et al.* 2002). This species was also found to have a significant reduction in growth in the presence of competition (75%), similar to that of *L. vulgare* (72%). These results suggest that in the natural system both species are competitive but when grown at a small scale with competitive grasses their ability to successfully compete is weakened. In the field *L. vulgare* was found growing in inter-tussock space suggesting that it lacks the ability to out-compete grasses, however this does not rule out the possibility of *L. vulgare* being competitively dominant to other herbaceous species.

The native daisy *Craspedia aurantia* was found to be the weakest competitor against the native grasses. With an overall reduction in biomass of 76%, this species, unlike *S. gunnii,* did not reach flowering during this experiment. A thickened rootstock allows *C. aurantia* to re-sprout after winter (Walsh & Entwisle 1999); the low competitive ability found for this species may be a trade off for these traits that allow it to increase tolerance to stress.

As tussock grasses are often used in competition experiments because of their known competitive ability these results show that *L. vulgare,* like most other species, is inferior in competitive ability against the strongest competitors in the landscape. This does not assist in our understanding of the impacts of *L. vulgare* on other herbaceous species for which *L. vulgare* predominantly co-exits. These results show that *L. vulgare* may be competitively dominant to other daisy species of similar traits to *C. aurantia* that have reduced competition and increased stress-tolerance.

Plant functional types of native and invasive daisies

The traits of invading species have often been used as an indicator of species invasiveness (Goodwin *et al.* 1999; Leffler *et al.* 2014; Rejmanek & Richardson 1996; Sharma *et al.* 2005). It has been suggested that comparing the traits of an invader to those of the system into which it is invading may be a more accurate measure of invasiveness (Darwin 1859;

Strauss *et al.* 2006). Darwin (1859), and many other invasion scientists since with variations on the theme (Hierro *et al.* 2005; Johnstone 1986; Shea & Chesson 2002), have suggested that a species ability to invade may be based on the availability of resources that are not used by the existing species pool. This theory of limiting similarity explains that an invading species should be functionally dissimilar from the existing species in order to exploit different resources (Emery 2007; Macarthur & Levins 1967).

Emery (2007) tested this hypothesis by manipulating the functional type richness of a system, without removing dominant species, as a way of testing whether an invasive species is functionally dissimilar from the existing community. She found that one third of species showed some evidence for limiting similarity, with the invasive species being hindered by functionally similar dominant natives (Emery 2007). It was concluded in this study that limiting similarity is limited to dominant species and that simple presence of particular traits does not hinder an invasives ability to succeed (Emery 2007).

When the CSR scores of 33 daisy species found at Mt Hotham were plotted with *L. vulgare,* a large spread of traits was found across all the species. Following the theory of limiting similarity *L. vulgare* would be expected to contained traits dissimilar from pre-existing daisies that allow it to exploit a differing resource supply. It was found that *L. vulgare*, much like the other exotic daisies found in the landscape, has traits leading to low disturbance tolerance (R) and high competitive ability (C). This result is unexpected as all other evidence from this study suggests that *L. vulgare* is a passenger responding to previous disturbance and therefore would have high tolerance to disturbance (R). These findings may be a result of the input to produce the CSR scores, as *L. vulgare* is tall relative to other herbaceous species in the landscape and plant height contributes a large amount to the competitive score. *Achillea millefolium* and *Cirsium vulgare,* two tall and well known invaders of disturbed habitats, were also found to come out with high C scores and low R scores, even though they are most commonly found on road sides and other disturbed habitats. When comparing the competitive ability of *L. vulgare* in the pot experiment *Senecio gunnii* was found to have a stronger competitive ability, when the traits of these daisies were plotted the opposite was found. *Senecio gunnii* was found to have lower competitive ability and higher disturbance tolerance than *L. vulgare*. As the input to produce the CSR scores does not incorporate time to first flowering of a species this could be why *S. gunnii* was given a lower C score than *L. vulgare.*

Broader significance of this work - weed risk assessments

Both the federal and state levels of government have regulations governing the classification and management of weeds in Australia. A list of Weeds of National Significance (WoNS) exists, as well as the complimentary National Environmental Alert List. The Commonwealth also maintains control over quarantine matters governed by the *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act) and the *Quarantine Act 1908.* The Australian Government Department of Agriculture (DAFF) uses a weed risk assessment to estimate the weed potential of plants proposed for import (http://www.daff.gov.au/ba/reviews/weeds/system/weed_risk_assessment). All other invasive and introduced species management is the responsibility of the relevant state or territory.

Weed risk assessments in Victoria are undertaken on newly introduced species to measure potential impacts for management prioritisation. Many weed impact assessments consider only species invasiveness as their measure of potential impact, and fail to decouple the terms of invasiveness and impact (e.g. the DAFF framework). The *Department of Environment and Primary Industries* (DEPI) in Victoria bases its weed risk assessment on the predicted invasiveness and measureable impacts of a species (http://vro.depi.vic.gov.au/dpi/vro/vrosite.nsf/pages/weeds_listing2_a). Under the DEPI weed assessment protocol invasiveness of species is based on establishment, growth/competition, reproduction and dispersal. Impacts of species are based on social, abiotic, community habitat, fauna, pest animal and agricultural factors as measures of impact.

Under the DEPI weed risk assessment *L. vulgare* is considered a noxious weed because it scores highly for both invasiveness and impact. While it is laudable that the DEPI system does not conflate invasiveness with impact, the assessment of impact is in most cases dependent on expert opinion rather than empirical data. *Leucanthemum vulgare* is no exception; DEPI rates *L. vulgare* at medium-high for impacts on community habitat, on the expert opinion of (Parsons & Cuthbertson 2001); ‘Ox-eye grows so densely it excludes almost all other vegetation’. Aside from dense stands being visually displeasing, no data was presented to support the statement of impact. Similar anecdotes have been used when assessing the potential impacts of *L. vulgare* in other parts of its invasive range. For example, an invasiveness assessment from Alaska states ‘Ox-eye displaces native plant species growing so densely it excludes all other vegetation' (Klein 2011). A fact sheet by Montana University suggests that impacts to natural ecosystems are high, and suggests that because *L. vulgare* is 'not highly competitive, establishment of a healthy plant community can reduce chances of invasion' (Mangold *et al.* 2009). In Victoria, the DEPI assessment describes *L. vulgare* as "Often a weed of neglected areas, degraded pastures and turf", suggesting, like the Montana assessment, a low competitive ability and a reliance on disturbance for invasion. The research reported here is consistent with those assessments – the data indicate L. vulgare may well be a 'passenger' of poor competitive ability in subalpine regions, whose invasion dynamics are dependent to some degree on the incidence and abundance of other invasive species. However due to the high chance of invasion in disturbed areas, and not being especially palatable to cattle, this species may pose a higher threat to agriculture than it does to intact natural vegetation.

Suggestions for future directions

This was a comparative study of areas invaded by the introduced species *L. vulgare*. The limited time available for the duration of this study lead to limitations for assessing impact. Any correlations found between *L. vulgare* and alterations in its invaded community cannot be directly attributed to *L. vulgare,* as the finding of a pattern does not always demonstrate process.

This study indicates that dense stands of *L. vulgare* are not consistently associated with any measures of impact, such as lower species density, species richness or changes in community organisation. However, further work is needed to demonstrate conclusively that despite being a visually impressive and rapidly expanding alien species, *L. vulgare* is not having any measurable impact of biodiversity values in subalpine communities of the Australian Alps and is not a priority for immediate management.

These future studies might include a before and after invasion comparison, sampling an expanding invasion front before and after encroachment. Alternatively experimental addition or removal component would be useful in concluding whether this species is hindering local species persistence. Both of these options require long periods of time to allow for detectable environmental response. The transects used in this study have now been marked permanently and could serve in the future as a before/after comparison. An experimental seed addition / plant removal study has been running for two years at Mt

Kosciuszko, and preliminary findings suggest no difference in native species richness in the presence and absence of *L. vulgare* (K. McDougall, unpublished data).

Conclusions

Leucanthemum vulgare is a species of high concern in the Australian Alps due to its perceived invasiveness and assumed impacts. Although it forms dense stands that are visually displeasing, this study found no consistent evidence for high negative impacts due to this species. The results suggest *L. vulgare* is a passenger to past disturbance, and the presence of other exotic species may be driving its distribution. However, this study was a snapshot, and further studies that compare native communities before and after invasion by *L. vulgare*, or experimental addition and removal studies, are required before *L. vulgare* can be confidently classified as a highly invasive weed with no measurable impact.

REFERENCES

Barney J. N., Tekiela D. R., Dollete E. S. J. & Tomasek B. J. (2013) What is the "real" impact of of invasive plant species? *Frontiers in Ecology and the Environment* **11**, 322-329.

Bauer J. T. (2012) Invasive species: "back-seat drivers" of ecosystem change? *Biological Invasions* **14**, 1295-1304.

Berman M., Andersen A. N. & Ibanez T. (2013) Invasive ants as back-seat drivers of native ant diversity decline in New Caledonia. *Biological Invasions* **15**, 2311-2331

Birdsall R. L., McCaughey W. & Runyon J. B. (2012) Roads impact the distribution of noxious weeds more than restoration treatments in a lodgepole pine forest in Montana, U.S.A. *Retoration Ecology* **20**, 517-523.

Bulleri F., Balata D., Bertocci I., Tamburello L. & Benedetti-Cecchi L. (2010) The seaweed *Caulerpa racemosa* on Mediterranean rocky reefs: from passenger to driver of ecological change. *Ecology* **91**, 2205-2212.

Byers J. E., Reichard S., Randall J. M., Parker I. M., Smith C. S., Lonsdale W. M., Atkinson I. A. E., Seasted T. R., Williamson M., Chornesky E. & Hayes D. (2002) Directing Research to Reduce the Impacts of Nonindigenous Species. *Conservation Biology* **16**, 630-640.

Clements D. R., Cole D. E., Darbyshire S., King J. & McClay A. (2004) The biology of Canadian weeds. 128. *Leucanthemum vulgare* Lam.. *Canadian Journal of Plant Science* **84**, 343-363.

Colautti R. I. & MacIsaac H. J. (2004) A neutral terminology to define 'invasive' species. *Diversity and Distributions* **10**, 135-141.

Colwell R. K. (2013) *EstimateS: Statistical Estimation of Species Richness and Shared Shared Species from Samples* (Software and User's Guide), Version 9.1.0. http://purl.oclc.org/estimates.

Cornelissen J. H. C., Lavorel S., Garnier E., Diaz S., Buchmann N., Gurvich D. E., Reich P. B., Steege H. t., Morgan H. D., Heijden M. G. A. v. d., Pausas J. G. & Poorter H. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**, 335-380.

Costin A., Gray M., Totterdell C. & Wimbush D. (1979) *Kosciuszko Alpine Flora*, 2nd edn. CSIRO publishing, Melbourne.

Darwin C. (1859) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. John Murray, London.

Davis M. A., Chew M. K., Hobbs R. J., Lugo A. E., Ewel J. J., Vermeij G. J., Brown J. H., Rosenzweig M. L., Gardener M. R., Carroll S. P., Thompson K., Pickett S. T. A., Stromberg J. C., Tredici P. D., Suding K. N., Ehrenfeld J. G., Grime P. J., Mascaro J. & Briggs J. C. (2011) Dont judge a species on their origins *Nature* **474**, 153-154.

Diamond J. M. (1975) Assembly of species communities. In: Cody M. L. & Diamond J. M. (eds.) *Ecology and evolution of communities,* pp. 342-444. Belknap Press, Harvard University Press, Cambridge.

Didham R. K., Tylianakis J. M., Hutchison M. A., Ewers R. M. & Gemmell N. J. (2005) Are invasive species the drivers of ecological change? *Trends in Ecology and Evolution* **20**, 470-474.

Dietz H. & Edwards P. J. (2006) Recognition the casual processes change during plant invasion helps explain conflicts in evidence *Ecology* **97**, 1359-1367.

Emery S. M. (2007) Limiting similarity between invaders and dominant species in herbaceous plant communities? *Journal of Ecology* **95**, 1027-1035.

Falk-Peterson J., Bohn T. & Sandlund O. T. (2006) On the numerous concepts in invasion biology. *Biological Invasions* **8**.

Godfree R., Lepschi B. & Mallinson D. (2004) Ecological filtering of exotic plants in an Australian sub-alpine environment. *Journal of Vegetation Science* **15**, 227-236.

Godoy O., Valladares F. & Castro-Diez P. (2011) Multispecies comparison reveals that invasive and native plants differ in their traits but not in their pasticity. *Functional Ecology* **25**, 1248-1259.

Goodwin B. J., McAllister A. J. & Fahrig L. (1999) Predicting invasiveness of plant species based on biological information. *Conservation Biology* **13**, 422-426.

Gotelli N. J. & Colwell R. K. (2001) Quantifying biodiversity procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4**, 379-391.

Gotelli N. J. & Colwell R. K. (2011) Estimating Species Richness. In: Magurran A. E.& McGIll B. J. (eds.) *Frontiers in measuring biodiversity*, pp 39-54. Oxford University Press, New york

Grime J. P. (1974) Vegetation classification by references to strategies. *Nature* **250**, 26-31.

Grime J. P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* **111**, 1169-1194.

Grime J. P., Thompson K., Hunt R., Hodgson J. G., Cornelissen J. H. C., Rorison I. H., Hendry G. A. F., Ashenden T. W., Askew A. P., Band S. R., Booth R. E., Bossard C. C., Campbell B. D., Cooper J. E. L., Davison A. W., Gupta P. L., Hall W., Hand D. W., Hannah M. A., Hillier S. H., Hodkinson D. J., Jalili A., Liu Z., Mackey J. M. L., Matthews N., Mowforth M. A., Neal A. M., Reader R. J., Reiling K., Ross-Fraser W., Spencer R. E., Sutton F., Tasker D. E., Thorpe P. C. & Whitehouse J. (1997) Integrated screening validates primary axes of specialisation in plants. *OIKOS* **79**, 259-281.

Gurevitch J. G. & Padilla D. K. (2004) Are invasive species a major cause of extinctions. *Trends in Ecology and Evolution* **19**, 470-474.

Hauser C. E. & McCarthy M. A. (2009) Streamlining 'search and destroy': cost-effective surveillance for invasive species management. *Ecology Letters* **12**, 683-692.

Hejda M. & Pysek P. (2006) What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation. *Biological Conservation* **132**, 143-152.

Hierro J. L., Maron J. L. & Callaway R. M. (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology* **93**, 5-15.

HilleRisLambers J., Yelenik S. G., Colman B. P. & Levine J. M. (2010) California annual grass invaders: the drivers or passengers of change? *Journal of Ecology* **98**, 1147-1156.

Hodgson J. G., Wilson P. J., Hunt R., Grime J. P. & Thompson K. (1999) Allocating C-S-R plant functional types: a soft approach to a hard problem. *OIKOS* **85**, 282-294.

Hulme P. E. (2012) Weed risk assessment: a way foward or a waste of time? *Journal of Applied Ecology* **49**, 10-19.

Hulme P. E., Pysek P., Jarosik V., Pergl J., Schaffner U. & Vila M. (2013a) Bias and error in understanding plant invasion impacts. *Trends in Ecology and Evolution* **28**, 212-218.

Hulme P. E., Pysek P., Pergl J., Jarosik V., Schaffner U. & Vila M. (2013b) Greater focus needed on alien plant impacts in protected areas. *Conservation Letters* **00**, 1-7.

Hulme P. E., Pysek P., Pergl J., Schaffner U. & Vila M. (2014) Pragmatism required to assess impacts of invasive plants. *Frontiers in Ecology and the Environment* **12**, 153-154.

Humphries S. E., Groves R. H. & Mitchell D. S. (1991) Plant invasions of Australian ecosystems: a status review and management directions. *Kowari* **2**, 1-134.

IPCC. (2007) *Climate change: impacts adaptations and vulnerability, fourth assessment report of working group II*. United Nations, Brussels.

Johnstone F. M. & Johnstone S. W. (2004) Impacts of road disturbance on soil properties and on exotic plant occurence in subalpine areas in the Australian Alps. *Arctic, Antarctic and Alpine Research* **36**, 201-207.

Johnstone F. M. & Pickering C. M. (2001) Alien Plants in the Australian Alps. *Mountain Research and Devlopment* **21**, 284-291.

Johnstone I. M. (1986) Plant invasion windows: a time-based classification of invasion potential. *Biological Reviews* **61**, 369-394.

Khuroo A. A., Malik A. H., Reshi Z. A. & Dar G. H. (2010) From ornamental to detrimental: plant invasion of *Leucanthemum vulgare* Lam. (Oxeye Daisy) in Kashmir valley, India. *Current Science* **98**, 600-602.

Klein H. (2011) *Ox-eye Daisy Leucanthemum vulgare Lam*. University of Alaska Anchorage.

Kolar C. S. & Lodge D. M. (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* **16**, 199-204.

Lass L. W. & Callihan R. H. (1997) Effect of phenological stage on detectability of yellow hawkweed (*Hieracium pratense*) and oxeye daisy (*Chrysanthemum leucanthemum*) with remote multispectral digital imagery. *Weed Technology* **11**, 248-256.

Lawrence R. E. (1999) Vegetation changes on the Bogong High Plains from the 1800's to 1950's. *Proceedings of the Royal Society of Victoria* **111**, xxix-lii.

Leffler J. A., James J. J., Monaco T. A. & Sheley R. L. (2014) A new perspective on trait differences between native and invasvie exotic plants. *Ecology* **95**, 298-305.

Levine J. M. & D'Antonio C. M. (1999) Elton revisited: a review of evidence linking diversity and invasability. *OIKOS* **87**, 15-26.

Levine J. M., Vila M., D'Antonio C. M., Dukes J. S., Grigulis K. & Lavorel S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London* **270**, 775-781.

Lonsdale W. M. (1999) Global patterns of plant invasions and the concept of invasability. *Ecology* **80**, 1522-1536.

Macarthur R. & Levins R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist* **101**, 377-385.

MacDougall A. S. & Turkington R. (2005) Are invasive species the drivers or passengers of change in degraded ecosystems. *Ecology* **86**, 42-55.

Mack R. N. & Lonsdale M. W. (2001) Humans as global plant dispersers: getting more than we bargained for. *Bioscience* **51**, 95-102.

Magee T. K., Ringold P. L., Bollman M. A. & Ernst T. L. (2010) Index of alien impact: a method for evaluating potential ecological impact of alien plant species. *Environmental Management* **45**, 759-778.

Makepeace W. (1985) Growth, reproduction, and production biology of the mouse-ear and king devil hawkweed in eastern South Island, New Zealand. *New Zealand Journal of Ecology* **23**, 65-78.

Makepeace W., Dobson A. T. & Scott D. (1985) Interference phenomena due to mouse-ear and king devil hawkweed. *New Zealand Journal of Ecology* **23**, 79-90.

Mangold J., Sheley R. & Brown M. (2009) *Oxeye daisy: Identification, Biology and Integrated Management.* Montana State University Extension - MontGuide.

Martin P. (2003) *A 2020 Vision Statement: Killing us softly - Australia's green stalkers*. CRC for Australian Weed Management, Bowden printing, Adelaide.

McCabe D. J. & Gotelli N. J. (2000) Effects of disturbance frequency, intensity and area on assemblages of stream invertebrates. *Oceologia* **124**, 270-279.

McDougall K. L., Morgan J. W., Walsh N. G. & Williams R. J. (2005) Plant invasions in treeless vegetation of the Australian Alps. *Perspectives in Plant Ecology, Evolution and Systematics* **7**, 159-171.

McIntosh P. D., Loeseke M. & Bechler K. (1995) Soil changes under mouse-ear hawkweed (*Hieracium pilosella). New Zealand Journal of Ecology* **19**, 29-34.

McIntosh P. O. & Allen R. B. (1993) Soil pH delines and organic carbon increases under hawkweed. *New Zealand Journal of Ecology* **17**, 59-60.

Meffin R., Miller A. L., Hulme P. E. & Duncan R. P. (2010) Experimental introduction of the alien plant Hieracium lepidulum reveals no significant impact on montane plant communities in New Zealand. *Diversity and Distributions* **16**.

Mitch L. W. (2000) Oxeye Daisy (*Chrysanthemum leucanthemum* L.), the white-flowered gold flower. *Weed Technology* **14**, 659-662.

Moore R. & William J. (1976) A Study of subalpine woodland-grassland boundary. *Australian Journal of Ecology* **1**, 145-153.

Murphy B. F. & Timbal B. (2008) Review: A review of recent climate variability and climate in southeastern Australia. *International Journal of Climatology* **28**, 859-879.

Olson B. E. & Wallander R. T. (1999) Ox-eye daisy. In: R. L. Sheley and J. K. Petroff (eds.) *Biology and management of noxious weeds,* pp. 282-289. Oregon State University Press. Corvalis, Ore.

Olson B. E., Wallander R. T. & Fay P. K. (1997) Intensive cattle grazing of ox-eye daisy (*Chrysantehmum leucanthemum). Weed Technology* **11**, 176-181.

Ordonez A. (2014) Global meta-analysis of trait consistency of non-native plants between their native and introduced areas. *Global Ecology and Biogeography* **23**, 264-273.

Parker I. M., Simberloff D., Lonsdale W. M., Goodell K., Wonham M., Kareiva P. K., Williamson M. H., Holle B. V., Moyle P. B., Byers J. E. & Goldwasser L. (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* **1**, 3-19.

Parks Vic (2010) Parks: Grater Alpine National Parks Discussion Paper. *Invasive species*.

Parsons W. & Cuthbertson E. (2001) *Noxious weeds of Australia*. Inkata Press, Melbourne.

Pauchard A., Keuffer C., Dietz H., Daehler C. C., Alexander J., Edwards P. J., Arevalo J. R., Cavieres L. A., Guisan A., Haider S., Jakobs G., McDougall K., Millar C. I., Naylor B. J., Parks C. G., Rew L. J. & Seipel T. (2009) Ain't no mountain high enough: plant invasions reaching new elevations. *Frontiers in Ecology and the Environment* **7,** 479-486.

Pheloung P. C., Williams P. A. & Halloy S. R. (1999) A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *Journal of Environmental Management* **57**, 239-251.

Pickering C. M., Harrington J. & Worboys G. (2003) Environmental impacts of tourism on the Australian Alps Protected Areas. *Mountain Research and Devlopment* **23**, 247-254.

Pysek P., Jarosik V., Hulme P. E., Pergl J., Hejda M., Schaffner U. & Vila M. (2012) A global analysis of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology* **18**, 1725-1737.

Ravi S., D'Odorico P., Collins S. L. & Huxman T. E. (2009) Can biological invasion induce desertification? *New Phytologist* **181**, 512-515.

Rejmanek M. (2000) Invasive plants: approaches and prediction. *Austral Ecology* **25**, 497-506.

Rejmanek M. & Richardson D. M. (1996) What attributes make some plant species more invasive? *Ecology* **77**, 1655-1661.

Ricciardi A. (2003) Predicting the impacts of an introduced species from its invasion history: an empirical approach to zebra mussel invasions. *Freshwater Biology* **48**, 972-981.

Ricciardi A. & Cohen J. (2007) The invasiveness of an introduced species does not predict its impact. *Biological Invasions* **9**, 309-315.

Richardson D. M., Pysek P., Rejmanek M., Barbour M. G., Panetta F. D. & West C. J. (2000) Naturalization and invasion of alien plants: concepts and defintions. *Diversity and Distributions* **6**, 93-107.

Rowe R. K. (1967) A Study of the Land in the Victorian Catchment of Lake Hume. *Soil Conservation Authority*.

Ruijven J. V., Deyn G. B. D. & Berendse F. (2003) Diversity reduces invasability in experimental plant communities: the role of plant species. *Ecology Letters* **6**, 910-918.

Sanders N., Gotelli N., Heller N. & Gordon D. (2003) Community disassembly by an invasive species. *PNAS* **100**, 2474-2477.

Sharma G. P., Singh J. S. & Raghubanshi A. S. (2005) Plant invasions: Emerging trends and future implications. *Current Science* **88**, 726-734.

Shea K. & Chesson P. (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* **17**, 170-176.

Stewart-Wade S. M., Neumann S., Collins L. L. & Boland G. J. (2002) The biology of Canadian weeds. 117. *Taraxacum officinale* G. H. Weber ex Wiggers. *Canadian Journal of Plant Science* **82**, 825-853.

Stone L. & Roberts A. (1990) The checkerboard score and species distributions. *Oceologia* **85**, 74-79.

Strauss S. Y., Webb C. O. & Salamin N. (2006) Exotic taxa less related to native species are more invasive. *PNAS* **103**, 5841-5845.

Thiele J., Kollmann J., Markussen B. & Otte A. (2010) Impact assessment revisited: improving the theoretical basis for management of invasive alien species. *Biological Invasions* **12**, 2025-2035.

Thomsen M. S., Olden J. D., Wernberg T., Griffin J. N. & Siliman B. R. (2011) A broad framework to organize and compare ecological invasion impacts. *Environmental Research* **111**, 899-908.

Thorsell J. (2003) A Global Overview of Mountain Protected Areas on the World Heritage List. *Mountain Research and Devlopment* **23**, 290-293.

Vila M., Espinar J. L., Hejda M., Hulme P. E., Jarosik V., Maron J. L., Pergl J., Schaffner U., Sun Y. & Pysek P. (2011) Ecological impacts of invasive alien plant: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* **14**, 702-708.

Vitousek P. M., D'Antonio C. M., Loope L. L., Rejmanek M. & Westbrooks R. (1997) Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology* **21**, 1-16.

Walsh N. G. & Entwisle T. J. (1999) *Flora of Victoria Volume 4: Dicotyledons Cornaceae to Asteraceae*. Inkata Press, Melbourne.

Wearne L. J. & Morgan J. W. (2001) Recent forest encroachment into Subalpine Grasslands near Mount Hotham. *Arctic, Antarctic and Alpine Research* **33**, 369-377.

White S. R., Tannas S., Bao T., Bennett J. A., Bork E. W. & Cahill Jr. J. F. (2013) Using structural equation modelling to test the passenger, driver and opportunist concepts in a *Poa pratensis* invasion. *OIKOS* **122**, 377-384.

WIlliams N. S. G. & Holland K. D. (2007) The ecology and invasion history of hawkweeds (*Hieracium* species). *Plant Protection Quarterly* **22**, 75-80.

APPENDICES

Appendix I. GPS coordinates of each transect within the sites sampled in the comparative field study component. Grassland = Airport, Woodland = Brandy Creek.

	START		FINISH	
	Easting	**Northing**	**Easting**	**Northing**
Grassland P1 HIGH	529554	5898906	529553	5898220
Grassland P1 LOW	529563	5898911	529561	5898922
Grassland P2 HIGH	0529549	5898904	0529550	5598916
Grassland P2 LOW	0529572	5898908	0529570	5898920
Grassland P3 HIGH	0529596	5898878	0529609	5898892
Grassland P3 LOW	0529604	5898877	0529615	5898888
Woodland P1 HIGH	0517163	5904199	0517172	5904206
Woodland P1 LOW	0517166	5904186	0517172	5904201
Woodland P2 HIGH	0517220	5904184	0517232	5904190
Woodland P2 LOW	0517219	5904179	0517230	5904187
Woodland P3 HIGH	0517070	5904126	0517069	5904136
Woodland P3 LOW	0517070	5904111	0517069	5904121

Appendix II. Input values for CSR calculator spread sheets following the methods in Hodgson *et al.* (1999).

Species	Canopy height	Dry matter content (%)	Flowering period	Lateral Spread	Dry weight (mg)	SLA (mg/mm$^{2)}$	Flowering start	C Score	S Score	R Score	Functional Type
Acaena agnipila	3	40.4	4	3	8.3	3.5	4	-1.026	0.605	-2.5	S/SC
Acaena novae-zelandiae	2	34.1	4	6	37.8	13.1	4	0.1	-0.205	-1.603	SC
Acetosella vulgaris	1	12.4	3	4	11.7	19.6	4	-1.268	-2.5	1.33	R/CR
Achillea millefolium	5	26.7	4	6	78.2	3.9	4	1.865	-2.5	-1.611	C
Agrostis cappillaris	3	36.7	2	2	10	5.7	-	-1.131	2.222	-2.109	S
Ajuga australis	2	14.5	3	3	47.8	3.6	3	-1.133	-2.5	-0.669	CR
Anthoxanthum odoratum	3	38.8	3	2	6.4	5.6	-	-1.131	2.342	-1.677	S
Arthropodium milleflorum	3	20.8	3	3	158.6	4.5	-	-0.751	1.98	-2.5	S/SC
Asperula gunnii	1	25.2	1	4	0.3	9.1	5	-1.623	-0.287	-0.96	SR
Asperula pusilla	2	23.5	1	4	0.2	21.5	5	-1.408	-0.903	-0.275	SR/CSR
Asterolasia trymalioides	3	45.6	2	2	2.5	5.2	3	-1.408	1.534	-2.5	S/SC
Brachyscome decipiens	1	15.3	3	3	49.6	12.7	5	-1.35	-2.499	0.933	R/CR
Brachyscome nivalis	1	26.3	4	4	14.1	6.6	3	-1.24	-0.667	-1.282	SC/CSR
Brachyscome rigidula	3	26.9	2	4	2.1	15.8	5	-0.859	-1.055	-0.581	CR/CSR
Brachyscome spathulata	3	14.3	4	2	11.3	4.7	3	-1.219	-2.5	0.122	R/CR
Bracteantha subundulata	3	26.4	2	4	37	10.7	6	-0.461	-1.679	-0.669	CR
Bulbine bulbosa	4	9.2	2	3	120.7	8.9	-	0.077	0.27	-2.5	SC
Carex breviculmis	2	35.8	4	2	12.3	15.2	-	-1.723	1.341	-0.612	S/SR
Celmisia costiniana	2	46.1	3	3	116	1.1	4	0.96	1.172	-2.5	S/SC
Celmisia pugioniformis	3	38.8	2	6	60.7	4.8	5	0.575	-0.072	-2.5	SC
Cerastium glomeratum	3	20.9	3	2	1.7	5.5	4	-1.446	-1.865	-0.488	CR
Chrysocephalum semipapposum	3	46.1	5	3	0.9	2.8	3	-1.265	1.734	-2.5	S/SC
Cirsium vulgare	4	23.3	2	3	248.1	2.4	5	0.136	-2.5	-2.064	C/CR
Convolvulus erubescens	2	22	2	3	13.9	4.5	4	-1.34	-1.668	-1.37	CR

Appendix II. Cont…

Species	Canopy height	Dry matter content (%)	Flowering period	Lateral Spread	Dry weight (mg)	SLA (mg/mm$^{2)}$	Flowering start	C Score	S Score	R Score	Functional Type
Craspedia aurantia	3	25.8	4	4	62.8	2.8	4	-0.364	-1.898	-1.708	C/CR
Craspedia coolaminica	3	27	3	3	97.2	3.3	4	-0.608	-1.85	-2.188	C/SC
Craspedia lamicola	3	20.7	3	5	97.7	3.1	4	0.148	-2.5	-1.368	C/CR
Craspedia maxgrayii	3	23.6	1	3	127.4	11.3	5	-0.553	-2.403	-1.174	CR
Cymbonotus preissianus	1	14.4	5	2	156.6	3.8	2	-1.365	-2.5	-0.42	CR
Cynoglossum suaveolens	3	28.3	3	3	89.9	2.6	3	-0.624	-1.647	-2.5	SC
Dichelachne rara	3	44.9	4	2	23.5	1.9	-	-2	2	-2	S
Dichondra repens	1	20.2	3	4	24.9	3.6	3	-1.15	-1.66	-1.354	CR
Elymus scaber	3	36.9	4	2	64.1	4.2	-	-1.131	2.427	-2.333	S
Epilobium billardierianum	3	32.5	3	4	3.7	4.1	4	-0.798	-0.357	-2.384	SC
Erigeron nitidus	1	26.6	2	3	14.9	10.8	4	-1.562	-0.637	-1.325	SR/CSR
Erigeron paludicola	1	26.9	3	3	23.4	9.2	4	-1.491	-0.695	-1.164	SR/CSR
Euchiton fordianus	1	32.9	3	3	5.6	14.5	4	-1.699	0.434	-1.535	S/SR
Festuca rubra	3	32.5	3	3	7.6	4.3	-	-0.751	2.5	-1.92	S
Galium gaudichaudii	2	30.3	3	4	0.4	5.2	3	-1.376	0.003	-2.121	S/SC
Geranium 2. (Tall)	3	24.7	3	3	82.6	4.2	4	-0.641	-2.126	-1.658	C/CR
Geranium antrorsum	2	27.6	4	3	32.9	9.3	4	-1.2	-1.08	-0.922	SR/CSR
Geranium sessiliflorum	1	23.4	3	3	32.3	2.8	4	-1.436	-1.26	-1.659	SC
Geranium sp.7	2	22.6	2	3	7.8	5.9	4	-1.423	-1.469	-1.171	CR/CSR
Geranuim potentilloides	2	26.4	3	3	51.7	4.8	4	-1.119	-1.361	-1.718	SC
Geum urbanum	3	30.1	2	3	142.3	3.6	5	-0.529	-1.527	-2.5	C/SC
Glycine latrobeana	2	28.3	1	3	17.7	4	4	-1.303	-0.839	-2.5	SC
Gonocarpus montanus	2	33.9	3	4	0.7	4.3	4	-1.34	0.457	-2.423	S/SC

Appendix II. Cont…

Species	Canopy height	Dry matter content (%)	Flowering period	Lateral Spread	Dry weight (mg)	SLA (mg/mm^{2})	Flowering start	C Score	S Score	R Score	Functional Type
Helichrysum scorpioides	3	31.7	4	5	11.7	4	3	-0.222	-0.679	-2.408	SC
Holcus lanatus	3	45.4	2	2	11.9	6.1	-	-1.131	2.5	-2.113	S
Hydrocotyle laxiflora	1	19.8	2	4	6.4	5.8	4	-1.351	-1.421	-0.779	CR/CSR
Hypochaeris radicata	3	14.7	2	3	42.8	19.6	5	-0.766	-2.5	0.854	R/CR
Juncus australis	5	40.6	6	2	408.9	1.8	-	0.762	1.661	-2.5	SC
Lagenophora stipitata	2	18.7	5	3	18.2	5.6	3	-1.298	-2.187	-0.024	R/CR
Leptorhynchos squamatus	2	34.6	2	3	3.3	9.8	5	-1.529	0.357	-1.897	S/SC
Leucanthemum vulgare	4	20.9	3	5	17.9	4.4	4	0.386	-2.5	-0.892	C/CR
Leucochrysum albicans	2	29.1	6	3	10.2	2.6	3	-1.385	-0.612	-1.615	SC
Lotus pedunculatus	4	20.4	3	4	11.7	6.4	5	-0.104	-2.5	-0.098	CR
Luzula acutifolia	3	34.6	2	2	15.8	8.3	-	-1.131	1.779	-1.943	S/SC
Luzula modesta	2	36.5	2	3	23	9.2		-1.343	2.5	-1.969	S
Luzula novae-cambriae	3	36.7	3	2	37.2	9.2	-	-1.131	1.769	-1.826	S/SC
Oreomyrrhis eriopoda	2	30.3	2	3	43.4	8.3	5	-1.151	-0.771	-1.865	SC
Oxalis exilis	1	18.7	3	4	5.9	9.9	5	-1.361	-1.561	0.547	R/CR
Plantago lanceolata	3	27.5	3	3	76.6	2.9	3	-0.656	-1.714	-2.5	C/SC
Poa costiniana	3	42.2	3	2	76.1	5.2	-	-1.131	2.5	-2.5	S
Poa fawcettiae	3	50.6	5	2	9.1	15.2	-	-1.131	1.696	-0.214	S/CSR
Poa hiemata	3	46.8	1	3	5.8	7.4		-0.751	2.5	-2.018	S
Poa hothamensis	3	47.5	5	2	47.8	13	-	-1.131	1.824	-0.943	S/CSR
Poa sieberiana	3	49.7	2	3	11.2	2.8	-	-0.751	2.5	-2.5	S
Podolepis robusta	2	18.3	3	3	268.3	10.4	6	-0.771	-2.5	0.234	CR
Prunella vulgaris	2	23.6	3	2	10.4	5.7	4	-1.619	-1.385	-0.994	SR
Ranunculus victoriensis	2	32.7	3	3	43.5	6.8	4	-1.151	-0.436	-2.43	SC

Appendix II. Cont…

Species	Canopy height	Dry matter content (%)	Flowering period	Lateral Spread	Dry weight (mg)	SLA (mg/mm$^{2)}$	Flowering start	C Score	S Score	R Score	Functional Type
Ranunculus graniticola	3	24.4	3	3	161.3	3.2	3	-0.502	-2.362	-2.307	C/CR
Rhodanthe anthemoides	3	34.7	3	3	1.2	4.4	5	-1.241	0.108	-2.172	S/SC
Rytidosperma nudiflorum	1	45.9	3	3	12.4	5.7	-	-1.698	2.5	-1.88	S
Rytidosperma pilosum	3	48.9	3	3	13	2.5	-	-0.751	2.5	-2.4	S
Scleranthus biflorus	1	32.3	3	3	0.3	2.2	4	-1.954	0.706	-2.5	S/SC
Senecio gunnii	3	21.1	3	1	38.1	3.4	4	-1.165	-2.427	-1.217	CR
Senecio linearifolius	4	37.1	3	3	158	4.2	4	0.036	-0.982	-2.5	SC
Senecio pectinatus	2	16.5	2	4	34.3	11.8	5	-0.862	-2.5	0.398	R/CR
Senecio pinnatifolius	5	21.6	4	6	68.8	4.8	3	1.84	-2.5	-1.098	C/CR
Senecio tenuiflorus	4	17.5	3	6	76.8	6	3	1.163	-2.5	-0.742	C/CR
Solenogyne gunnii	1	18.9	3	3	51.4	2.6	3	-1.353	-2.005	-1.53	CR
Stellaria pungens	2	28.4	4	4	0.6	19.9	3	-1.351	-0.297	-0.634	SR/CSR
Stylidium graminifolium	2	25.4	2	3	33.5	9.2	4	-1.197	-1.392	-1.376	CR/CSR
Taraxacum officinale	3	14.4	5	3	361.8	6.7	2	0.319	-2.5	-0.108	CR
Themeda triandra	3	45.4	3	3	30.9	9.3	-	-0.751	2.5	-1.755	S
Trifolium arvense	3	28.2	2	2	3.5	5.9	5	-1.371	-0.95	-1.493	SC/CSR
Trifolium campestre	2	27.2	2	2	3.1	2.7	4	-1.772	-0.668	-2.331	S/SC
Trifolium repens	2	24.1	2	4	17.1	7.3	3	-0.978	-1.419	-1.667	SC
Verbascum thapsus	3	24.6	3	3	221.2	6	4	-0.433	-2.431	-1.515	C/CR
Veronica serpyllifolia	2	24	2	1	1.9	4.1	4	-1.965	-1.044	-1.533	SR
Vicia benghalensis	2	24.4	2	2	15.3	6.1	4	-1.562	-1.353	-1.466	SR/CSR
Viola betonicifolia	2	19.5	4	3	47.4	4.7	3	-1.135	-2.303	-0.773	CR
Viola bicolor	3	15.6	2	2	10.1	2.6	4	-1.235	-2.5	-0.873	CR
Wahlenbergia gloriosa	3	26.5	3	1	11.6	4.7	5	-1.357	-1.404	-1.187	CR/CSR
Xerochrysum subundulatum	3	40.3	3	5	20	2.6	5	-0.14	0.409	-2.5	SC

Appendix III. SIMPER analysis of the contribution of each species to the dissimilarities found for species composition within each pair of Low and High density transects.

Grassland P1 (G1)

Average dissimilarity = 70.33

	High	Low				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Galium gaudichaudii	0.17	0.84	5.16	1.46	7.33	7.33
Helichrysum scorpioides	0.67	0.08	4.45	1.25	6.33	13.66
Hypochaeris radicata	0.33	0.75	4.14	1.12	5.88	19.54
Anthoxanthum odoratum	0.33	0.68	4.04	1.05	5.75	25.29
Asperula pusilla	0.47	0.74	3.7	0.98	5.25	30.54
Cerastium glomeratum	0.21	0.53	3.54	0.99	5.03	35.57
Trifolium repens	0.59	0.56	3.49	0.93	4.97	40.54
Trifolium campestre	0.17	0.45	3.06	0.9	4.35	44.9
Poa sieberiana	0.95	0.58	3.02	0.81	4.3	49.2
Holcus lanatus	0.29	0.35	2.89	0.85	4.11	53.31
Trifolium arvense	0	0.42	2.72	0.82	3.87	57.18
Rytidosperma pillosa	0	0.41	2.6	0.81	3.69	60.87
Acaena novae-zelandiae	0.3	0.14	2.37	0.72	3.37	64.24
Elymus scaber	0.04	0.32	2.19	0.69	3.12	67.36
Dichondra repens	0	0.29	2.13	0.61	3.04	70.4
Carex breviculmis	0.01	0.27	1.97	0.59	2.81	73.2
Carex appressa	0.18	0.02	1.38	0.46	1.97	75.17
Poa hothamensis	0.16	0.06	1.38	0.48	1.97	77.13
Solenogyne gunnii	0	0.19	1.3	0.47	1.84	78.98
Scleranthus biflorus	0.12	0.09	1.29	0.46	1.83	80.81
Prunella vulgaris	0.17	0.01	1.2	0.45	1.7	82.51
Euchiton fordianus	0.17	0.01	1.19	0.45	1.69	84.2
Geranium sp. 7	0	0.2	1.19	0.49	1.69	85.89
Geranium sessiliflorum	0.13	0.05	1.07	0.44	1.53	87.41
Acetosella vulgaris	0.02	0.15	1.02	0.44	1.46	88.87
Leptorhynchos squamatus	0.13	0.03	1	0.41	1.43	90.3
Unknown 3	0	0.15	0.98	0.41	1.4	91.7
Oreomyrrhis eriopoda	0.14	0	0.91	0.39	1.3	92.99
Stellaria pungens	0.12	0	0.81	0.36	1.14	94.14
Epilobium billardierianum	0	0.12	0.78	0.36	1.11	95.25
Taraxacum officinale	0.04	0.07	0.67	0.34	0.96	96.21
Vicia benghalensis	0.03	0.04	0.44	0.27	0.63	96.84
Plantago lanceolata	0	0.07	0.41	0.27	0.58	97.41
Gonocarpus montanus	0.06	0	0.39	0.24	0.55	97.97
Acaena agnipila	0	0.06	0.37	0.25	0.52	98.49
Oxalis exilis	0.04	0	0.27	0.2	0.38	98.87
Geranium C	0	0.03	0.22	0.17	0.31	99.18
Scleranthus diander	0.02	0	0.13	0.14	0.19	99.37
Cymbonotus preissianus	0.02	0	0.13	0.14	0.19	99.56
Hypericum gramineum	0.01	0	0.07	0.1	0.11	99.67
Ajuga australis	0.01	0	0.06	0.1	0.09	99.75
Viola betonicifolia	0.01	0	0.06	0.1	0.09	99.84
Craspedia sp.	0	0.01	0.06	0.1	0.08	99.92
Brachyscome sp.	0.01	0	0.05	0.1	0.08	100

Appendix III. Cont…

Grassland P2 (G2)

Average dissimilarity = 58.83

	Low	**High**				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Trifolium campestre	0.74	0.27	3.82	1.21	6.49	6.49
Trifolium arvense	0.64	0.09	3.75	1.22	6.37	12.87
Helichrysum scorpioides	0.46	0.9	3.31	1.03	5.63	18.49
Hypochaeris radicata	0.77	0.48	3.28	0.99	5.58	24.07
Trifolium repens	0.4	0.63	3.28	1.02	5.57	29.63
Elymus scaber	0.56	0.15	3.26	1.06	5.54	35.17
Galium gaudichaudii	0.54	0.08	3.2	1.04	5.44	40.61
Anthoxanthum odoratum	0.59	0.52	3.13	0.95	5.32	45.93
Rytidosperma pillosa	0.46	0.03	2.72	0.9	4.62	50.56
Asperula pusilla	0.84	0.64	2.64	0.8	4.49	55.04
Carex breviculmis	0.36	0.19	2.47	0.82	4.2	59.24
Cerastium glomeratum	0.35	0.15	2.33	0.79	3.96	63.2
Solenogyne gunnii	0.35	0.06	2.17	0.75	3.68	66.88
Leptorhynchos squamatus	0.22	0.19	2.05	0.68	3.49	70.37
Scleranthus biflorus	0.12	0.26	1.94	0.67	3.3	73.67
Holcus lanatus	0.12	0.24	1.85	0.65	3.15	76.81
Geranium sessiliflorum	0.32	0	1.85	0.67	3.14	79.96
Acaena novae-zelandiae	0.06	0.27	1.83	0.64	3.1	83.06
Rytidosperma pensilata	0	0.25	1.53	0.57	2.61	85.67
Oreomyrrhis eriopoda	0.11	0.13	1.23	0.51	2.09	87.76
Oxalis exilis	0	0.14	0.82	0.4	1.39	89.15
Geranium C	0	0.12	0.69	0.37	1.17	90.32
Carex appressa	0	0.1	0.63	0.33	1.08	91.39
Acetosella vulgaris	0.09	0.01	0.62	0.32	1.06	92.45
Stellaria pungens	0.04	0.06	0.6	0.32	1.02	93.47
Poa sieberiana	0.92	0.99	0.57	0.3	0.96	94.44
Vicia benghalensis	0.02	0.07	0.55	0.3	0.93	95.37
Gonocarpus montanus	0	0.08	0.49	0.29	0.83	96.2
Poa hothamensis	0.04	0.03	0.42	0.27	0.72	96.92
Ranunculus graniticola	0.04	0.02	0.32	0.25	0.55	97.47
Acaena agnipila	0.05	0	0.3	0.23	0.51	97.98
Dichondra repens	0	0.04	0.25	0.2	0.42	98.4
Prunella vulgaris	0.04	0	0.25	0.2	0.42	98.83
Hypericum gramineum	0	0.04	0.22	0.2	0.37	99.2
Geranium sp. 7	0.02	0	0.12	0.14	0.2	99.4
Themeda triandra	0.02	0	0.11	0.14	0.19	99.59
Cymbonotus preissianus	0.01	0	0.07	0.1	0.12	99.71
Stylidium graminifolium	0	0.01	0.07	0.1	0.11	99.82
Verbascum thapsus	0.01	0	0.06	0.1	0.1	99.92
Euchiton fordianus	0	0.01	0.05	0.1	0.08	100

Appendix III. Cont…

Grassland P3 (G3)

Average dissimilarity = 65.14

	High	Low				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Festuca rubra	0.86	0.31	4.85	1.22	7.45	7.45
Themeda triandra	0.21	0.69	4.68	1.17	7.19	14.63
Anthoxanthum odoratum	0.54	0	4.39	1	6.74	21.37
Trifolium repens	0.64	0.2	4.24	1.12	6.51	27.88
Carex appressa	0.42	0.5	3.82	0.94	5.86	33.74
Asperula pusilla	0.55	0.43	3.81	0.96	5.84	39.59
Trifolium campestre	0.55	0.25	3.78	1.01	5.81	45.39
Hypochaeris radicata	0.7	0.65	3.53	0.85	5.41	50.8
Poa hothamensis	0.09	0.49	3.46	0.94	5.31	56.11
Elymus scaber	0.11	0.42	3.12	0.84	4.8	60.91
Holcus lanatus	0.36	0.03	2.66	0.74	4.09	65
Cerastium glomeratum	0.96	0.76	2.28	0.57	3.5	68.5
Poa sieberiana	0.07	0.26	2.15	0.61	3.3	71.79
Galium gaudichaudii	0.25	0.06	1.92	0.61	2.95	74.74
Rytidosperma pensilata	0.08	0.2	1.71	0.56	2.62	77.37
Cynoglossum suaveolens	0.14	0.11	1.57	0.51	2.41	79.78
Viola betonicifolia	0.21	0.03	1.52	0.53	2.34	82.11
Solenogyne gunnii	0.12	0.07	1.17	0.44	1.79	83.91
Trifolium arvense	0.11	0.07	1.05	0.44	1.61	85.51
Helichrysum scorpioides	0.13	0.02	0.94	0.4	1.44	86.96
Oxalis exilis	0.03	0.1	0.81	0.37	1.24	88.2
Vicia benghalensis	0.07	0.04	0.74	0.33	1.13	89.34
Ranunculus graniticola	0.08	0.03	0.68	0.34	1.05	90.38
Scleranthus biflorus	0	0.09	0.67	0.31	1.03	91.41
Plantago lanceolata	0.03	0.06	0.56	0.3	0.87	92.28
Leptorhynchos squamatus	0	0.08	0.55	0.29	0.85	93.13
Carex breviculmis	0.06	0.01	0.47	0.27	0.72	93.84
Hypericum gramineum	0.02	0.04	0.41	0.24	0.62	94.47
Rytidosperma pillosa	0.05	0.01	0.39	0.25	0.61	95.07
Acetosella vulgaris	0.01	0.05	0.37	0.25	0.57	95.64
Acaena novae-zelandiae	0.05	0	0.36	0.22	0.56	96.2
Luzula sp.	0	0.05	0.34	0.23	0.52	96.72
Cirsium vulgare	0.04	0	0.3	0.2	0.46	97.18
Geranium sessiliflorum	0.01	0.03	0.27	0.2	0.41	97.59
Dichelachne rara	0.03	0.01	0.26	0.2	0.41	98
Parentucellia latifolia	0.03	0	0.22	0.17	0.34	98.34
Ajuga australis	0.03	0	0.2	0.17	0.3	98.64
Eucalyptus sp.	0.02	0	0.14	0.14	0.21	98.86
Oreomyrrhis eriopoda	0.02	0	0.13	0.14	0.21	99.06
Stellaria pungens	0.02	0	0.12	0.14	0.19	99.25
Acaena agnipila	0.01	0	0.08	0.1	0.12	99.37
Senecio sp.	0	0.01	0.07	0.1	0.11	99.49

Cymbonotus preissianus	0.01	0	0.07	0.1	0.11	99.6
Craspedia sp.	0	0.01	0.07	0.1	0.11	99.7
Euchiton fordianus	0	0.01	0.07	0.1	0.11	99.81
Taraxacum officinale	0.01	0	0.06	0.1	0.1	99.91
Brachyscome sp.	0	0.01	0.06	0.1	0.09	100

Appendix III. Cont…

Open Woodland P1 (W1)
Average dissimilarity = 65.78

	Low	High				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Trifolium repens	0.29	0.99	5.68	1.41	8.63	8.63
Oreomyrrhis eriopoda	0.77	0.18	5.2	1.31	7.91	16.54
Agrostis capillaris	0.27	0.69	4.41	1.13	6.7	23.24
Poa costiniana	0.8	0.41	4.22	1.05	6.42	29.66
Bulbine bulbosa	0.57	0.13	4.17	1.04	6.34	36
Hypochaeris radicata	0.54	0.65	3.85	0.94	5.85	41.85
Dichondra repens	0.48	0.47	3.83	0.95	5.81	47.67
Cerastium glomeratum	0.16	0.48	3.53	0.93	5.37	53.04
Hydrocotyle laxiflora	0	0.48	3.36	0.93	5.11	58.15
Anthoxanthum odoratum	0.89	0.68	2.98	0.71	4.53	62.68
Prunella vulgaris	0.16	0.36	2.83	0.8	4.3	66.98
Elymus scaber	0.25	0.13	2.31	0.65	3.51	70.5
Viola betonicifolia	0.28	0.01	2.12	0.61	3.22	73.72
Luzula sp.	0.03	0.26	1.92	0.6	2.93	76.64
Acetosella vulgaris	0	0.24	1.64	0.55	2.5	79.14
Asperula pusilla	0.04	0.17	1.37	0.48	2.08	81.22
Ranunculus spp.	0.16	0.04	1.34	0.47	2.03	83.25
Eriochilus cucullatus	0	0.18	1.23	0.46	1.87	85.13
Poa hothamensis	0.16	0.01	1.19	0.44	1.81	86.94
Poa helmsii	0	0.12	1.06	0.35	1.61	88.55
Rytidosperma pensilata	0.08	0.08	0.99	0.41	1.51	90.06
Solenogyne gunnii	0	0.12	0.81	0.36	1.22	91.28
Veronica serpyllifolia	0.01	0.11	0.8	0.36	1.22	92.5
Geranium 1	0	0.1	0.73	0.33	1.1	93.6
Juncus sp.	0.04	0.06	0.67	0.32	1.02	94.62
Grass A	0	0.09	0.63	0.31	0.96	95.59
Geranium sessiliflorum	0.08	0	0.54	0.28	0.82	96.41
Geum urbanum	0	0.06	0.53	0.24	0.81	97.22
Geranium 2	0	0.05	0.36	0.22	0.55	97.77
Ranunculus eicherianus	0.03	0	0.28	0.17	0.43	98.2
Carex appressa	0.03	0.01	0.28	0.2	0.43	98.63
Taraxacum officinale	0.01	0.02	0.2	0.17	0.31	98.94
Oxalis exilis	0	0.02	0.17	0.14	0.26	99.21
Acaena novae-zelandiae	0.02	0	0.13	0.14	0.2	99.41
Unk 3: Fam. Caryophyllaceae	0.01	0	0.09	0.1	0.14	99.55
Stellaria pungens	0	0.01	0.08	0.1	0.13	99.68
Wahlenbergia gloriosa	0	0.01	0.08	0.1	0.13	99.8
Geranium 3	0	0.01	0.07	0.1	0.1	99.91
Holcus lanatus	0.01	0	0.06	0.1	0.09	100

Appendix III. Cont…

Open Woodland P2 (W2)

Average dissimilarity = 60.06

Species	Low Av.Abund	High Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Anthoxanthum odoratum	0.78	0.1	4.86	1.5	8.09	8.09
Viola betonicifolia	0.64	0.45	3.51	0.99	5.84	13.93
Dichondra repens	0.55	0.95	3.39	0.88	5.65	19.57
Asperula pusilla	0.19	0.51	3.39	0.97	5.65	25.22
Poa hothamensis	0.45	0.47	3.35	0.95	5.59	30.81
Acaena novae-zelandiae	0.29	0.47	3.28	0.94	5.47	36.27
Elymus scaber	0.45	0.13	2.92	0.9	4.87	41.14
Poa costiniana	0.37	0.07	2.76	0.76	4.59	45.73
Hakea microcarpa	0.3	0.22	2.49	0.77	4.15	49.87
Hypochaeris radicata	0.81	0.77	2.4	0.68	3.99	53.87
Cerastium glomeratum	0.26	0.24	2.38	0.75	3.97	57.84
Poa helmsii	0.08	0.31	2.35	0.7	3.91	61.75
Veronica serpyllifolia	0.1	0.31	2.14	0.71	3.57	65.32
Agrostis capillaris	0.25	0.17	2.12	0.69	3.53	68.84
Oreomyrrhis eriopoda	0.24	0.18	2.1	0.69	3.49	72.34
Rytidosperma pensilata	0.24	0.06	1.63	0.6	2.71	75.04
Hydrocotyle laxiflora	0	0.25	1.62	0.56	2.7	77.75
Trifolium repens	0.8	0.96	1.61	0.52	2.68	80.42
Carex appressa	0.13	0.15	1.59	0.55	2.64	83.07
Ranunculus spp.	0.07	0.14	1.18	0.47	1.96	85.02
Acetosella vulgaris	0.11	0.09	1.15	0.46	1.91	86.94
Luzula spp.	0.09	0.06	0.9	0.39	1.5	88.44
Geranium 2	0	0.13	0.85	0.38	1.41	89.85
Eriochilus cucullatus	0.02	0.11	0.8	0.37	1.32	91.18
Unknown H	0.07	0.05	0.71	0.35	1.17	92.35
Geranium 1	0.01	0.09	0.64	0.32	1.07	93.42
Grass B	0.08	0	0.61	0.29	1.01	94.42
Scleranthus biflorus	0.09	0	0.53	0.31	0.87	95.3
Oxalis exilis	0.06	0.01	0.42	0.27	0.69	95.99
Epacris gunnii	0.05	0	0.4	0.23	0.66	96.65
Brachyscome aculeata	0.04	0.02	0.36	0.25	0.6	97.25
Leptospermum grandifolium	0.05	0	0.31	0.23	0.51	97.77
Senecio gunnii	0.04	0.01	0.3	0.22	0.5	98.27
Bulbine bulbosa	0.05	0	0.3	0.23	0.49	98.76
Geranium 3	0	0.04	0.27	0.2	0.45	99.21
Grevillea australis	0.02	0	0.13	0.14	0.21	99.42
Prunella vulgaris	0.01	0.01	0.12	0.14	0.2	99.62
Eucalyptus sp.	0	0.02	0.11	0.14	0.18	99.8
Juncus sp.	0.01	0	0.07	0.1	0.11	99.91
Ajuga australis	0.01	0	0.05	0.1	0.09	100

Appendix III. Cont…

Open Woodland P3 (W3)

Average dissimilarity = 61.32

	Low	High				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Agrostis capillaris	0.71	0.29	4.86	1.12	7.93	7.93
Cerastium glomeratum	0.06	0.6	4.44	1.14	7.24	15.17
Oreomyrrhis eriopoda	0.46	0.69	4.19	0.98	6.83	22
Festuca rubra	0.62	0.53	4	0.93	6.52	28.52
Hypochaeris radicata	0.75	0.58	3.82	0.89	6.22	34.75
Poa hothamensis	0.31	0.4	3.75	0.87	6.11	40.86
Stellaria pungens	0.11	0.4	3.51	0.81	5.72	46.57
Prunella vulgaris	0.21	0.39	3.24	0.86	5.28	51.86
Anthoxanthum odoratum	0.32	0.3	3.24	0.84	5.28	57.14
Acaena novae-zelandiae	0.16	0.33	2.98	0.76	4.86	62
Hydrocotyle sp.	0.02	0.35	2.61	0.72	4.25	66.25
Helichrysum scorpioides	0.32	0.09	2.56	0.72	4.17	70.42
Acetosella vulgaris	0.2	0.23	2.44	0.7	3.97	74.39
Geranium 2	0.08	0.24	2.07	0.61	3.38	77.77
Trifolium repens	0.84	0.96	1.7	0.47	2.77	80.54
Geranium antrorsum	0.17	0.02	1.52	0.46	2.48	83.01
Geranium 3	0.06	0.13	1.33	0.45	2.16	85.18
Carex appressa	0.02	0.14	1.12	0.42	1.83	87.01
Scleranthus biflorus	0	0.14	1.04	0.4	1.69	88.7
Carex breviculmis	0.11	0	0.79	0.35	1.28	89.99
Acaena agnipila	0	0.09	0.67	0.31	1.09	91.07
Asperula pusilla	0.1	0	0.64	0.33	1.05	92.12
Ranunculus sp.	0.04	0.05	0.59	0.3	0.96	93.08
Senecio tenuiflorus	0	0.06	0.46	0.25	0.75	93.82
Geranium 1	0.01	0.05	0.43	0.25	0.7	94.52
Wahlenbergia gloriosa	0.03	0.03	0.42	0.24	0.69	95.2
Elymus scaber	0.02	0.03	0.38	0.22	0.62	95.83
Lotus pedunculatus	0.03	0	0.31	0.17	0.5	96.33
Lagenophora stipitata	0.04	0	0.29	0.2	0.47	96.8
Gonocarpus montanus	0.04	0	0.26	0.2	0.43	97.23
Olearia erubescens	0.04	0	0.25	0.2	0.41	97.64
Arthropodium milleflorum	0.04	0	0.24	0.2	0.4	98.03
Veronica serpyllifolia	0	0.03	0.22	0.17	0.36	98.39
Dichondra repens	0.03	0	0.22	0.17	0.36	98.75
Oxalis exilis	0.02	0	0.18	0.14	0.29	99.04
Rytidosperma pensilata	0.02	0	0.15	0.14	0.24	99.28
Taraxacum officinale	0.01	0.01	0.14	0.14	0.23	99.51
Epilobium billardierianum	0.01	0	0.09	0.1	0.15	99.66
Brachyscome decipiens	0.01	0	0.08	0.1	0.13	99.79
Eucalyptus spp.	0.01	0	0.07	0.1	0.11	99.9
Luzula sp.	0.01	0	0.06	0.1	0.1	100