

PROCESSES EXPLAINING EXOTIC PLANT OCCURRENCE IN AUSTRALIAN MOUNTAIN SYSTEMS



by
Mellessa Schroder
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Certificate of Authorship

I hereby declare that this submission is my own work and to the best of my knowledge and belief, understand that it contains no material previously published or written by another person, nor material which to a substantial extent has been accepted for the award of any other degree or diploma at Charles Sturt University or any other educational institution, except where due acknowledgement is made in the thesis. Any contribution made to the research by colleagues with whom I have worked at Charles Sturt University or elsewhere during my candidature is fully acknowledged. I agree that this thesis be accessible for the purpose of study and research in accordance with normal conditions established by the Executive Director, Library Services, Charles Sturt University or nominee, for the care, loan and reproduction of thesis, subject to confidentiality provisions as approved by the University.

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ABSTRACT

Mountain systems support diverse ecological communities and species adapted to extreme climatic conditions. They are also important for the ecosystem services they provide such as water resources for hydroelectricity generation and irrigation of lowland areas. Inaccessibility and extreme climate have largely protected mountains from wide scale disturbance. In the last century the richness of exotic plant species in mountains has increased on a world wide scale as these landscapes became more accessible through human activities and as temperatures increase under climate change.

Research on exotic plant species in mountains has focussed on exotic species richness in disturbed areas such as roadsides or human nodes such as ski resorts. Other exotic plant studies in mountains have focused on the strong inverse correlation between elevation and exotic species richness at higher elevations. There has been limited study on the role of abiotic (not including temperature) and biotic factors in explaining exotic species richness or abundance.

A smaller number of exotic plant species occur in undisturbed habitats in the Australian Alps when compared with many other lowland Australian natural systems although richness has increased since the 1950s. Exotic plant programs in the Australian Alps remain largely focused on disturbed areas with the greatest extent of exotic plant invasion. There is an increasing need to develop strategies to identify the potential invaders of undisturbed areas (natural habitats). However in order to detect these species we need to have a greater understanding of the processes which lead to exotic plant occurrence in disturbed and undisturbed habitats and the abiotic and biotic factors which may promote invasive species.

This study focussed on improving our understanding of the processes and had two main objectives to: (1) determine the degree to which elevation filtering can explain exotic plant occurrence in disturbed and undisturbed habitats and (2) establish the degree to which biotic and abiotic factors (other than elevation and temperature) explain differences in exotic plant richness and composition between disturbed and undisturbed habitat types. The research was

undertaken in the montane, sub-alpine and alpine areas of Kosciuszko National Park, New South Wales. The park is part of the Australian Alps. Study sites were located at roadsides, human nodes and undisturbed habitats across an elevation gradient of 1000 – 2200 m. Data collection included abiotic and biotic factors such as exotic plant cover, soil samples and elevation.

My results confirmed expectations that disturbed roadsides and human nodes had greater richness and cover of exotic species than undisturbed sites. I found patterns of occurrence between roadsides and human nodes vary and management may need to be approached differently in the two areas. I also found that species composition and soil physical and chemical properties varied between disturbed and undisturbed habitats.

My results suggest that whilst elevation is important in explaining richness in undisturbed habitats, in disturbed habitats exotic plant richness can be explained by understanding interactions between elevation and soil attributes. I also found that exotic species composition in undisturbed and disturbed habitats is explained by a combination of mean temperature and soil attributes. It would appear that elevation (climate) may not prevent exotic plant species establishment at higher elevations and areas where soil disturbance has occurred are more vulnerable to exotic species establishment.

The results from this thesis improve our understanding of the drivers of exotic plant richness and composition in Australian mountain systems. To reduce the potential for increases in exotic species richness and cover anthropogenic disturbances must be minimised. This is even more important in light of predicted changes to climate. Future management should focus on predicting and targeting species which may pose the greatest threat to biodiversity.

CHAPTER 1 INTRODUCTION

1.1 General introduction

Biological systems globally have been impacted by increased anthropogenic disturbance. One component of this change has been the increased human movement of exotic plant species around the globe (Dukes and Mooney 1999, Stohlgren *et al.* 2011, Stohlgren *et al.* 2013). Changes in land use practices through the development of human settlements and agriculture have provided conditions conducive for exotic plant establishment. A number of processes interact to facilitate suitable conditions for exotic plant growth such as altered soil nutrient regimes, changes in water cycles, reduction in biotic resistance and release from natural predators (Hobbs 1989, Tillman 1997, Lonsdale 1999, Davis *et al.* 2000).

Exotic plant richness and distribution are globally on the increase (Alpert *et al.* 2000, Becker *et al.* 2005, Pyšek *et al.* 2011). Many exotic plant species will persist in disturbed areas; however some species have the potential to invade natural areas and some of these species are a threat to endemic plant and animal communities (Kolar and Lodge 2001, Pyšek *et al.* 2004).

Many lowland systems where human development is greatest have had the most rapid change and have been found to have the highest richness and cover of exotic plant species (Drake *et al.* 1989). Continents and islands which have been geographically isolated, such as Australia, have demonstrated a high vulnerability to exotic plant invasion (Di Castri 1989). The evolutionary and geological isolation of the Australian continent has led to a high degree of biological endemism which has made ecological systems susceptible to exotic plant invasion (Williams and West 2000). It has been estimated from herbarium records that 10-15% of the Australian flora is now exotic (Groves 2002, ABG 2009).

Many mountains globally, including the Australian Alps, are important biologically due to their high endemism. They support diverse ecological communities and species adapted to extreme climatic conditions (Costin 2000, Körner 2003). They are also important for the ecosystem services they provide such as water resources for hydroelectricity generation and irrigation of lowland areas (Körner 2004, Viviroli 2007, Worboys *et al.* 2011).

Due to their inaccessibility and extreme climate, mountains have a lower incidence of exotic plant species compared with many lowland systems (Daehler 2003, McDougall *et al.* 2011a). Low species richness at high elevations may be attributed to the reduced spatial area at high elevations (Rahbek 1995, Rahbek 2005, Romdal and Grytness 2007). The smaller area of alpine environments could mean that fewer species are available for dispersal. Low species richness at high elevations may also be influenced by gravity as propagules are more likely to be dispersed downhill than uphill or in water (Daehler 2003, Pyšek *et al.* 2007). Despite these factors, exotic plant richness is increasing in mountains as human dispersal of seeds overcomes gravitational constraints and propagules are dispersed along roadsides, into ski resorts or around huts (Mallen-Cooper 1990, Johnston 2005, McDougall *et al.* 2005, Morgan and Carnegie 2009). Increased exotic species richness is predicted to continue as land use change has made mountains more accessible to agriculture and recreation pursuits (Pauchard *et al.* 2004, Johnston 2005, Becker *et al.* 2005). In addition, climate change, increased temperatures and reduced snow cover and duration have been linked to increases in species richness at higher elevations (Pauchard *et al.* 2009, Jump *et al.* 2011, Pyšek *et al.* 2011).

The Australian Alps have a lower number of exotic plant species than adjoining lowland areas (McDougall *et al.* 2005). This provides an opportunity to improve our understanding of the processes which lead to exotic plant occurrence in mountain systems and develop strategies to manage exotic plants before they may become widespread. Many exotic species were first recorded in recent decades (Mallen-Cooper 1990, Johnston and Pickering 2001, Johnston 2005) and may not have reached their full extent (Haider *et al.* 2010). Managers need to be able to distinguish between those species that will be invasive in undisturbed natural areas and those that are not. To achieve this we must develop an understanding of the processes which influence exotic plant occurrences in the Australian Alps. This information can then be used to guide strategies which can separate the future potential invaders of natural habitats from the larger pool of species present in disturbed habitats.

1.2 Definition of an exotic plant species

In this thesis the term **exotic plant species** encompasses all plants which have been introduced into a new geographic locality. Exotic plant species may demonstrate different

levels of invasiveness based on their traits or the environmental conditions in the area they are introduced to (Richardson and Pyšek 2006). Because of this, Pyšek *et al.* (2004) proposed the following terms be adopted globally to describe exotic (alien) plant species.

- **Casual (alien) exotic plants** may flourish and reproduce occasionally outside cultivation but will eventually die out.
- **Naturalized plants** are those species that can produce self-sustaining populations and establish without human intervention.
- **Invasive plants** are a subset of naturalized species and have the ability reproduce in large numbers and are capable of spreading over a large area.
- **Transformer plants** are a subset of invasive plants that have the ability to alter ecosystem function.

1.3 Definition of elevation versus altitude

There has been ongoing debate over the interchangeable use of the word 'elevation' and 'altitude' in scientific literature (Körner 2007, McVicar and 2013). In this thesis the word **elevation** is used to describe the vertical distance between a point on the land surface and a reference point. The term **elevational gradient** is used to describe the increasing elevation in a mountain range and its influence on climatic factors (McVicar and Körner 2013).

The term **elevational filtering** has been used to describe how increasing elevation and its associated effects on climate, and the uphill movement of plant propagates can explain patterns in exotic species occurrence, i.e increasing elevation may explain a reduction in the richness of species (Alexander *et al.* 2011, Seipel *et al.* 2011).

1.4 Definition of disturbed and undisturbed habitats

In this thesis disturbed habitats are considered those localities where major land use change has occurred such as along roadsides or in ski resorts. Human nodes is the term used in this thesis to encompass ski resorts, huts and camping areas. Undisturbed sites in this study are those localities where past land use may have modified soils, but sites support a successional advanced plant community (Rejmánek 1989, Rejmánek *et al.* 2005).

1.5 Background and study area

The Australian Alps is a mountainous landscape comprising a contiguous group of National Parks straddling a 340 km length of the Great Dividing Range that extend from the Australian Capital Territory through the Snowy Mountains in New South Wales to the high areas of Victoria (Figure 2.1). Kosciuszko National Park is the largest park (690,000 hectares) in the Australian Alps and is the location for this study.

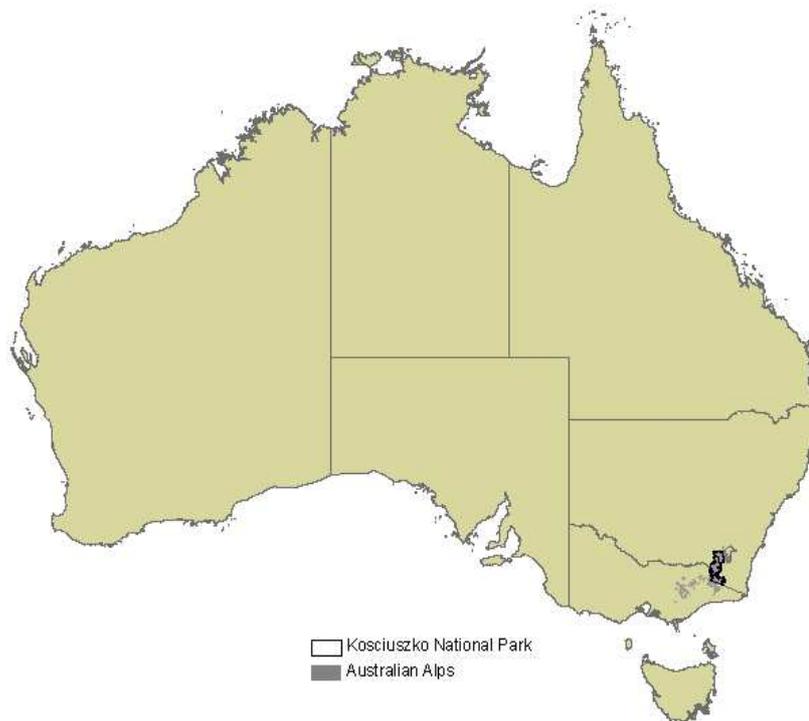


Figure 1.1. Australian mainland, Kosciuszko National Park is identified by the black outline. The Australian Alps are identified by the grey shading.

The Australian Alps differ from many other mountain systems due to their low-set topography and deep alpine humus soil cover (Kirkpatrick 2003). They support a number of endemic plants and animals. The alpine portion of Kosciuszko National Park represents a small area (0.001%) of the Australian mainland (Costin 1954, Costin *et al.* 2000).

The Australian Alps can be divided into three main vegetation zones. The montane area, 1100-1400 m above sea level (ASL), is dominated by *Eucalyptus pauciflora*, *E. dalrympleana*,

E. delegatensis, *E. rubida* and *E. viminalis* forests. The sub-alpine occurs from 1400-1850 m and is dominated by *E. niphophila* woodland interspersed with wet and dry heathlands, bogs and grasslands. Alpine areas above the treeline at 1850 m are dominated by low-growing shrubs, herb fields, grasslands, feldmark and bogs (Costin 1954, Costin *et al.* 2000).

Soil characteristics in the higher elevation areas are driven by climate, parent material, topographic position and vegetation type (Kirkpatrick *et al.* 2014). The additional influence of aeolian dust deposits from the western plains mixes with parent material increasing nutrients and changing soil characteristics (Johnston 2001). Bare soils in the alpine and sub alpine may experience needle ice which can accelerate erosion and inhibit re-vegetation (Lynch and Kirkpatrick 1995).

Humus soils are dominant above 1400 m where they cover all but a few rocky areas and support almost complete vegetation cover. The humus soils are developed largely from the breakdown of plant material and have low pH due to the leaching of minerals and nutrients as a result of high rainfall. Humus soils and organic peat soils (bogs and fens) are important for their water holding capacity (Costin 1954, Good 1992). Most of the study sites in this thesis occur in areas of humus soil with the exception of some montane sites on friable loams and grey-brown podsolics of various depths (Costin 1954).

The past impact on vegetation and the loss of soil from grazing took many decades to recover once grazing was removed (Wimbush and Costin 1979, Scherrer 2003). Equally the loss of soil after fire has also influenced the recovery of vegetation (Kirkpatrick and Bridle 2013).

The climate is characterized by low temperatures and is influenced by continental westerly circulation systems and coastal effects from the Southern Ocean. The north-south orientation of the mountain range intersects the west-to-east weather patterns resulting in an average yearly precipitation of 2000 mm (Costin *et al.* 2000). Snow lies on the ground for 1-4 months in the sub-alpine zone and 6-9 months in the alpine zone (Green and Osborne 2012).

1.6 Land-use history

Cattle and sheep were introduced into the Australian Alps in the 1800s and by the end of the 19th century the practice of summer grazing and burning of vegetation to promote regrowth was common (Good 1992). These practices impacted on soil and vegetation (Costin 1954) and led to the introduction of the first exotic plant species (Maiden 1898). Grazing ceased in the main range alpine areas in 1944 and in the broader Kosciuszko National Park by the 1960s due to its impact on soils and vegetation (DEC 2006). To stabilise soils after stock were removed, a range of exotic plant species were selected due to their ability to grow in shallow nutrient deficient soils (Clothier and Condon 1968). These species still remain widespread in disturbed habitats today and include *Agrostis capillaris*, *Festuca rubra*, *Trifolium repens* and *Phleum pratense* (Johnston 2005, McDougall *et al.* 2005). *Festuca* species are still used for road side and ski slope stabilisation (DECC 2007).

The Snowy Mountains Hydro Electrical Scheme was constructed between 1949 and 1972 and this altered the hydrology, topography and ecology of Kosciuszko National Park by expanding road networks, electricity easements and urban development (Good 1992). This new infrastructure provided the means for exotic plants to be transported on vehicles and machinery and to establish in disturbed areas (Mallen-Cooper 1990, Johnston 2005, McDougall *et al.* 2005, Jeuch 2006). Roadside stabilization practices varied based on the extent of disturbance. At some localities *Salix* species were used to stabilize steep road batters on the Alpine Way and Guthega Road (OEH 2012). Other road stabilization practices are less obvious and the methods used at the time unknown.

Fire is a natural component of Australian mountains with extensive widespread fires occurring every 50 -100 years (Williams *et al.* 2009). Fire has had major impacts on some communities with bogs and fens being vulnerable to loss of soil and erosion (Good 2006). In 2003 fires burnt 71% of Kosciuszko National Park (Zystra 2006). This fire has led to an expansion in some exotic species distributions, such as *Hieracium aurantiacum* (Caldwell & Wright 2011) and *Leucanthemum vulgare* (OEH 2013).

Other exotic species were directly introduced into gardens in the villages which formed as part of this new infrastructure, and more recently in ski resorts (McDougall and Appleby

2000, Pickering *et al.* 2002). Ski resort infrastructure has expanded since the 1960s and a range of exotic species have been introduced inadvertently through construction processes (Johnston 2005). In more recent decades, increased recreation into more remote areas to access huts continues to transport exotic species throughout the Australian Alps (Morgan and Carnegie 2009, Mount and Pickering 2009).

Many of the studies on exotic plant species undertaken in the Australian Alps provide lists of exotic species at a particular point (a snap-shot) in time. Johnston (2005) documented the increase in exotic species by analysing ten studies undertaken from 1898 to 1999. Although the studies varied in locality and methodology, they provide valuable information on the increase in species diversity in the sub-alpine and alpine areas over the last century. In 1898, six species (Maiden 1898) were recorded, by 1954 this had increased to 44 (Costin 1954), by 1986 to 135 (Mallen-Cooper 1990) and by 1999, 175 exotic species were recorded in the sub-alpine and alpine zones of the Australian Alps, 165 of these in Kosciuszko National Park (Johnston 2005). This increase in species was directly associated with changes in land use patterns since the 1950s.

Australian mountains are consistent with other global mountain systems as disturbance, in particular roads, has been linked to exotic species dispersal and establishment (Mallen-Cooper 1990, Scherer-Lorenzen *et al.* 2000, Kalin Arryo *et al.* 2000, Petryna *et al.* 2002, Johnston 2005, McDougall *et al.* 2005, Becker *et al.* 2005, Jakobs *et al.* 2010, Haider 2010, Paiaro *et al.* 2010). Since the 1950s, species associated with cattle and sheep grazing have been joined by species dispersed along roadsides, used in revegetation programs and ornamental species grown in high elevation gardens (Mallen-Cooper 1990, Johnston and Pickering 2001, McDougall and Appleby 2000, McDougall *et al.* 2005).

1.7 Why undertake this study?

Exotic plant management in Kosciuszko National Park is largely focused on species which are an issue in lowland agricultural systems (with some exceptions, *Hieracium auranticum* and *Cytisus scoparius*, OEH 2012). Control programs in much of the lower elevation areas of the park are focused on meeting neighbour and visitor expectations, and target roadsides and recreational areas. Programs remain focused on disturbed areas with the greatest extent of

exotic plant invasion (OEH 2012). There are no strategies (predictive tools) currently available to identify future invaders in the Australian Alps.

With the exception of *Hieracium auranticum* (Caldwell and Wright 2012) minimal resources are directed towards educating park users and staff in detecting and controlling new incursions. At present undisturbed areas at high elevation have low levels of invasion of exotic plant species (McDougall *et al.* 2005). However, the richness of species is increasing in disturbed areas (Mallen-Cooper 1990, Johnston, 2005). This is likely to continue as a result of increased infrastructure development, recreation and climate change.

There is an increasing need to develop strategies to identify the potential invaders of undisturbed areas (natural habitats). However in order to detect these species we need to have a greater understanding of the processes which lead to exotic plant occurrence in disturbed and undisturbed habitats and the abiotic and biotic factors which may promote invasive species in the Australian Alps.

1.8 Study aims

Previous studies have identified the significant role of elevation in explaining low exotic species richness at high elevations in disturbed global and Australian mountain systems (Becker *et al.* 2005, McDougall *et al.* 2005, Haider *et al.* 2005, Mallen-Cooper and Pickering 2008). Given the complexity of other factors which occur as part of disturbance, such as changes in resources (Davis *et al.* 2000, Burke and Grime 2006), it is likely that other abiotic and biotic factors may play a significant role which has been overlooked.

This study will focus on improving our understanding of the processes underlying exotic species occurrence in the Australian Alps and has two main objectives:

- 1. Determine the degree to which elevation filtering can explain exotic plant occurrence in disturbed and undisturbed habitats.**
- 2. Establish the degree to which biotic and abiotic factors (other than elevation and temperature) explain differences in exotic plant richness and composition between disturbed and undisturbed habitat types.**

1.9 Thesis outline and research questions

The thesis is presented in a series of chapters.

Chapter 1 Provides a general introduction

Chapter 2 reviews the literature on exotic plants in mountain systems and examines documented relationships between exotic plant species and abiotic and biotic attributes. This chapter identifies where further investigation may improve our understanding of the processes which influence exotic plant patterns in Australian mountain systems.

Chapter 3 Investigates the relationships between elevation, soil attributes and exotic plant richness in disturbed mountain systems and seeks to answer the following research questions;

1. Does exotic species richness decline with increasing elevation in different disturbance types (roadsides and human nodes)?
2. Are exotics at high elevations a nested subset of those at lower elevations?
3. Can elevation and soil attributes explain patterns of exotic species richness in roadsides and human nodes?
4. Do areas with different disturbance regimes (human nodes and roadsides) have different exotic species and if so do these patterns reflect differences in underlying abiotic attributes?

Chapter 4 examines the role of elevation and soil attributes in explaining exotic plant richness in undisturbed ('natural') mountain systems and addresses the following research questions;

1. Does exotic species richness decline with increasing elevation in natural areas?
2. Do the exotic species which occur in natural areas change along an elevation gradient?
3. Are the exotic species which occur in natural areas a subset of those which occur in adjacent disturbed areas at the same elevation?
4. Can elevation and soil attributes explain patterns of exotic species richness in natural areas?

Chapter 5 investigates associations between exotic species composition and soil attributes and temperature in disturbed and undisturbed mountain systems. Specifically I address the following questions:

1. How does the composition of exotic species vary between disturbed and undisturbed habitat types?
2. How do soil attributes vary between disturbed and undisturbed habitat types?
3. What is the relationship between exotic plant composition and soil attributes and temperature?
4. Does the influence of abiotic and biotic factors vary for different species?

Chapter 6 summarises the main findings from the thesis and provides recommendations for exotic plant management and future research in the Australian Alps.

CHAPTER 2 LITERATURE REVIEW

2.1 Introduction

This literature review will encompass exotic species research undertaken globally in mountain systems and studies at regional and local scales in the Australian Alps. It will examine the relationship of exotic plant species to abiotic and biotic factors and identify where further examination may improve our understanding of the processes contributing to exotic plant patterns in Australian mountain systems.

The review is divided into the following sections:

1. Exotic plant species literature from global mountain regions.
2. Exotic plant species research undertaken in the Australian Alps.
3. The role of disturbance and changes to soil physical and chemical properties in explaining exotic plant species richness and cover.
4. Exotic species traits studies and their relevance to mountain systems.

2.2 Exotic plant species literature from global mountainous regions

Inaccessibility and extreme climate have largely protected mountain systems from wide scale disturbance (Körner 2004). In the last century the richness of exotic plant species in mountains has increased on a world wide scale as these landscapes became more accessible through human activities and as temperatures increase under climate change (Pauchard *et al.* 2009, Pysek *et al.* 2011).

Whilst the ecology of mountain systems varies across continents, increased natural or anthropogenic disturbance has been the common denominator in the establishment of exotic species in mountains (McDougall *et al.* 2011a). Anthropogenic disturbance has increased rapidly in the last century. Studies undertaken in the mountainous regions of Europe, North America, South America, Hawaii, Canary Islands, New Zealand and Australia have all identified the significant role that anthropogenic disturbance has played in providing conditions suitable for the establishment of a range of exotic species (Mallen-Cooper 1995, Jesson *et al.* 2000, Scherer-Lorenzen 2000, Kalin Arryo *et al.* 2000, Petryna *et al.* 2002, Becker *et al.* 2005, Jakobs *et al.* 2010, Haider 2010, Paiaro *et al.* 2010).

Co-operative global studies on exotic plants in mountainous regions (McDougall *et al.* 2011, Alexander *et al.* 2011, Seipel *et al.* 2011) have assisted in unravelling previous misconceptions that mountains were at a low risk of invasion (Humphries *et al.* 1991). In a global study of 13 mountain systems 1000 species from over 100 families were found to be naturalised (McDougall *et al.* 2011a). Despite these findings the number of exotic plant species in natural mountain systems remains significantly less than in many lowland environments (Daehler 2003, McDougall *et al.* 2011a).

The region of origin has been found to be a key factor in determining the successful establishment of an exotic plant species (Kolar and Lodge 2001). Exotic plant species fall into two distinct categories based on their origin (Di Castri 1989). This includes those species categorised as 'old world' exotics, which originated in Europe and the Mediterranean, and 'new world' species derived from more geographically isolated locations such as Australia, South America or the Pacific. The 'old world' localities are dominated by exotic species with origins from Asia and the Americas, whilst the 'new world' is dominated by Eurasian species (Di Castri 1989). In eight mountainous regions, including the Australian Alps, South Chile, Central Chile, Swiss Alps, Canary Islands, Hawaiian Islands and North America, more than half of the exotic species were of Eurasian origin (Seipel *et al.* 2011).

Steep mountain terrain can slow the uphill movement of species, and the extreme climate experienced in the higher elevations of mountains may prevent or reduce establishment of exotic plant species. This has been described as an elevation or climatic filter (Alexander *et al.* 2011). The smaller land area at high elevation sites may also influence low species richness. A number of studies on exotic species in mountains have described the strong inverse correlation between exotic species richness and elevation, although patterns do vary. A linear pattern has been demonstrated for higher latitude areas including the Swiss Alps (Becker *et al.* 2005), Chile (Pauchard and Alaback 2004), with species numbers declining as elevation increases. Other more temperate regions, such as the Canary Islands (Haider 2010) and Australia (McDougall *et al.* 2005, Mallen-Cooper and Pickering 2008), show a unimodal pattern with a 'hump' in exotic species richness at mid-elevations. Whilst the elevation filter may help to preclude many species, the presence of species with the ability

to adapt to extreme climatic conditions is accelerated if they are dispersed through direct introduction (Alexander *et al.* 2011).

With predicted changes in climate such as increased temperatures and reduced snow cover, elevation filtering may become less effective in preventing exotic species establishment at higher elevations (Pickering *et al.* 2004, Pauchard *et al.* 2009, Steffen *et al.* 2009). Studies have already indicated an increase in exotic plant species. In the Czech Republic exotic species increases have been attributed to warming in the last two centuries (Pyšek *et al.* 2011). In Taiwan similar trends have led to an increase in elevational ranges of both endemic and introduced species (Jump *et al.* 2011).

Many species with a broad climatic range have demonstrated the ability to establish in mountains (Pyšek 2009, Haider 2010, Shah *et al.* 2011). In a global study of 13 mountain regions, over a third of exotic species were elevational generalists rather than mountain specialists (McDougall *et al.* 2011). Many of the species found at the top of mountains are a sub-set of the species which are also located in the surrounding lowlands. These species are considered climatic generalists as they have the ability to adapt to a range of conditions (Alexander *et al.* 2011). Ongoing movement of exotic species from lowland areas to mountainous areas is likely particularly where exotic plant richness is high and modes of dispersal such as transport corridors exist.

Global and regional studies indicate that the movement of exotic species into mountain systems has been promoted by an expansion in road networks (Becker *et al.* 2005, Haider 2010, Paiaro *et al.* 2010, Seipel *et al.* 2011). Road verges are often the first point of introduction for exotics (Daehler 2003, Pauchard *et al.* 2004, McDougall *et al.* 2005, Kosaka *et al.* 2010, Pollnac *et al.* 2012). With the increasing use of mountain systems not only for agriculture, but for winter sports and summer based tourism, the potential for dispersal has increased (Johnston and Pickering 2001, Pauchard *et al.* 2009).

A number of studies have shown a positive correlation between time since introduction and a species' maximum elevation (Becker *et al.* 2005, Haider *et al.* 2010, Pyšek *et al.* 2011). Biogeographic information for residence time from other mountain systems with similar

climates but with longer histories of exotic species introduction could be used to assist in detecting potential new invaders.

Nutrient cycles have also been altered in many mountains. Atmospheric deposition of nitrogen from the burning of fossil fuels and the use of fertilizers has increased nitrogen availability, making systems more conducive for the establishment of exotic species (Vitousek *et al.* 1997, Scherer–Lorenzen *et al.* 2000). Studies from lowland environments (Hobbs and Huenneke 1992, Burke and Grime 1996) indicate the significant role increased nutrients can play in the establishment of exotic species in environments that naturally have low levels of soil nutrients. In addition, the establishment of nitrogen fixing exotic species such as *Lupinus polyphyllus* and *Cytisus scoparius* can also contribute to increases in nitrogen availability (Waterhouse 1988, Scherer-Lorenzen *et al.* 2000).

Away from areas of disturbance, exotic species richness and cover are low in natural communities or National Parks in mountains (McDougall *et al.* 2005, Chytry *et al.* 2008, Pyšek *et al.* 2011). In these areas exotic species are unable to compete with native plant communities (Seipel *et al.* 2011). Due to the complexity of examining multiple species, most research on ecological impacts in mountains has focussed on individual invasive species, such as *Hieracium* spp. and *Bromus tectorum* (Rose *et al.* 1995, Larson *et al.* 2011).

2.3 Existing exotic plant species research undertaken in the Australian Alps

Many studies undertaken in the Australian Alps provide lists of exotic species at a particular point in time. Over time, species associated with cattle and sheep grazing have been joined by species used in revegetation and ornamental species grown in high elevation gardens (Clothier and Condon 1968, Mallen-Cooper 1990, McDougall and Appleby 2000, McDougall *et al.* 2005). Other species have arrived through direct movement along roadways from lowland areas (Johnston and Pickering 2001, Jeuch 2006, Mallen-Cooper and Pickering 2008). Recent research suggests that in Kosciuszko National Park infrastructure construction has had a greater impact on the richness and abundance of species than past grazing (Mallen-Cooper 1990, Johnston 2005). Increasing elevational distribution records and the establishment of new species are a frequent occurrence (Schroder 2010).

Past grazing was implicated in the impact on soil and vegetation (Costin 1954) but after grazing ceased in the 1960s monitoring of sites on the Main Range and at Gungaharten in Kosciuszko National Park demonstrated recovery of native vegetation communities (Wimbush and Costin 1979).

Roadsides have been the focus for most of the exotic species studies in the Australian Alps with some additional studies around remote huts, ski resorts and different walking track types (Mallen-Cooper 1990, McDougall and Appleby 2000, McDougall 2001, Godfree *et al.* 2004, Johnston and Johnston 2004, Johnston 2005, Jeuch 2006, McDougall *et al.* 2005, Mallen-Cooper and Pickering 2008, Morgan and Carnegie 2009). Riparian and wetland systems in alpine and sub alpine regions of the Australian Alps have had insufficient study of exotic species. These systems appear to be vulnerable to invasion when close to disturbed areas (pers. observ.).

Most exotic species in Australian mountain systems are from Europe, including 90% of the 128 species recorded by McDougall *et al.* (2005). The most common species at higher elevations also occur in the lowlands surrounding the Australian Alps (McDougall *et al.* 2005). Of the 175 species recorded across the Australian Alps (Johnston and Pickering 2001), 90% were grasses, herbs or rushes, the remaining 10% shrubs and trees. Many of the shrubs and trees such as *Cytisus scoparius* and *Salix* spp. are considered priority pests and are targeted in control programs (DEC 2009, OEH 2012).

Global studies indicate that natural environments with intact natural communities have capacity to resist establishment of exotic plant species (Daehler 2003, D'Antonio and Chamber 2006, Seipel *et al.* 2011). In the Australian Alps exotic cover was found to be rarely greater than 5% and generally less than 1% in natural communities, except on limestone (McDougall *et al.* 2005). In the northern part of Kosciuszko National Park, Godfree *et al.* (2004) examined the resistance of different habitat types to exotic plant species and found grasslands and woodlands contained more cover of exotic species than tall *Eucalyptus* forest and montane bogs.

To understand the vulnerability of natural habitats to exotic species invasion, some studies have focussed on a single exotic species. Wearne and Morgan (2004) identified the impact

on sub-alpine woodland in the Australian alps of the exotic species *Cytisus scoparius*, which is recognised as a transformer species. It changes the soil structure and soil moisture levels and reduces light through shading (Waterhouse 1988). Ultimately these changes lead to a decline in native species diversity (Wearne and Morgan 2004, Hosking *et al.* 2013). *Achillea millefolium* was identified as an emerging invasive exotic in Kosciusko National Park (Johnston 2005) and became a target for weed control in the late 1990s (Sanecki *et al.* 2003) due to its competitive growth with native species such as *Poa fawcettiae* (Johnston 2005).

Nutrients promote exotic species establishment and persistence in a number of lowland systems in Australia (Hobbs 1989, Prober *et al.* 2002, Leishman and Thomson 2005), but have not sufficiently been investigated in mountain systems. Investigation of soils along a road verge in the Bogong High Plains in the Australian Alps indicated differences in soil chemistry between the road verge (which contained predominantly exotic vegetation) and adjoining natural habitat. The disturbed site had higher phosphorus and lower potassium levels than the native community (McDougall 2001). A study investigating changes in soil properties at varying distances from road verges in the sub-alpine in Kosciuszko National Park demonstrated that road sides and verges showed significant differences in soil chemistry and physical condition (Johnston and Johnston 2004). Soil nutrients such as nitrogen and pH were higher in undisturbed vegetation. In road verges pH and calcium were much higher and nitrogen and organic carbon much lower than undisturbed vegetation. Exotic species richness was found to be greater in areas of disturbance where the soils physical and chemical characteristics of soils had been altered

The implications of climate change on existing naturalised species in the Australian Alps are largely unknown, with the exception of modelling undertaken for *Hieracium* species (Beaumont *et al.* 2009) and *Achillea millefolium* (Johnston 2005). The alpine areas of the Australian Alps have warmed at the rate of 0.2° C per decade over the past 35 years and it is predicted that the current snow line will rise and the duration of snow cover will decline (Hennessy *et al.* 2003). These changes may provide conditions more suited for expansion of existing exotic plants and for new species to establish (Pickering *et al.* 2004, Duursma *et al.* 2013). Climate change highlights the need to increase our understanding of the processes behind exotic species invasions.

2.4 The role of disturbance and changes to soil physical and chemical properties in explaining exotic plant species richness and cover

Disturbance is an important part of all ecosystems and often causes changes in resources such as water, nutrients and light (Hobbs and Huenneke 1992). Disturbance can be from natural events, such as flood and fire, or anthropogenic, such as land clearing and infrastructure construction. Disturbance in natural habitats may provide advantageous conditions for exotic species to invade (Davis *et al.* 2000). Once a plant propagule is transported into a new system, abiotic and biotic factors affect the recruitment and establishment of a species (Lonsdale 1999). Different species may be affected by changes following disturbance. (Mack and D'Antonio 1998, Davis *et al.* 2000, Jesson *et al.* 2000).

Increases in available soil nutrients have been identified as a major driver of exotic plant invasions in lowland systems (Hobbs 1989, Burke and Grime 1996, Leishman and Thomson 2005). In a number of low nutrient Australian habitats, higher levels of available soil nutrients – in particular nitrogen and phosphorus – have been linked to an increase in exotic species occurrence (Hedde and Specht 1975, Hobbs 1989, Prober *et al.* 2002, Leishman and Thomson 2005).

Elevated soil nutrients associated with disturbance can increase exotic species cover (Hobbs 1989, Stohlgren *et al.* 1999). Exotic species cover can be highest in areas where a combination of anthropogenic disturbance and nutrient application has occurred (Hobbs and Atkins 1988, Burke and Grime 1996). Fire can have a negative effect on soils by removing organic matter and changing nutrient cycles (Certini *et al.* 2005). In the Australian Alps soil exposure following fire can lead to wind and water erosion which may impede regeneration of plant species (Williams *et al.* 2009).

Other studies have identified the ability for exotic species to increase with nutrient addition alone. Fertilization of Californian grassland on soils which are low in nutrients promoted the invasion and dominance of non-native grasses (Huenneke 1990). In glass house experiments, exotic species had faster growth rates than native alpine species following nutrient addition (Mallen-Cooper 1990, Johnston 1995).

The source of nutrients may be through application of fertilizer (Burke and Grime 1996), through imported materials such as road base (Cale and Hobbs 1991) or through atmospheric deposition (Vitousek *et al.* 1997). All three could be considered for the Australian Alps. Fertilizer has been used in revegetation programs (McDougall *et al.* 2005) and gravel has been used in the development of roads, which may be different from the surrounding geology (Mallen-Cooper 1990, McDougall 2001, Johnston and Johnston 2004). Atmospheric dust can also contribute to soil nutrients (Johnston 2001).

Low productive environments with low soil nutrients have less exotic species richness and cover than higher productive environments (McIntyre and Lavorel 1994, Bashkin *et al.* 2003). Soils in the alpine and subalpine areas of Kosciuszko National Park are largely derived from granite geology and are low in nutrients, however the basalt and limestone derived soils in the north of the park are much more fertile (Costin 1954) and exotic species cover is higher in these areas (McDougall *et al.* 2005).

Establishment of exotic species can lead to major increases or decreases in soil nutrients (Ehrenfield *et al.* 2003). Once a species is established it may continue to alter ecosystem processes or favour the establishment of new species at a site (Corbin and Antonio 2004, King and Downey 2008, Turner *et al.* 2009). At localities where soil nutrients are high a short term reduction in nutrient availability can be achieved through fire or the addition of organic matter low in nutrients such as sawdust or sugar (Blumenthal *et al.* 2003, Prober *et al.* 2005).

Disturbance and exotic species may also impact on soil biota (Wardle *et al.* 2004, Wolfe and Klironomos 2005, Reinhart and Callaway 2006). The relationship between native alpine plant species and the symbiotic root fungi, arbuscular mycorrhizal fungi (AMF) is important in Australian mountains. The paucity of AMF in disturbed habitats could advantage exotic plant species (Johnston and Ryan 2000).

Understanding the role that soil factors play in preventing or facilitating invasion of exotic plant species is important because of increased anthropogenic disturbance in mountain systems. The relationship between disturbance and soil resource changes has been recognised on a global and national scale as a key mechanism in facilitating exotic species occurrence in many lowland systems. Understanding if soil attributes can explain exotic

species richness and cover in Australian mountain ecosystems could assist in future management.

2.5 Exotic species trait studies and their relevance to mountain systems

Plant functional trait studies have attempted to differentiate which attributes may be associated with invasive exotic plant species (Pausas *et al.* 2003, Lake and Leishman 2004, Hamilton *et al.* 2005, Grotkopp and Rejmanek 2007, Tecco *et al.* 2010). A succession of traits has been used to separate invasive from non-invasive exotic species this includes, high specific leaf area, early and longer phenology, leaf area allocation and shoot allocation (Lake and Leishman 2004, Grotkopp and Rejmanek 2007, Pyšek and Richardson 2007, Ordonez *et al.* 2010, Tecco *et al.* 2010, Van Kluennen *et al.* 2010).

As factors leading to exotic species establishment may change with time, differing traits may be used under different biogeography and climate (van Kleunen 2010). A study of native species in mountains demonstrated that the same species can have very different growth responses along altitudinal gradients (Körner 2003). Therefore it is also possible that the types of species traits which make exotic species invasive in lowland systems may change at higher elevations. Plant species with cold tolerant adaptations such as perennial underground storage and early flowering times may be important at higher elevations when seasons are short (Körner 2003).

Some studies suggest that the very traits that make a successful exotic species are the same traits which make a successful native plant (Thompson and Davis 2011). Two studies in the Australian Alps were unable to separate the traits of exotic plants (excluding *Trifolium repens*) from native species (Godfree *et al.* 2004, Pickering and Venn 2013). Exotic plants in the Alpine area demonstrated contrasting functional traits – common species showing different traits from less common species. Traits were also different between exotic plants in the alpine and sub-alpine (Pickering and Venn 2013).

2.6 Synthesis

Research on exotic plant species in mountains has focussed on exotic species richness in disturbed areas such as roadsides or human nodes such as ski resorts (Haider *et al.* 2010,

Alexander *et al.* 2011, Seipel *et al.* 2011). Much research has focussed on the strong correlation of reduced exotic plant richness with increasing elevation. There has been limited study on the combined role of abiotic and biotic factors in explaining exotic species richness or cover.

Based on the literature review, Figure 2.1 describes the major processes which have led to the introduction of exotic plant species into the Australian Alps. Exotic plant species are dispersed around the globe into lowland systems (Stohlgren *et al.* 2011). These species can then be dispersed from lowland systems along roads or through direct introductions for ornamental use into mountain systems (McDougall and Appleby 2001, Becker *et al.* 2005, Alexander *et al.* 2011). The species which reach the higher elevations are capable of tolerating cold climates (Seipel *et al.* 2011) and some of these have the ability to invade natural habitats (McDougall *et al.* 2011, 2011a).

Many of the factors associated with this model will be investigated in later chapters.

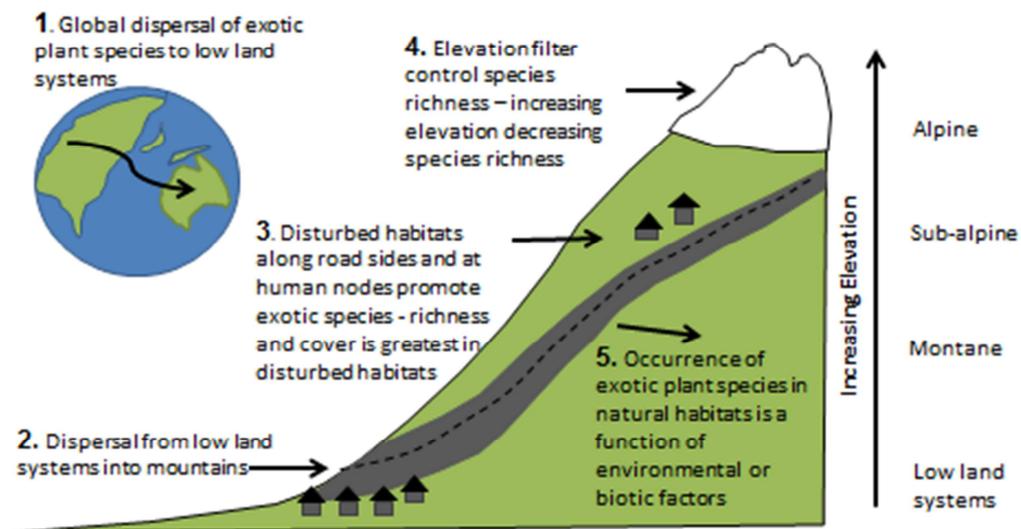


Figure 2.1. The major processes involved in the introduction of exotic plant species into alpine landscapes.

CHAPTER 3 THE ROLE OF ELEVATION AND SOIL ATTRIBUTES IN EXPLAINING EXOTIC PLANT RICHNESS IN DISTURBED MOUNTAIN SYSTEMS

3.1 Introduction

Mountain systems around the world are under increasing pressure from changes in land use. Mountains which were difficult to access due to their harsh climate remained protected from wide scale anthropogenic impacts. In the last century the invasion of mountain systems by exotic plant species has increased across the globe as these landscapes become more accessible through increased human activities and as climate change weakens biotic resistance (Pauchard *et al.* 2009, Pyšek *et al.* 2011, McDougall 2011a).

Many mountain systems globally provide habitats for a range of plant and animal species specifically adapted to cold climates (Körner 2003). Mountain systems are also important for the ecosystem services they provide such as the collection and supply of water to low land systems (Körner 2004). Mountain systems still remain much less invaded by exotic plant species than adjoining lowland systems and the distribution of exotic species away from areas of disturbance in protected mountains (i.e. land conserved as national parks) is limited (Daehler 2003, McDougall *et al.* 2005, Pickering and Hill 2007, McDougall *et al.* 2011a). By understanding the processes which promote exotic plant occurrence in disturbed mountain systems there may be an opportunity to both prevent and manage exotic species before they have the opportunity to invade undisturbed natural systems.

The source of exotic species in mountain systems can be traced to the global increase in the dispersal of exotic species across the landscape by humans for agriculture, food production and horticulture (Lonsdale 1999, Stohlgren *et al.* 2011). Increasing numbers of species are being transported across the globe, usually into lowland systems, as the majority of human settlements and agriculture occurs in these environments (Dukes and Mooney 1999, Seipel *et al.* 2011). Lowland areas are more likely to support modified habitats as a result of agriculture or human settlement. This modification, through disturbance and changes in resource availability and biotic resistance, provides conditions conducive for the

establishment of exotic species (Davis *et al.* 2000). From these lowlands exotic species can be dispersed into mountains.

Global and regional studies indicate that the ingress of exotic species into mountains is promoted by an expansion in road networks (Becker *et al.* 2005, Haider 2010, Paiaro *et al.* 2010, Seipel *et al.* 2011). A road network provides a linear corridor for the dispersal of species. Road construction alters soil chemical properties (including nutrient content), causes soil compaction, increases runoff and available light and modifies the soil seed bank (Hobbs 2006, Hobbs 2009, Jimenez *et al.* 2011). Road verges have been found to be the first point of introduction of exotic species into mountain systems (Daehler 2003, Pauchard *et al.* 2004, McDougall *et al.* 2005, Alexander *et al.* 2009, Kosaka *et al.* 2010, Pollnac *et al.* 2012). Seed may then continue to be dispersed along the road verge through the movement of traffic, from road upgrades such as resurfacing, and drainage changes (Christen and Matlack 2006, Paiaro *et al.* 2010).

Many studies in mountain systems have focused on roadsides to understand patterns of invasion. However other nodes of human activity, such as ski resorts, huts and camping grounds also provide opportunities for establishment of exotic plants (Pickering *et al.* 2000, Morgan and Carnegie 2009). Exotic plants have been planted as ornamentals in gardens and introduced as food plants around these human nodes (McDougall and Appleby 2000). Different disturbance types on roadsides and human nodes may influence plant establishment and growth leading to the presence of different species in these two environments.

Exotic plant species are most likely to enter mountain systems through human nodes or road networks (Morgan and Carnegie 2009, McDougall *et al.* 2005, Alexander *et al.* 2011). Whilst other dispersal modes occur, such as wind and animal dispersal, the geographic distance between lowland systems and high mountains is likely to reduce the occurrence of these.

3.1.1 Exotic plants in the Australian Alps

Exotic plant species were first recorded in the Australian Alps in flora surveys in the 1800s. These species were, *Acetosella vulgaris*, *Taraxacum officinale*, *Hypochaeris radicata*, which were recorded by Maiden (1898) in the sub-alpine zone and *Vulpia bromoides*, *Hordeum*

murinum and *Lotus corniculatus* which were recorded in the montane zone. All six species are now widespread in Australia. Since the 1950s, dispersal pathways have altered and species richness of exotic plants has increased in association with ongoing infrastructure development. The development of the Snowy Mountains Hydro Electricity scheme (1949-1972) led to the construction and establishment of road networks and villages (Good 1992). This infrastructure increased the introduction of exotic plant species into areas of the mountains previously not accessible (Mallen-Cooper 1990, Johnston 2005). Soil restoration works in the 1960s and 1970s also introduced species through the use of a sown exotic grass and legume mix and the use of straw mulch (Clothier and Condon 1968). Other major developments have continued since this time, with an expansion of ski resort infrastructure from the 1960s and an increase in summer recreational activities including mountain bike trails (McDougall *et al.* 2005, Hill and Pickering 2006, Pickering and Johnston 2007). Figure 3.1 displays the increase in exotic plant species in surveys undertaken in Kosciuszko National Park. Although surveys differ in scale, timing and methodology they indicate the overall trend of increasing species richness (Johnston 2005).

In mountains the number and type of exotic species recorded along roadways has been shown to decline with increasing elevation (Becker *et al.* 2005, McDougall *et al.* 2005, Haider *et al.* 2010, Mallen-Cooper and Pickering 2008). A linear decline in exotic species richness with increasing elevation has been demonstrated for high latitude areas including the Swiss Alps (Becker *et al.* 2005) and Chile (Pauchard and Alaback 2004). Surveys from other regions including the Canary Islands (Haider *et al.* 2010) and Australia (McDougall *et al.* 2005, Mallen-Cooper and Pickering 2008) show a hump in exotic species richness; i.e. higher species richness at intermediate elevations with a sharp decline at high elevations.

These patterns have been attributed to an elevation filtering model (Fig 3.2), which is based on regional and global studies that include data from the Australian Alps (Alexander *et al.* 2011, Seipel *et al.* 2011).

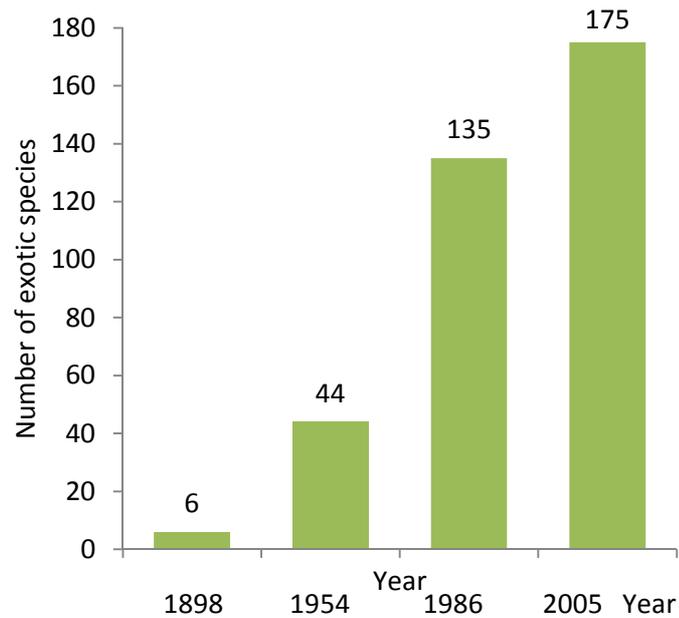


Figure 3.1. Increased exotic plant species richness over time in the sub-alpine and alpine areas of Kosciuszko National Park (Compiled from data in Maiden 1898, Costin 1954, Mallen-Cooper 1990, Johnston 2005)

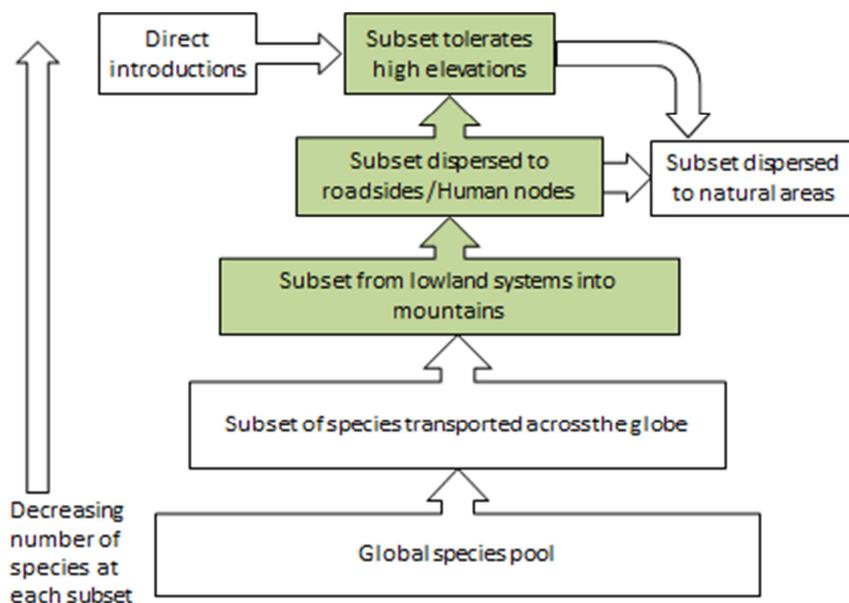


Figure 3.2. The elevation filtering model has been proposed to explain the processes leading to the introduction of exotic plant species into the Australian Alps (Alexander *et al.* 2011, Seipel *et al.* 2011).

Explanation of the elevation filtering model (Figure 3.2)

1. Global species pool

All plant species which occur across the globe.

2. Subset of species transportation across the globe

The global dispersal of exotic plant species has intensified in the last century as species are transported more rapidly for agriculture and ornamental use (Lonsdale 1999, Stohlgren 2011). Most of these species are introduced from lowlands to other lowland systems. The majority of human settlements and agriculture occur in these lowland environments. These modified habitats provide conditions conducive to the establishment of lowland specialists and climate generalists.

3. Subset of exotic species dispersed from lowland systems into mountains

Roadsides are an important dispersal pathway for exotic plant species in mountain systems (Becker *et al.* 2005, Seipel *et al.* 2011). In the Australian Alps most species are introduced from lowlands, predominantly species of European origin (McDougall *et al.* 2005).

4. Subset of exotic species dispersed to roadsides and in human nodes

Propagules are dispersed from roadways in lowland systems to roadside edges and human nodes at higher elevations. These areas of disturbance provide ideal conditions for the establishment of exotic species (Becker *et al.* 2005, Mallen-Cooper and Pickering 2008, Haider 2010).

5. Subset tolerates high elevations

At the highest elevations, only those species with the widest climatic tolerances persist. Species which are often found in disturbed areas at the top of mountains have been found to be a sub-set of the species which are also located in surrounding lowlands (Alexander *et al.* 2011). These species are considered climatic generalists as they have the ability to adapt to a range of conditions. This includes cold temperatures, frost and snow (Seipel *et al.* 2011). Additionally some species may reach higher elevations through direct introductions of mountain specialists into domestic gardens at high elevations (McDougall and Appleby 2000).

The elevation climate filter was thought in the past to be a barrier preventing establishment of many species at high elevations (Humphries *et al.* 1991). Whilst many studies support this (Mallen-Cooper 1990, Johnston and Pickering 2001, Haider 2010, Alexander *et al.* 2011, Seipel *et al.* 2011), some studies have questioned the role of a climate filter and indicate that other processes may also influence the distribution of exotic species. Paiaro *et al.* (2010) found exotic species richness peaked at low and high ends of the elevation spectrum, whilst Alexander *et al.* (2009) suggested that elevation and climate conditions are likely to pose only limited constraints to exotic species establishment. Morgan (2009) found only a weak negative relationship with elevation and exotic species richness in and around remote mountain huts, indicating other processes may explain the distribution of exotics.

In both disturbed and natural lowland systems, available soil nutrients are a major driver of exotic plant invasions (Hobbs 1989, Burke and Grime 1996, Leishman and Thomson 2005). Higher levels of available soil nutrients, in particular nitrogen and phosphorus which have been introduced to some low nutrient soils, have been linked to the proliferation of exotic species (Hedde and Specht 1975, Hobbs 1989, Prober *et al.* 2002, Leishman and Thomson 2005). Elevated soil nutrients associated with disturbance have been found to increase exotic species diversity (Hobbs 1989, Stohlgren *et al.* 1999) and abundance (Prober *et al.* 2002). Nutrients can be applied directly in fertilizer (Burke and Grime 1996) or indirectly through imported materials such as road base (Cale and Hobbs 1991) or through atmospheric deposition (Vitousek *et al.* 1997).

Increased soil nutrients have been considered a major factor in exotic plant occurrence in a number of low nutrient ecosystems in lowland Australia (Hobbs 1989, Prober *et al.* 2002, Leishman and Thomson 2004) but have not been sufficiently investigated in mountains. An investigation of soils on a road verge in the Bogong High Plains in the Australian Alps found differences in soil chemistry between the road verge which contained predominantly exotic vegetation, and an adjoining area of natural vegetation (McDougall 2000). Similarly, Johnston and Johnston (2004) found that road verges had lower nitrogen, pH and organic carbon than undisturbed soils but higher levels of calcium.

Nutrients have been introduced into the Australian Alps in fertilizers used in soil stabilization programs during road development (McDougall *et al.* 2005). Fertilizers were used widely in

alpine rehabilitation programs in Kosciuszko National Park in the 1960s and 1970s (Good 1992) to increase vegetation cover in eroded areas after the cessation of grazing. Low phosphorus, slow release fertilizers are still used in rehabilitation programs throughout KNP (NPWS 2005). Materials used to surface roads and walking trails (concrete, bitumen, gravel) are brought into the alps from other regions which may alter soil chemistry (Mallen-Cooper 1990, McDougall 2001, Johnston and Johnston 2004). Aeolian dust particles have also been identified as a source of nutrients (Johnston 2001) which may increase during periods of drought when top soil is vulnerable to wind erosion in western parts of the continent. De-icing salts are also used on the main roadways during winter. This may lead to a loss of soil stability, changes in pH through increased levels of sodium and calcium, and impacts on soil micro-organisms (Hoffman *et al.* 2012).

3.2 Chapter aims

The above review indicates that further research is required on relationships of exotic species with soil factors and elevation gradients in the Australian Alps. This study will examine the relationships between exotic species richness and both soil attributes and elevation (climate). This is important to investigate given the contribution of soil attributes to exotic plant occurrences in lowland systems and that climate change will reduce the effectiveness of an elevation filter.

Whilst exotic species richness on roadsides has been examined there have been few studies of exotic species in other disturbance types. Given that human nodes occur throughout the Australian Alps and are a potential source of exotic plant species, this study will also consider the processes which explain exotic richness in disturbed human nodes.

This chapter will investigate if patterns of exotic plants in roadsides and human nodes conform to expectations based on the elevation filtering model, i.e. species richness will decline with increasing elevation and species at higher elevations will be a subset of the species which also occur at lower elevations (as shown in the shaded area of Figure 3.2).

Data from both roadside and human nodes will address the following questions.

1. Does exotic species richness decline with increasing elevation in different disturbance types (roadsides and human nodes)?

2. Are exotics at high elevations a nested subset of those at lower elevations ?
3. Can elevation and soil attributes explain patterns of exotic species richness in roadsides and human nodes?
4. Do areas with different disturbance regimes (human nodes and roadsides) have different exotic species and if so do these patterns reflect differences in underlying abiotic attributes?

3.3 Study area

The Australian Alps comprise a contiguous group of National Parks straddling a 340 km length of the Great Dividing Range in south-east Australia (Figure 1.1). Alpine ecosystems cover only 0.001% of the Australian mainland and contain many endemic species that do not occur in surrounding lowland areas (Costin *et al.* 2000). Snow lies on the ground for 1-4 months in the sub-alpine and 6-9 months in the alpine area (Green and Osborne 2012).

This study was located in montane, sub-alpine and alpine areas in Kosciuszko National Park (673 542 ha). The montane area, 1100 – 1400 m above sea level (ASL), generally supports forests dominated by *Eucalyptus pauciflora*, *E. dalrympleana*, *E. delegatensis*, *E. rubida* and *E. viminalis*. The sub-alpine zone occurs from 1400 – 1850 m ASL and is dominated by *E. niphophila* woodland interspersed with wet and dry heathlands, bogs and grasslands. Alpine areas above the treeline at 1850 m are dominated by low growing shrubs, herb fields, grasslands, feldmark and bogs (Costin 1954, 2000).

3.4 Methods

Study sites were chosen across an altitudinal gradient of 1000 – 2200 m in two different disturbance types: roadsides and human nodes. Roadsides consisted of main roads with a bitumen or gravel surface that are frequently used and actively maintained. The four highest road side sites occur on a gravel road closed to public vehicles but is frequently used by National Parks and Wildlife Service staff, contractors and research vehicles. This road is also used extensively by walkers and bicycle riders. Human node sites included frequently utilised huts, recreational camping areas and ski resorts. Figure 3.3 identifies the locality of study sites in Kosciuszko National Park.

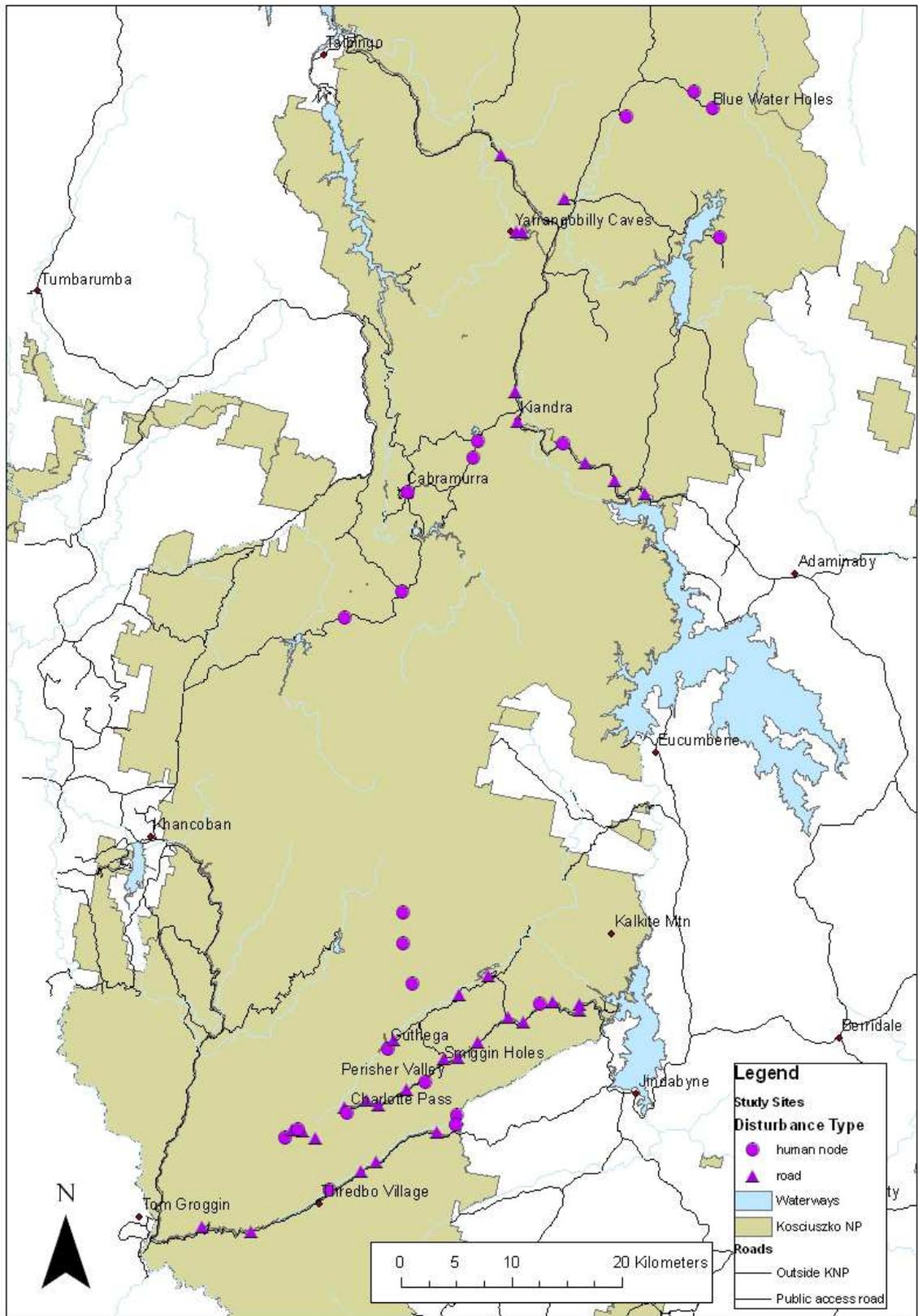


Figure 3.3. Locality of study sites within Kosciuszko National Park.

Using an Arc Map™ geographic information system (GIS), sites were stratified based on elevation to allow for an elevation spread across montane, sub alpine and alpine zones.

Geology was also considered to ensure sites were established in all three common geological types including, granite, basalt and limestone. Sites were located on a GIS as part of the desktop exercise and then this information was installed on a handheld IPAQ using the ArcPad™ geographic information program fitted with a geographic positioning system (GPS). The handheld device was then used to locate sites in the field.

Once in the field the main criterion for the selection of the disturbed field site was to have a minimum of 30% cover of exotic species. For human nodes all sites identified in the desktop exercise met the criterion. In the case of a roadside if the site did not exceed 30% exotic cover the road was followed until an appropriate location was identified. A 40 m² plot was established at each of the 55 disturbed sites (23 roadsides, 32 human nodes) and an additional plot was located in an undisturbed area in the surrounding vegetation community (data from undisturbed plots are presented in Chapter 4).

Sites were identified from October to November 2010, the date depending on snow melt. Available nutrient levels are likely to be the greatest at this time in sub alpine and alpine soils (Johnston 2011). Soil samples were collected and abiotic information recorded. Floristic sampling was undertaken from December 2010 to February 2011, when most plant species were identifiable.

At each plot the following abiotic factors were recorded; geology, soil type, aspect, elevation and slope. Information on bare soil was collected but not considered in the analysis. Bare soil in alpine and sub alpine areas may impede plant establishment due to unfavourable temperature extremes, high temperatures in summer followed by soil freezing in winter (Chambers 1990, Körner 2003). Elevation and locality data (latitude and longitude) were collected in the field at each site using a GPS. All exotic and native species were recorded in each plot. If the species was not easily identified a sample was collected and identified later. Eighty voucher specimens from the survey were lodged at the Australian National Herbarium. Percentage cover of all exotic and native species was visually estimated using the scale 0-1, >1-5, >5-10, >10-25, >25-50, >50-75, >75-94, 94-100. The species growth form and

ornamental use were recorded (GRIN 2014, The Royal Botanic Garden and Domain Trust 2014).

Ten random top soil samples were collected from each plot. A soil auger was used to remove samples from the top 5 cm of soil (4 cm depth x 5 cm width). The samples were bulked to obtain a representative sample and mixed well. Samples were chilled to prevent microbial activity and were sent to CSPB Soil Analysis & Plant Laboratory in Western Australia. Soil testing included Colwell phosphorus and potassium (Colwell 1965), nitrate and ammonium (Searl 1984, Rayment and Lyons 2011), pH and electrical conductivity (Rayment and Lyons 2011), organic carbon (Walkely and Blake 1934, Rayment and Lyons 2011), sulphur (Blair et al 1991), available phosphorus and exchangeable cations (aluminium, magnesium, calcium, potassium, sodium), total nitrogen and total phosphorus (Rayment and Lyons 2011). Soil classification was undertaken using the Australian Soil Classification System (Isbell 1996).

The locality information collected in the field for each plot was downloaded into ArcMap Version 9™ and using Hawth's Tool the mean annual temperature for each plot was extracted from the Worldclim 30 second climate grid (Hijmans *et al* 2005).

3.5 Statistical analysis

In order to establish if there was a difference in exotic plant richness between the two disturbance types, roadsides and human nodes, a Wilcoxon Rank test was undertaken using S-Plus Statistical Analysis Software (Tibco 2010).

To confirm whether exotic species at higher elevations comprised a nested subset of species from lower elevations, following Alexander *et al.* (2011), sites were ordered by increasing elevation (matrix rows) and species by decreasing number of occurrence (columns). Next, 1,000 random matrices were generated using a null model that constrained species richness within sites while randomizing the occurrence of species. The analysis was undertaken with the nestedness metric based on overlap and decreasing fill (Almeida-Neto *et al.* 2008) using the vegan package (Oksanen *et al.* 2009) in R software (R development core team, 2012). To test if elevation was correlated with exotic species richness in both roadsides and human nodes Spearman's rank correlation was undertaken using S-Plus Statistical Analysis Software (Tibco 2010). The variables, elevation and annual mean temperature were tested.

Generalized linear models (GLM) were then developed to identify explanatory variables for the response variable exotic species richness in roadsides and human nodes. Model selection was the preferred option due to the complexity of interrelationships with the predictor variables (Johnson and Omland 2004). To reduce the potential for error I tested all variables for collinearity (Graham 2003) using Spearman's rank correlation (non-normal data). For all variables that showed a cross correlation of $r > 0.6$ only one of each pair of variables was included in the models. Cross correlation was undertaken on 19 independent variables and eight were used in the final GLM for both disturbance types. These were soil depth, nitrate nitrogen, phosphorus, potassium, sulfur, pH, extractable sodium and mean annual temperature. As elevation and mean annual temperature were strongly correlated with each other but no other variables, mean annual temperature alone was used in the GLM. As elevation and mean annual temperature were strongly correlated with each other but no other variables, mean annual temperature alone was used in the GLM. This was chosen over elevation as temperature has a more direct relationship with plant growth (Went 1953). Steep slopes on different aspects at the same elevation can have significant differences in temperature (Moser 1977, Körner 2003). Mean temperature was considered appropriate as it has been used as an ecological indicator in other vegetation studies in mountains (Kirkpatrick and Bridle 1998, Jakobs 2010). Nitrate nitrogen was also used over total nitrogen and ammonium nitrogen as it is most available in the soil for plant uptake (Harmsen and Kohlenbrandner 1965).

The response variable, exotic species richness (count data) was transformed using Poisson to assume a normal distribution. Using S-Plus software, Akaike Information Criterion (AIC) was undertaken (Johnson and Omland 2004). AIC provides an objective way to determine the most parsimonious model from a set of models. The AIC was adjusted for a small sample size due to the high proportion of predictor variables compared with the sample size. The best model has $AIC = 0$ and only models with $AIC \leq 2$ have substantial support and were included in the results (Burnham and Anderson 2002).

3.6 Results

3.6.1 Exotic species richness between disturbance types

In total, 41 exotic species were recorded on roadsides and 55 in human nodes. Table 3.1 displays the breakdown of the species into plant growth forms. Both disturbance types had the same ten frequently occurring species (Table 3.2). Human nodes contained more forbs (36) and other species which were introduced for both food and ornamental purposes (9), such as *Lupinus polyphyllus* than roadsides (5). However despite these differences, when the richness of exotic plant species was compared between roadsides and human nodes there was no significant difference in mean richness between the disturbance types ($P = 0.08$). Mean species richness was 9.3 species in roadsides and 8.2 species in human nodes.

Table 3.1. The number of exotic species broken up into growth forms at roadside and human node.

Site Type	Tree	Grass	Forb	Shrub	Sedge	Total
Roadside	1	14	24	1	1	41
Human node	1	15	36	1	2	55

Table 3.2. The frequency (%) of the ten most common exotic plant species on all roadside and human node sites.

Species	Roadsides	Human nodes
<i>Hypochaeris radicata</i>	91	47
<i>Acetocella vulgaris</i>	74	47
<i>Trifolium repens</i>	70	62
<i>Achillea millefolium</i>	57	38
<i>Anthoxanthum odoratum</i>	52	40
<i>Festuca rubra</i>	50	53
<i>Agrostis capillaris</i>	48	44
<i>Poa pratensis</i>	31	41
<i>Holcus lanatus</i>	30	31
<i>Dactylis glomerata</i>	26	34

The nested analysis was used to determine if the species at high elevations were a subset of species from lower elevations. This analysis replicates other exotic species studies in mountains which included data from the Australian Alps (Alexander *et al.* 2011). The results differed from other mountain studies as nestedness was not significant in either disturbance

type. However, the results did vary between each disturbance type with nestedness approaching significance along roadsides ($Z = 1.97$, Nest 27.68, $P = 0.07$) whilst human nodes were highly un-nested ($Z = 0.12$, Nest 22.46, $P = 0.9$). The nested analyses included species which were only recorded at one location (human nodes 26 species, roadsides 12 species). Even though the nestedness results were not significant the general trend for both disturbance types is that the most abundant species that occur at the highest elevations (> 2000 m) also occur commonly at lower elevations.

The patterns were illustrated in Figure 3.4 and Figure 3.5 so readers could view the distribution of all analysed species. Figure 3.4 and Figure 3.5 illustrate the altitudinal range of those species which were recorded at more than one site at a different elevation (± 100 m) in each disturbance type.

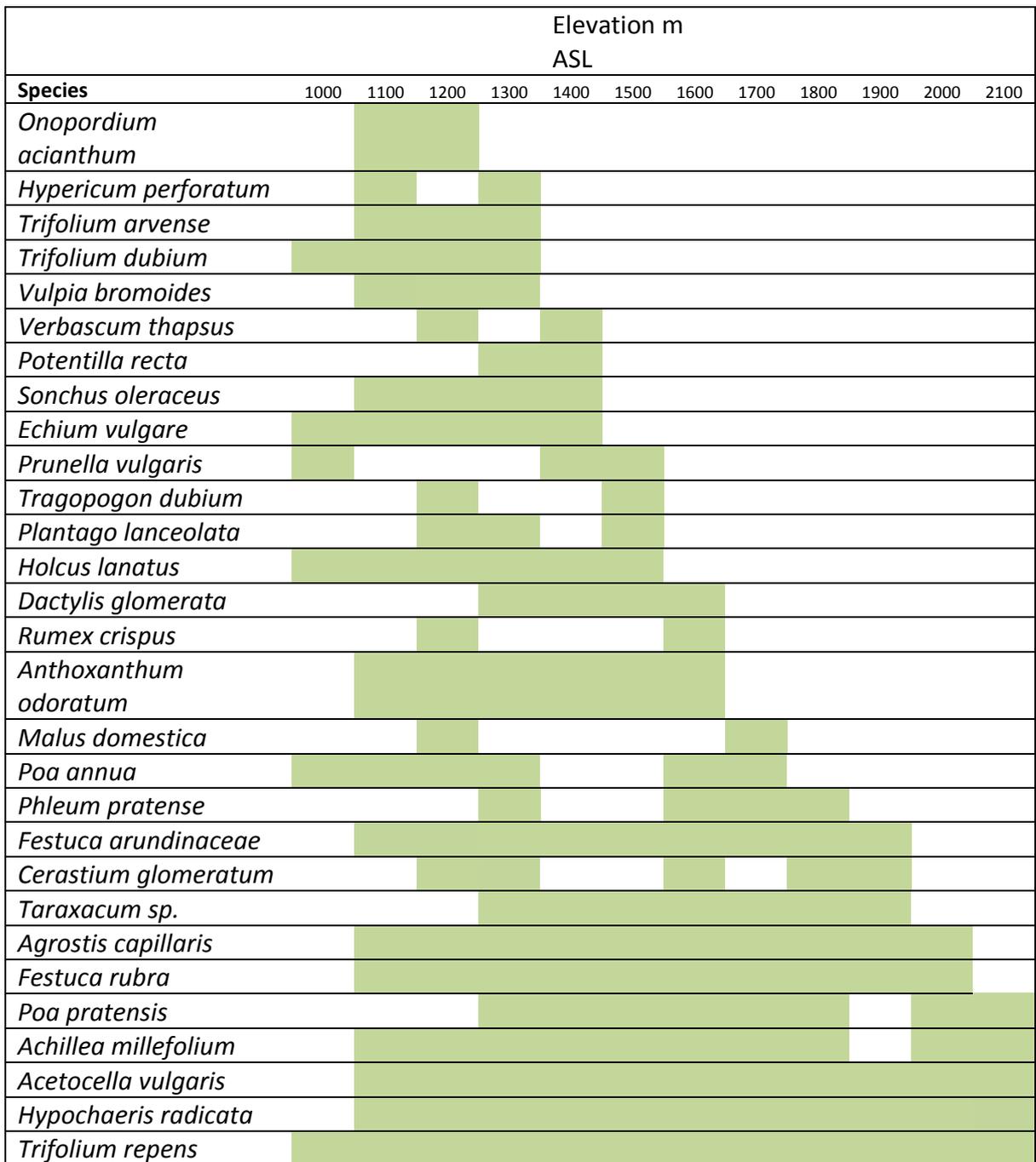


Figure 3.4. Elevational ranges of the 29 exotic plant species which were recorded in two or more human nodes.

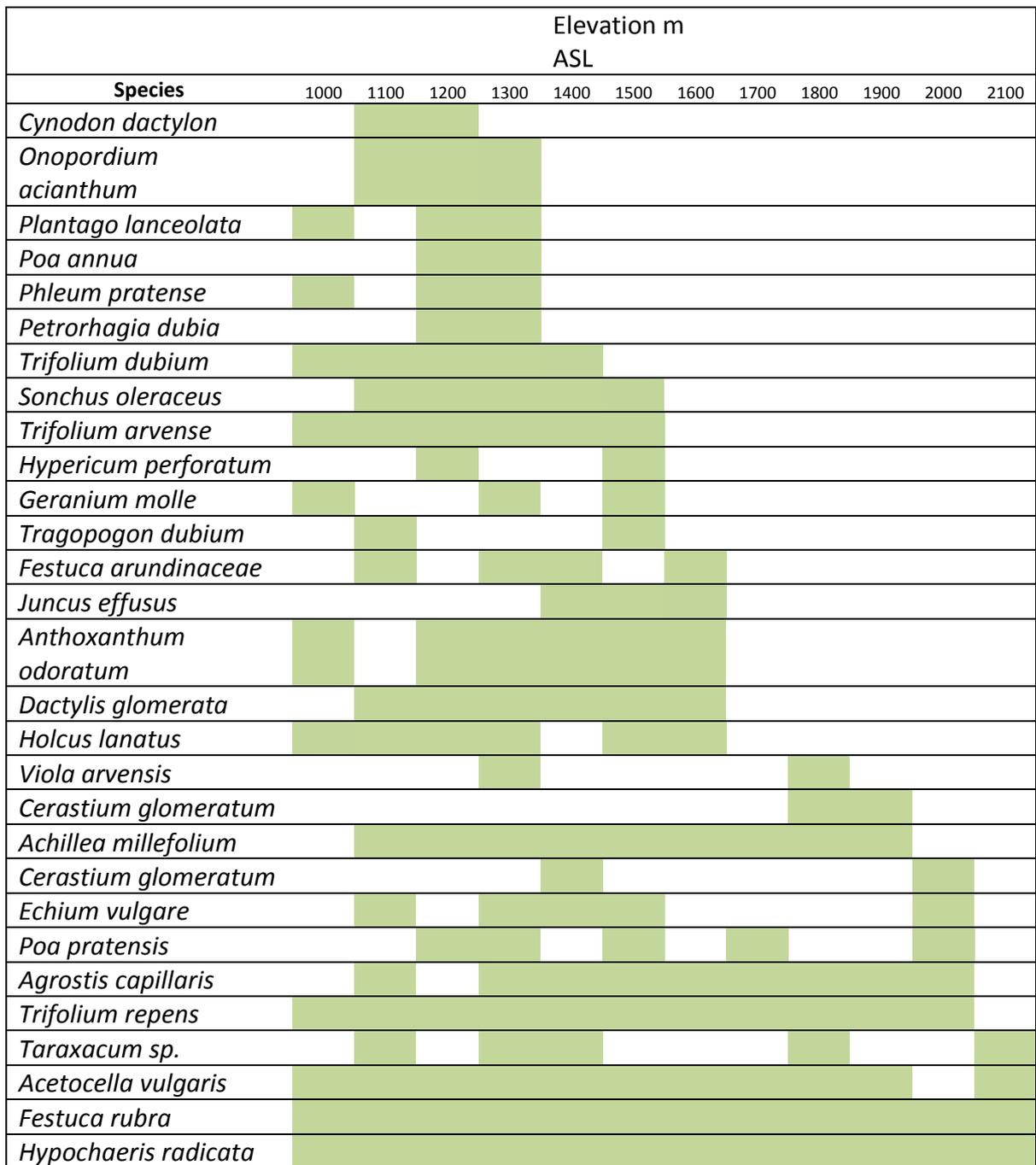


Figure 3.5. Elevational ranges of the 29 exotic plant species which were recorded in two or more roadside sites.

3.6.2 Elevation and soil attributes

Roadsides contrary to expectations, exotic richness on roadsides was not significantly correlated with elevation ($r = -0.26$, $P = 0.22$) or mean annual temperature ($r = 0.18$, $P = 0.38$). Instead richness was highly variable below 1700 m but consistently low above 1700 m (Figure 3.6).

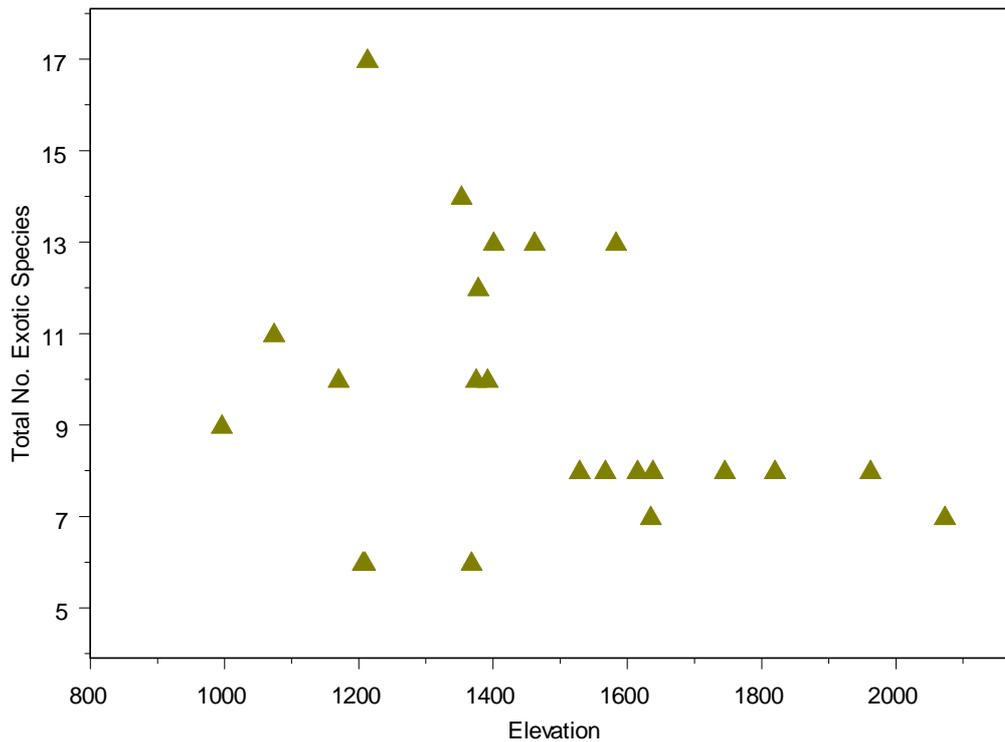


Figure 3.6. Relationship between total number of exotic species and elevation (m ASL) on roadsides.

Using AIC for roadside data there were three models within $\Delta AICc \leq 2$ (Table 3.3). Model 1 indicated potassium was the main predictor variable. Model 2 indicated potassium and sulphur, and Model 3 sulphur and nitrate. All predictor variables were positively associated with exotic species richness.

Table 3.3. Comparison of models fitting exotic species richness with explanatory variables for roadside sites ($\Delta AICc \leq 2$)

Model rank	model	K	AICc	R2	$\Delta AICc$	w_i
1	ESR~k	2	18.18	0.25	0.00	0.12
2	ESR~k+s	3	20.09	0.29	1.91	0.05
3	ESR~nn+s	3	20.14	0.29	1.97	0.04

ESR, exotic species richness, K, number of estimated parameters, AICc – Akaike’s Information Criterion corrected for small sample sizes, R2 – adjusted R², $\Delta AICc$ – difference in AICc, w_i , Akaike weights- for each variable are summed across all candidate models in the set, k, potassium, s, sulphur, nn, nitrate nitrogen

Human Nodes

Unlike roadsides, at human nodes there was a significant negative correlation between exotic species richness and elevation ($r = -0.48$, $P = 0.006$) and annual mean temperature ($r = 0.47$, $P = 0.008$), although the general pattern was similar to roadsides, with variable richness at low elevations and low richness at the highest elevations (Fig. 3.7).

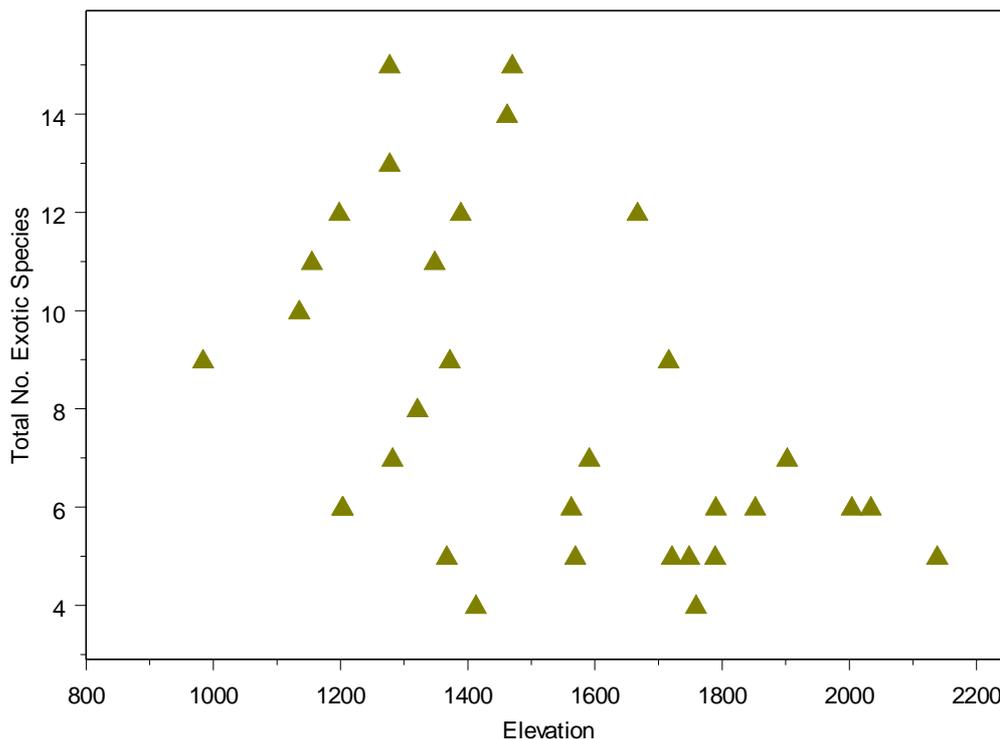


Figure 3.7. Relationship between total number of exotic species and elevation (m ASL) at human nodes.

The AIC models for human nodes indicated 18 models had an $\Delta AICc \leq 2$ (Table 3.4). This indicates a number of predictors are likely to contribute to the patterns associated with exotic species richness. Because of the lack of a single best model the relative importance of individual variables was determined by summing the Akaike weights (Burnham and Anderson 2002). Mean annual temperature had the highest summed Akaike weight at $\sum wi = 0.32$ followed by nitrate $\sum wi = 0.17$, soil depth $\sum wi = 0.16$, sulphur, $\sum wi = 0.11$ and pH $\sum wi = 0.11$. The remaining variables sodium and phosphorus had summed Akaike weights of less than 0.05. The results suggest a combination of climate and various soil attributes contribute to exotic species richness in human nodes.

Table 3.4. Comparison of models fitting exotic species richness with various explanatory variables for human nodes ($\Delta AICc \leq 2$).

Model Rank	Model	K	AICc	R2	$\Delta AICc$	wi
1	ESR~SD+MAT	3	36.32	0.28	0.00	0.04
2	ESR~SD+NN+MAT	4	36.37	0.34	0.05	0.03
3	ESR~NN+MAT	3	36.60	0.27	0.28	0.03
4	ESR~SD+pH+MAT	4	36.65	0.34	0.33	0.03
5	ERS~MAT	2	36.68	0.21	0.36	0.03
6	ESR~S+MAT	3	36.83	0.27	0.51	0.03
7	ESR~pH+MAT	3	36.90	0.26	0.58	0.03
8	ESR~NN+S	3	37.18	0.26	0.86	0.02
9	ESR~S	2	37.71	0.19	1.40	0.02
10	ESR~SD+S+MAT	4	37.77	0.31	1.45	0.02
11	ESR~NN+S+MAT	4	37.85	0.31	1.54	0.02
12	ESR~Na+MAT	3	37.87	0.24	1.55	0.02
13	ESR~SD+Pcol+MAT	4	37.89	0.31	1.57	0.02
14	ESR~NN	2	37.98	0.18	1.66	0.02
15	ESR~SD+NN+pH+M AT	5	38.01	0.37	1.69	0.02
16	ESR~NN+Na+MAT	4	38.05	0.30	1.73	0.02
17	ESR~pH+Na+MAT	4	38.06	0.30	1.75	0.01
18	ESR~NN+pH+MAT	4	38.14	0.30	1.82	0.01

K, number of estimated parameters, AICc – Akaike’s Information Criterion corrected for small sample sizes, R2 – adjusted R², $\Delta AICc$ – difference in AICc, wi, Akaike weights for each variable are summed across all candidate models in the set. ESR, exotic species richness, SD, soil depth, MAT, mean annual temperature, NN, nitrate nitrogen, S, sulphur. Na, sodium, PCol, Phosphorus Colwell

Mean annual temperature was positively associated and nitrate, soil depth and sulphur were negatively associated with exotic species richness. Interestingly, nitrate levels at human nodes at high elevations were high (Figure 3.8) although exotic richness remained low.

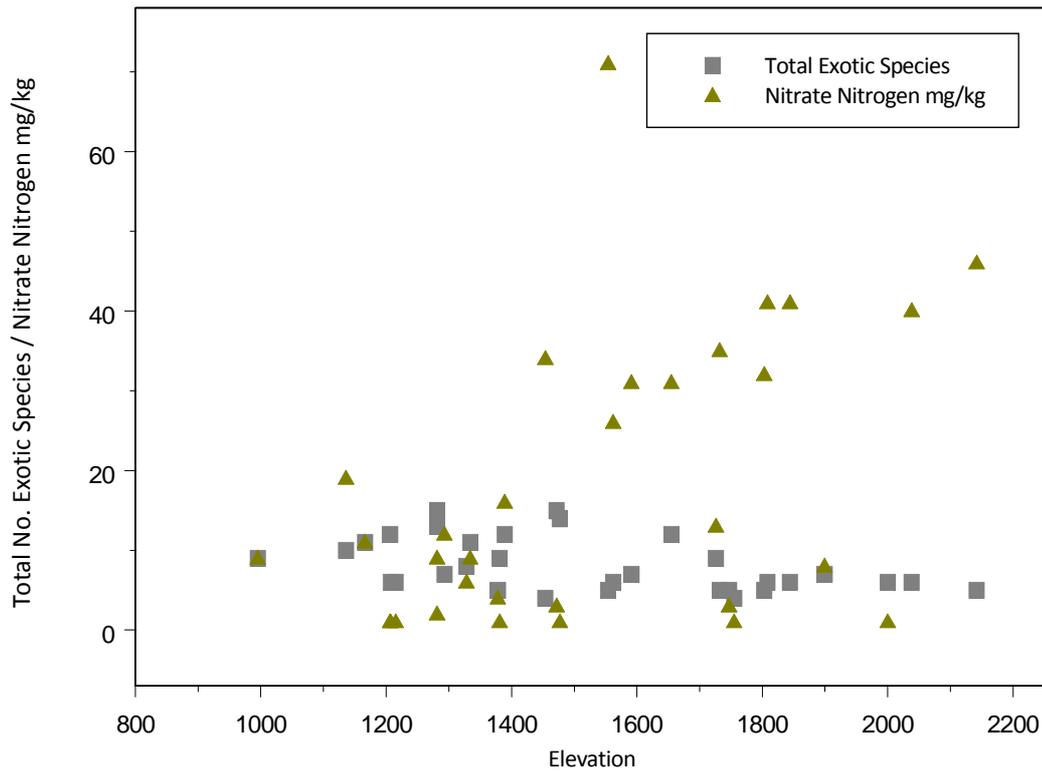


Figure 3.8. Relationship between soil nitrate (mg/kg), total exotic species and elevation (m ASL) at human nodes.

3.7 Discussion

These results suggest that the relationship between elevation and exotic species richness may vary between different disturbance types. Elevation was significantly correlated with the richness of exotic plants in human nodes but not along roadsides. Different processes may influence exotic species richness in the two disturbance types. Soil attributes were associated with exotic species richness on roadsides, while a combination of elevation and soil attributes contributed to exotic species richness at human nodes.

Exotic species richness was significantly and negatively correlated with altitude in human nodes. This finding is consistent with Morgan and Carnegie's (2009) study on exotic species near huts in the Australian Alps. Past studies in mountains including the Australian Alps have indicated that elevation can explain exotic species richness along roadsides (Mallen-Cooper 1995, Johnston and Pickering 2005, Becker *et al.* 2005, Haider *et al.* 2010). My study of roadsides did not support this finding. However I did find a decline in exotic species richness along roadsides above 1700 m elevation which was consistent with other studies (Mallen-Cooper 2000, Seipel *et al.* 2011) although not reflected in the correlation analysis.

Other studies have indicated that factors other than elevation may influence exotic species richness on roadsides (Alexander *et al.* 2009, Paiaro *et al.* 2010). Mallen-Cooper and Pickering (2008) identified that variation in richness of exotic species at similar elevations along roadsides in Kosciuszko National Park indicated that other factors were likely to be influencing species density, although their study did not investigate the potential role of soil attributes.

Three of the species which had a high frequency of occurrence from low to high elevations were previously used in rehabilitation programs in the Australian Alps. These three species are *Agrostis capillaris*, *Festuca rubra*, *Trifolium repens* (Clothier and Condon 1968) and their presence on roadsides and in human nodes may be due to direct introduction in the past. Artificial fertilizers were also associated with early stabilisation works in the 1960s and 1970s (Good 2006). Apart from some long term monitoring on the main range (Scherrer and Pickering 2006) there is limited information on the locality of rehabilitation programs.

My results suggest that a variety of factors may influence exotic species richness at low elevations, with many factors reducing richness below potential maximums at a particular elevation level. Soil attributes such as potassium and to a lesser extent nitrate nitrogen and sulphur, were all positively associated with exotic species richness along roadsides in this study. On roadsides higher levels of potassium and sulphur were associated with higher exotic species richness. Other studies have found roadside construction alters roadside soils (Cale and Hobbs 1991, Christen and Matlack 2006, Jimenez *et al.* 2007) resulting in conditions suitable for exotic species establishment. Roadside soil nutrients can vary as a result of maintenance activities and lead to variations in richness at different elevations.

Previous work by Johnston and Johnston (2005) indicated that exotic species were favoured by changes to physical and chemical soil structure along roadside verges in the sub alpine region in Kosciuszko National Park. Although not investigated here, changes in soil attributes may favour particular plant species over others (Godefroid and Koedam 2004). High potassium levels have been linked previously to increased occurrence and growth of *Taraxacum officinale* along road verges (Densmore 2008) and its ability to outcompete exotic grasses (Tillman 1999). High nitrate has also been linked to exotic grass cover and richness along roadsides in lowland areas (Hobbs 1989, Prober *et al.* 2002). This study highlights the need to understand the changes in soil properties which occur as the result of road construction and the potential impact of road construction activities on exotic species.

Elevation and soil attributes both contributed to exotic plant richness in human nodes. A wide range of soil attributes were associated with exotic species richness in human nodes, including nitrate, sulphur, pH, soil depth. This wide range of soil conditions is indicative of the variation in the land use history and current management at human nodes.

This study found that nitrate nitrogen levels in human nodes were highest at high elevations. Despite this exotic richness remained low at these sites (Figure 3.8). This was an important finding as it suggests that climate filters may be reducing richness at high elevations despite high nutrient levels. With predicted increases in temperature as a result of climate change (Steffen *et al.* 2009) high nutrients at these sites could lead to an increase in exotic species richness in the future.

Exotic richness along roadsides can be best explained by directional elevation filtering (Alexander *et al.* 2011) i.e. species are dispersed along road corridors and only those species with a wide climatic tolerance persist at higher elevations. The variation in richness patterns along roadsides (low and high richness at the same elevations) was likely to have influenced nested results. This variation is associated with the influence roadside construction can have on soil nutrients (Cale and Hobbs 1991, Christen and Matlack 2006, Jimenez *et al.* 2007). Despite the results Figure 3.5 illustrates a nested like pattern of exotic species occurrence on roadsides. The three most common species (Table 3.2) occurred from low to high elevations, *Acetocella vulgaris*, *Festuca rubra* and *Hypochaeris radicata*. Other common species, *Holcus lanatus*, *Anthoxanthum odoratum* occurred from low to mid-elevations but did not persist at higher elevations.

Human nodes can be geographically isolated and are not always linked by road corridors (Morgan and Carnegie 2009) therefore some human nodes may only receive exotic species through direct introduction. The results suggest that in human nodes two dispersal patterns may be operating. Some of the species located in human nodes were uncommon and found to be located at disjunct elevations (Figure 3.4). These species included *Cerastium glomeratum*, *Malus domestica* and *Prunella vulgaris*. Despite the un-nested results in human nodes three of the four most common species (Table 3.2) occurred from the lowest to the highest elevation and some other species were common from low to mid elevations but did not persist at higher elevations (Figure 3.4).

A greater number of species were recorded at human nodes (55) than roadsides (41). If two dispersal patterns operate in human nodes, directional elevation filtering and direct introduction, they may have the potential to contain more diversity of species and be a greater source of potential invasive exotic species to surrounding natural areas.

Revised models

The original model, Figure 3.2 was proposed to explain the processes leading to the occurrence of exotic plant species in the Australian Alps. Considering the study findings differ from the original proposed model, two separate models have been developed. The shaded components of the models indicate the components investigated in this chapter.

Exotic plant occurrence and richness at roadsides and human nodes in the Australian Alps are explained in Figure 3.9 and Figure 3.10. The roadside model (Figure 3.9) identifies that the overall richness of species along an elevation gradient can be explained through a nested like pattern, with elevation filtering occurring above 1700 m. The influence of soil attributes on species richness is included in the model. Soil conditions can vary along roadsides due to maintenance activities and can lead to low richness at low elevations. The human node model (Figure 3.10) illustrates that species occurrence patterns can be explained by direct and indirect introduction and that different species may be introduced into human nodes at varying elevations. The model also identifies the influence of elevation and soil attributes on species occurrence and richness.

The patterns of occurrence between roadsides and human nodes may vary and therefore the prevention and management of exotic species in these nodes may need to be approached differently. Preventing direct introductions of new plant species at human nodes may be achieved by restrictions on the use of local native plant species. Changes to roadside construction and maintenance practices could reduce the spread of exotic species: e.g. cleaning of all machinery before and during construction activities to prevent propagule movement; minimising disturbance to soil by limiting a road footprint, the use of road materials consistent with the local geology and free of exotic seed, and implementing rehabilitation practices which promotes the establishment of native species.

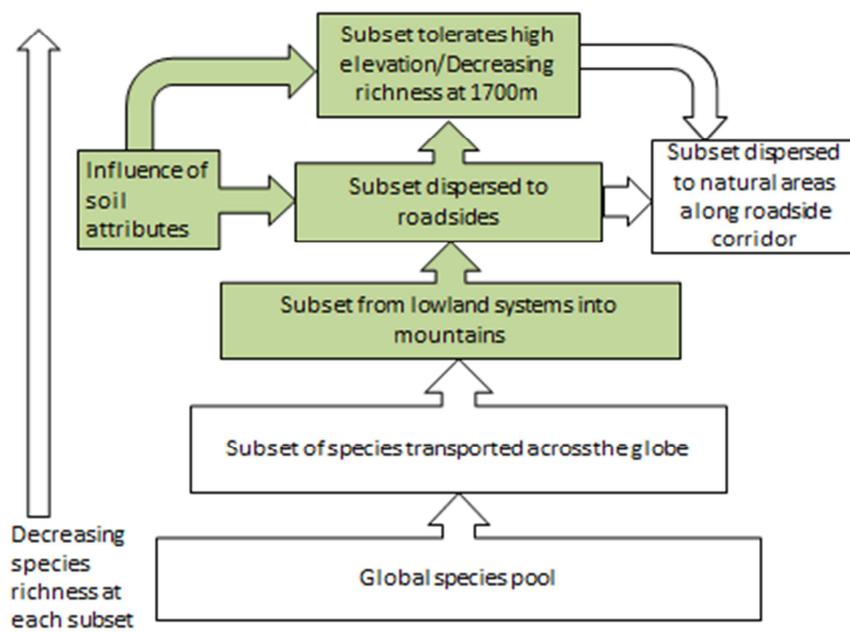


Figure 3.9. A model to explain the occurrence and richness of exotic plant species in roadsides in the Australian Alps.

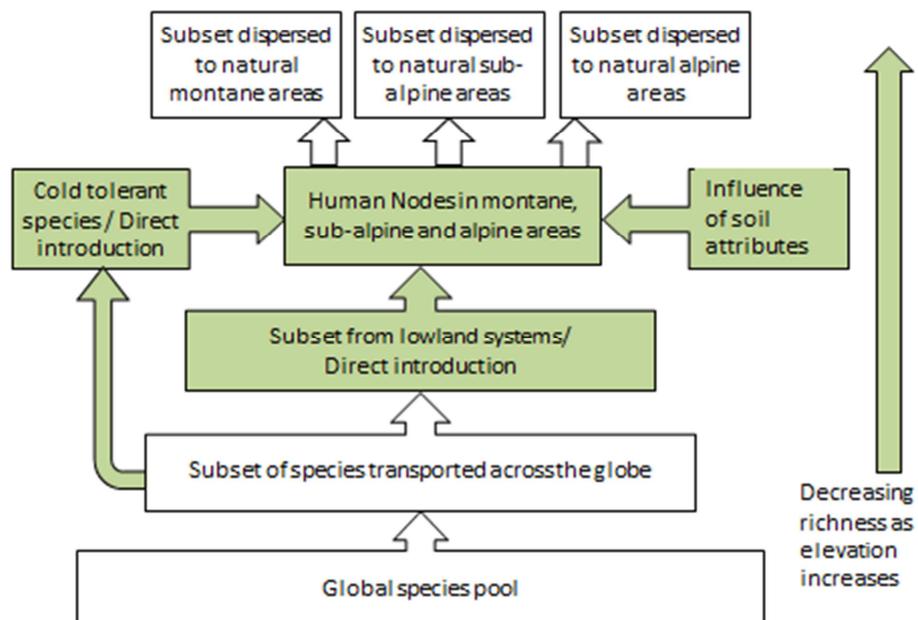


Figure 3.10. A model to explain the occurrence and richness of exotic plant species in human nodes in the Australian Alps.

This survey was static and given residence time is an important factor in other mountain studies (Haider *et al.* 2010) changes in species patterns may occur in the future. Therefore the detection and control of exotic species on roadsides at lower elevations may prevent the movement of species into higher elevations. A number of the species recorded at disturbed sites in this survey are considered invasive exotic species at higher elevations in other mountain regions, including *Leucanthemum vulgare*, *Verbascum thapsus* and *Potentilla recta* (Whipple 2001, Clements *et al.* 2003, Conn *et al.* 2008, Ansari and Daehler 2010). These species may not have reached their full extent but could be transported along roads or directly into high elevations areas as the models illustrate (Figure 3.9 and Figure 3.10).

3.8 Conclusion

The study suggests that the richness of exotic species may be explained by understanding the interaction between elevation (including temperature) and soil attributes. Perhaps the strong correlation of elevation and species richness in other studies (Becker *et al.* 2005, McDougall *et al.* 2005, Haider *et al.* 2010, Mallen-Cooper and Pickering 2008) has led to other important factors being overlooked, such as soil attributes. Whilst managers have no direct control over elevation or climate there is a greater capacity to manage soils to reduce conditions which may be conducive to exotic species growth. The first approach would be to minimize any further impact to soils. This may be achieved by reducing road and human node footprints, altering the materials used in road construction and having a commitment to rehabilitation which improves the soil condition and promotes native vegetation.

The study also suggests that the patterns of occurrence between roadsides and human nodes vary and therefore detection and management of exotic species in these two habitats should be approached differently.

Whilst this Chapter has focused on areas of disturbance the real key is to determine which species in roadsides and human nodes have the greatest potential to disperse into natural communities and become invasive. The species we should be most interested in for future management of natural mountain systems are those species which pose the greatest threat to biodiversity; i.e. those species that have the ability to invade a landscape, replace, compete with native species and transform vegetation communities (McDougall *et al.* 2011).

Given soil attributes help explain exotic plant richness in disturbed areas of mountain systems, in Chapter 4 I will further explore this by comparing exotic richness in natural areas to determine if we can understand the role elevation (climate) and soil attributes play in explaining exotic species richness in these habitats.

CHAPTER 4 THE ROLE OF ELEVATION AND SOIL ATTRIBUTES IN EXPLAINING EXOTIC PLANT RICHNESS IN UNDISTURBED MOUNTAIN SYSTEMS

4.1 Introduction

Mountain systems support unique biological systems, evolved to withstand extreme climatic conditions. They are important for their diverse flora and fauna and the water resources they provide to lowland systems (Körner 2004, Viviroli 2007). Their harsh climate and steep elevation has largely protected them until the last century from human induced change. Expansion in human activities has made these once protected systems more accessible and vulnerable to impacts including the introduction of exotic plant species (Pauchard *et al.* 2009). Despite this, the number and abundance of exotic plants remains low in natural areas in protected mountain systems (Daehler 2003, McDougall *et al.* 2011a).

The distribution of exotic plant species has been examined in global and local studies of disturbed mountains (Mallen-Cooper 1990, Johnston 2005, Daehler 2005, Alexander *et al.* 2009, Haider 2010, Jakobs *et al.* 2010, Paiaro *et al.* 2010, Seipel *et al.* 2011). Dispersal in disturbed mountain systems is via two main pathways: along road ways (Alexander *et al.* 2011) or through direct introductions into human nodes i.e. ski resorts (McDougall and Appleby 2000, Pickering *et al.* 2002). Changes to the abiotic environment in disturbed sites provide conditions favourable for exotic plant establishment (Gelbard and Belnap 2003, Johnston and Johnston 2004, Hobbs *et al.* 2006).

A smaller number of exotic species occur in undisturbed (natural) communities in mountain systems (Daehler 2003, McDougall *et al.* 2005, Pickering and Hill 2007, Pysek *et al.* 2009). In natural mountain systems the richness of exotic plants declines at higher elevations (Mallen-Cooper 1990, McDougall *et al.* 2005, Daehler 2005). A study of 32 different habitats in the Czech Republic using 20 468 vegetation plots found that higher elevation and natural sites were less invaded than low elevation and disturbed sites (Chytry *et al.* 2008).

Intact natural systems with minimal disturbance have been found to be more resistant to exotic plant invasion than communities impacted by anthropogenic disturbance (Rejmánek

2000, Daehler 2003, D'Antonio and Chambers 2006). Whilst climate (elevation) has been correlated with low exotic richness in undisturbed mountain systems it is unlikely to be the only factor that limits richness. A number of factors can contribute to the successful colonisation of an exotic species in an undisturbed or semi-undisturbed system (Richardson and Pysek 2006). Invasion may be explained by climate, disturbance history, dispersal ability, timing of phenology, time since introduction or characteristics of the abiotic and biotic environment (Crawley 1989, Lonsdale 1999, Davis *et al.* 2000).

Mountain systems are subject to a range of natural and anthropogenic disturbance regimes including, fire, soil disturbance by human or other animals, frost heave, wind events and extreme climate, including inundation by snow for several months of the year (Körner 2003). Natural disturbance is an important component of all natural systems (Hobbs and Huenneke 1992). Many native alpine species rely on natural disturbance to facilitate seedling recruitment (Chambers *et al.* 1990, Chambers 1993). Disturbances may also facilitate establishment of exotic species.

Changes in available resources including light or soil nutrients may have differing effects on different plant species and vegetation communities (Lonsdale 1999, Davis *et al.* 2000).

Changes to soil nutrients have been associated with exotic species occurrence in many low nutrient natural systems (Hobbs 1989, Prober *et al.* 2002, Leishman and Thomson 2005, Turner *et al.* 2008). However few studies have examined the effects of soil nutrients on exotic plant richness in natural mountain systems (McDougall 2001, Johnston and Johnston 2004).

4.1.1 Exotic plants in natural areas of the Australian Alps

The widespread disturbance to soils in the Australian Alps commenced with cattle and sheep grazing in the 1800s. Grazing has had widespread impacts throughout Kosciuszko National Park (KNP) with extensive loss of soils and erosion of waterways particularly in alpine areas (DEC 2006). Large scale revegetation programs were undertaken when grazing ceased in the 1960s (Good 1992). Revegetation programs covered large areas of the Main Range (1550 ha) in KNP and used an exotic grass and legume mix and straw mulch (Clothier and Condon 1968). Some of these species still persist in alpine areas today (McDougall *et al.* 2005). From the 1950s a major expansion in infrastructure occurred. This included the development of ski

resorts and hydroelectricity which has led to a significant increase in the richness of exotic species (refer Figure 3.1) in disturbed environments (Mallen-Cooper 1990, Pickering and Johnston 2001, Hill and Pickering 2006,).

Natural or undisturbed areas are those localities which support a successional advanced plant community (Rejmánek 1989, Rejmánek *et al.* 2005) and have no visual soil disturbance (Costin 2000). Undisturbed sites in this study are those localities where modification to soils may have occurred by past land use but was not visually apparent compared with disturbed sites, such as roadsides. Previous studies have found that few natural areas in KNP have greater than 5% cover of exotic species (Godfree *et al.* 2004, Johnston and Johnston 2004), except on limestone and basalt soils where cover is sometimes greater (McDougall *et al.* 2005). Godfree *et al.* (2004) found sub-alpine vegetation communities were largely resistant to invasion by most naturalized exotic plants compared to other grassland communities (Hobbs and Atkins 1992, Prober *et al.* 2002). The low number of exotic species in Australian mountain systems has been linked to a number of factors including climate (Costin *et al.* 2000, McDougall *et al.* 2005), limited ability for species to spread along elevation gradients (Alexander *et al.* 2011), competition from existing native plant communities (Godfree *et al.* 2004) and time since introduction (Johnston 2005). There have been few studies on the effects of soil attributes (such as soil nutrients) in explaining exotic plant richness in mountain systems. Two studies found significant differences in soil chemistry and physical conditions between road verge and adjoining native vegetation communities in the Australian Alps (McDougall 2000, Johnston and Johnston 2004). Both studies found higher levels of calcium and phosphorus in the road verge. McDougall (2005) found no differences in nitrogen or pH whilst Johnston and Johnston (2004) found higher levels of nitrogen and low pH in adjoining native vegetation communities. Both studies concluded that exotic species were mainly confined to disturbed road edges.

Given past and present land use history, changes in soil attributes may influence exotic species richness in natural areas. Fertilizers were used widely in alpine rehabilitation programs in KNP in the 1960s and 1970s (Good 1992). Aeolian dust particles have also been identified as a source of nutrients (Johnston 2001) which may increase during periods of drought when top soil is vulnerable to wind erosion in western parts of the continent.

Changes to soil nutrients may also occur through the increase in feral herbivore populations of horse, deer and rabbit (Dawson 2009, OEH 2013).

4.1.2 Exotic plant occurrence and richness in roadsides and human nodes

In Chapter 3 I investigated the role of elevation and soil attributes in explaining exotic plant richness in two different disturbance types, human nodes and roadsides. Based on these results, two models were developed which explained the differing patterns in exotic species occurrence and richness in disturbed areas.

The roadside model (Figure 4.1) identifies that the overall richness of species along an elevation gradient can be explained through a nested-like pattern. The species occurring at higher elevations are a subset of the species which also occur in lower elevations, suggesting exotic species are dispersed along roadsides. The model indicates that elevation filtering was most apparent above 1700 m (ASL); below this the influence of soil attributes on species richness was more significant.

The human mode model (Figure 4.2) illustrates that species occurrence patterns may be best explained by direct and indirect introduction. The most common exotic species occurring across the elevation gradient and less common species are scattered at various elevations. As more exotic species were found at human nodes than along roadsides, a greater variety of species have the potential to be introduced from human nodes into adjacent natural areas. The model also identifies the influence of a combination of elevation and soil attributes on species richness.

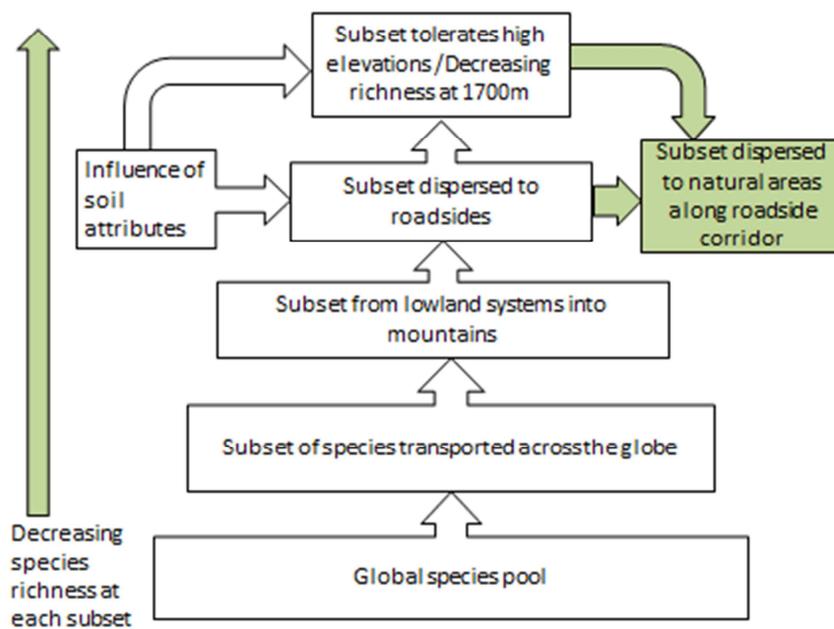


Figure 4.1. This model explains exotic plant species occurrence and richness in roadsides in the Australian Alps.

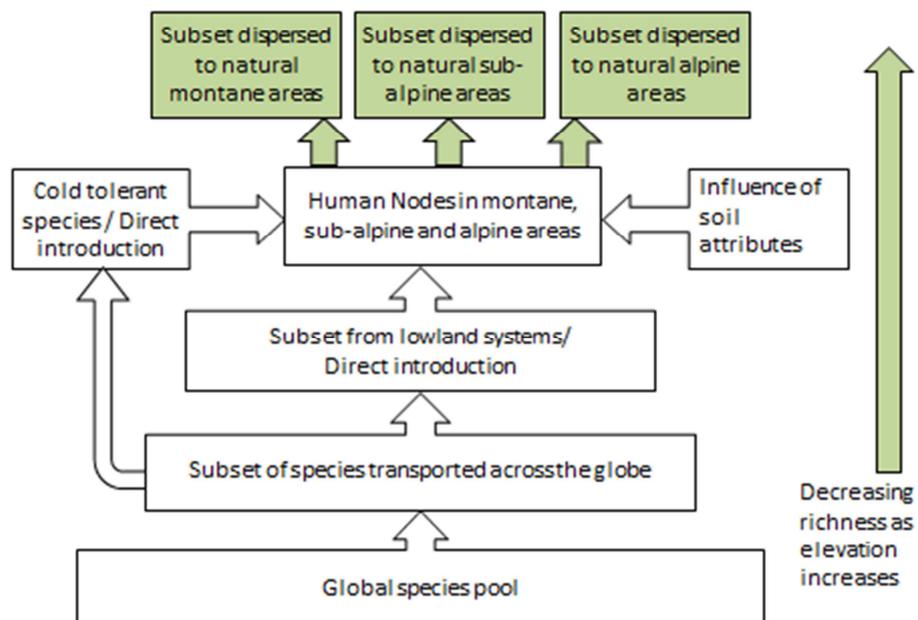


Figure 4.2. This model explains exotic plant species occurrence and richness in human nodes in the Australian Alps.

Based on these patterns, what patterns are likely to occur in undisturbed habitats? I hypothesise, there will be differences in the elevation patterns of exotic species richness between areas adjoining undisturbed roadsides (hereafter called undisturbed roadsides) and areas adjoining human nodes (hereafter called undisturbed human nodes). I suspect undisturbed roadsides receive plants from indirect pathways and undisturbed human nodes receive them from direct and indirect pathways. Given that the undisturbed areas have no obvious soil disturbance compared with the adjacent disturbed areas, I hypothesise that soil variables will have less influence on species richness compared to roadsides and human nodes, and that elevation (climate) will be an important factor.

The role of soil attributes may also vary. As roadsides are linear in shape, and undisturbed sites were > 50 m from the disturbed roadside area, undisturbed areas near roadsides may have less potential for soil changes than those near human nodes (Gelbard and Belnap 2003, Jimenez *et al.* 2011). Areas surrounding alpine huts were often used as a base for large sheep or cattle camps (Morgan and Carnegie 2009) and gold mining occurred in the northern part of KNP (DEC 2006). Thus, past activities may have altered soil conditions around human nodes.

There is also the potential for geology of the area to influence the exotic species richness in natural areas. McDougall *et al.* (2005) found higher exotic plant richness and cover in soils derived from basalt and limestone geology.

4.2 Chapter aims

There have been few studies on the factors that promote exotic species richness in mountain systems in Australia. Elevation, biotic resistance and residence time have been shown to be associated with exotic species richness (Godfree *et al.* 2004, McDougall *et al.* 2005, Mallen-Cooper and Pickering 2008) but other factors such as soil nutrients have not been considered in undisturbed areas. It is important to understand the early dynamic stages of invasion given that few exotic species are widespread and abundant in the Australian Alps. This is particularly important in relation to ongoing human disturbance and climate change predictions (Pauchard *et al.* 2009).

The above review indicates that further research is required to understand how elevation and soil factors are associated with exotic species in undisturbed mountain systems. This study will examine whether the patterns of richness in undisturbed areas are similar to those in adjacent disturbed areas. It will also investigate the role of elevation and soil attributes to explain exotic species richness in natural areas.

This chapter will investigate the patterns of exotic plants in undisturbed mountain areas and whether they conform to the model predictions for natural areas (shaded area Figure 4.1, 4.2). The data collected from natural areas will address the following.

1. Does exotic species richness decline with increasing elevation in natural areas?
2. Do the exotic species which occur in natural areas change along an elevation gradient?
3. Are the exotic species which occur in natural areas a subset of those which occur in adjacent disturbed areas at the same elevation?
4. Can elevation and soil attributes explain patterns of exotic species richness in natural areas?

4.3 Study area

This study was located in montane, sub-alpine and alpine areas in Kosciuszko National Park (673 542 ha). The alpine areas of KNP have one of the world's highest proportions of endemic alpine flora but represent only a small percentage (0.001%) of vegetation on the Australian mainland (Costin *et al.* 2000). The montane area 1100-1400 m above sea level (ASL) generally supports forests dominated by *Eucalyptus pauciflora*, *E.dalrympleana*, *E.delegatensis*, *E.rubida* and *E.viminalis* forests. The sub-alpine area occurs from 1400-1850 m ASL and is dominated by *E.niphophila* woodland interspersed with wet and dry heathlands, bogs and grasslands. Alpine areas above the tree line at 1850 m are dominated by low growing shrubs, herb fields, grasslands, feldmark and bogs (Costin 1954, Costin *et al.* 2000).

Humus soils are dominant above 1400 m where they completely cover all but a few rocky areas and support almost 100% vegetation cover. The humus soils are developed largely from the breakdown of plant material and are characterized by low pH due to the leaching of minerals and nutrients as a result of high rainfall. These along with organic peat soils (bogs

and fens) are important for their water holding capacity. Most of the study sites occur in areas of humus soil except some montane sites which occurred on friable loams and grey-brown podsolics of various depths (Costin 1954, Good 1992).

4.4 Methods

Chapter 3 describes data collection methods. In summary, 55 study sites (110 plots) were chosen across an altitudinal gradient of 1000-2200 m in two different disturbance types: roadsides and human nodes. Once the initial plot was established a paired plot was established in an undisturbed area >50m from the last obvious point of disturbance. The data used in this analysis (Chapter 4) are from the undisturbed plots.

4.5 Statistical analysis

The undisturbed plots were divided into undisturbed human nodes and undisturbed roadsides. In order to establish if there was a difference in exotic plant richness in the two undisturbed zones a Wilcoxon Rank test was undertaken using S-Plus Statistical Analysis Software (Tibco 2010). In order to establish if there was a difference between richness of undisturbed and disturbed areas a Wilcoxon rank test was undertaken using S-plus statistical analysis software (Tibco 2010).

To test if elevation was correlated with exotic species richness in undisturbed roadsides and undisturbed human nodes, Spearman's rank correlation was undertaken using S-Plus Statistical Analysis Software (Tibco 2010). The variables, elevation and annual mean temperature were tested.

To confirm whether exotic species at higher elevations comprised a nested subset of species from lower elevations, following Alexander *et al.* (2011), sites were ordered by increasing elevation (matrix rows) and species by decreasing number of occurrence (columns). Next 1,000 random matrices were generated using a null model that constrained species richness within sites while randomizing the occurrence of species. The analysis was undertaken with the nestedness metric based on overlap and decreasing fill (Almeida-Neto *et al.* 2008) using the *vegan* package (Oksanen *et al.* 2009) in R software (R development core team, 2012). Generalized linear models were then developed to identify explanatory variables for the response variable exotic species richness in undisturbed roadsides and human nodes. Model

selection was the preferred option due to the complexity of interrelationships with the predictor variables (Johnson and Omland 2004). To reduce the potential for error, I tested all variables for collinearity (Graham 2003) using Spearman's rank correlation (non-normal data). For all variables that showed a cross correlation of $r > \pm 0.6$ only one of each pair of variables was included in the models. Cross correlation was undertaken on 19 independent variables. There were some differences in the variables used in the final GLM for both types. For undisturbed roadsides, ammonium nitrate, sulphur, potassium, phosphorus and mean temperature were used, whilst for undisturbed human nodes, nitrate nitrogen, soil depth, phosphorus, potassium and mean temperature. As pH, elevation and mean annual temperature were strongly correlated with each other mean annual temperature alone was used in the GLM. This was chosen over elevation and pH as temperature has a more direct relationship with plant growth. Phosphorus (colwell) was also chosen over total phosphorus as it is a measurement of phosphorus available for plants to use (Colwell 1963).

The response variable, exotic species richness (count data) was transformed using Poisson to assume a normal distribution. Using S-Plus software the Akaike Information Criterion (AIC) was calculated (Johnson and Omland 2004). AIC provides an objective way to determine which model from a set of models is most parsimonious. The AIC was adjusted for a small sample size due to the high proportion of predictor variables compared with the sample size. The best model has $AIC = 0$ and only models with $AIC \leq 2$ have substantial support (Burnham and Anderson 2002).

4.6 Results

4.6.1 Exotic species richness in undisturbed areas

Twelve exotic species were recorded in undisturbed roadsides and 23 in undisturbed human nodes. The number of forbs and shrubs in undisturbed human nodes was higher than undisturbed roadsides (Table 4.1). These included species that have been used in ornamental plantings in nearby disturbed human nodes, such as, *Rubus* sp., *Rosa rubiginosa* and *Lynchis coronaria*. There was no significant ($P = 0.74$) difference in the means between exotic species in undisturbed roadsides (1.9) and undisturbed human nodes (2.4). Both undisturbed areas shared the same five common exotic species as shown in Table 4.2.

Table 4.1. The number of exotic species broken up into growth forms in natural areas.

Location	Tree	Grass	Forb	Shrub	Sedge	Succu- lent	Total
Undisturbed							12
Roadside	1	3	8	0	0	0	
Undisturbed							
Human node	1	2	17	2	0	1	23

Table 4.2. Frequency (%) of occurrence of the five most common exotic species

Species	Undisturbed roadside	Undisturbed human node
<i>Acetocella vulgaris</i>	43	44
<i>Anthoxanthum odoratum</i>	43	31
<i>Hypochaeris radicata</i>	43	53
<i>Sonchus oleraceus</i>	17	16
<i>Trifolium repens</i>	22	13

4.6.2 A comparison in exotic species richness between disturbed and undisturbed areas

Exotic species richness in natural areas was compared with the richness of disturbed areas. As expected there was a significant difference ($P < 0.001$) between mean exotic richness in disturbed roadside (9.3) areas and undisturbed roadsides (1.9). There was also a significant difference ($P < 0.001$) in the means of disturbed (8.2) and undisturbed human nodes (2.4).

4.6.3 Change in species along an elevation gradient

Nested analysis was undertaken to determine if the species which occur at high elevations were a subset of those at lower elevations. All species were included in the analysis. The results were different for each undisturbed type with nestedness significant at undisturbed roadsides ($Z = 2.91$, Nest 15.07, $P = 0.03$) and highly un-nested at disturbed human nodes ($Z = 1.33$ Nest 22.13 $P = 0.22$). Figures 4.3 and Figure 4.4 illustrate the altitudinal range of those species which were recorded at more than one site at a different elevation ($\pm 100\text{m}$) in each undisturbed type. Even though the nestedness results were not significant for undisturbed human nodes the general trend is that similar patterns occur between both undisturbed types with the species which occur more than once.

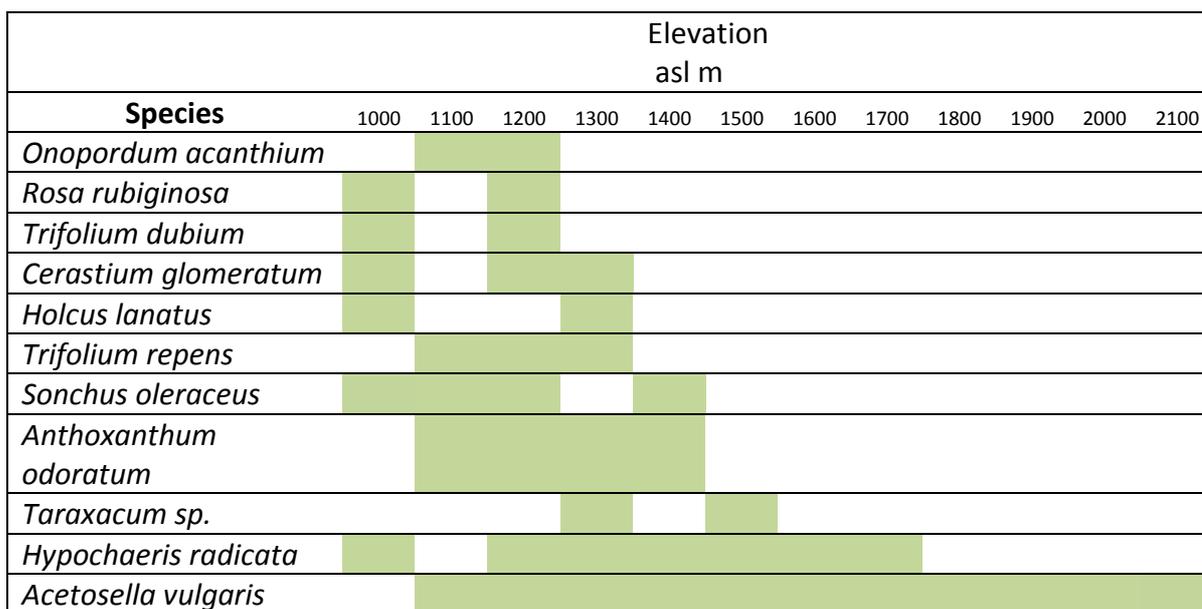


Figure 4.3. Altitudinal range of 11 exotic plant species which were recorded in two or more undisturbed human nodes.

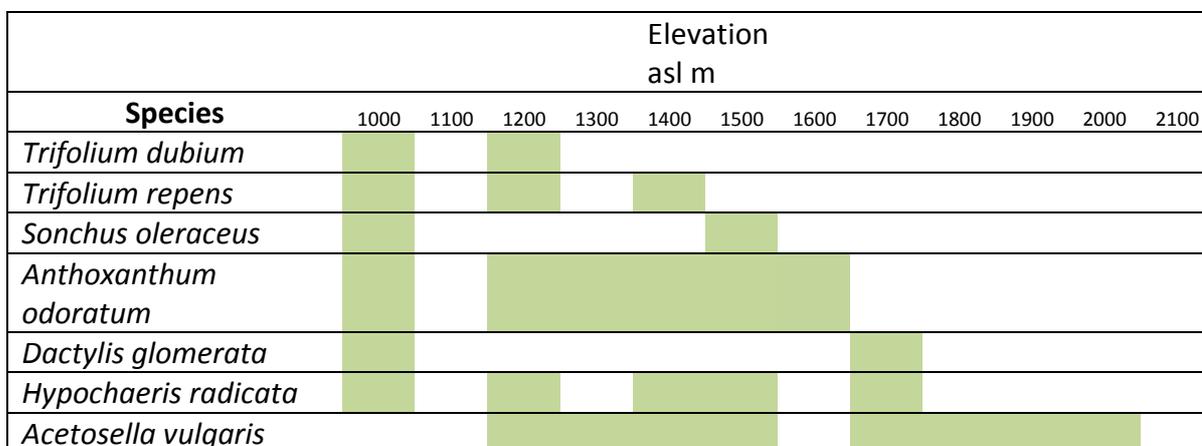


Figure 4.4. Altitudinal range of 7 exotic plant species which were recorded in two or more undisturbed roadsides.

Undisturbed areas beside roadsides

Exotic richness in undisturbed roadsides was significantly negatively correlated with both elevation ($P = 0.04$) and mean temperature ($P = 0.04$).

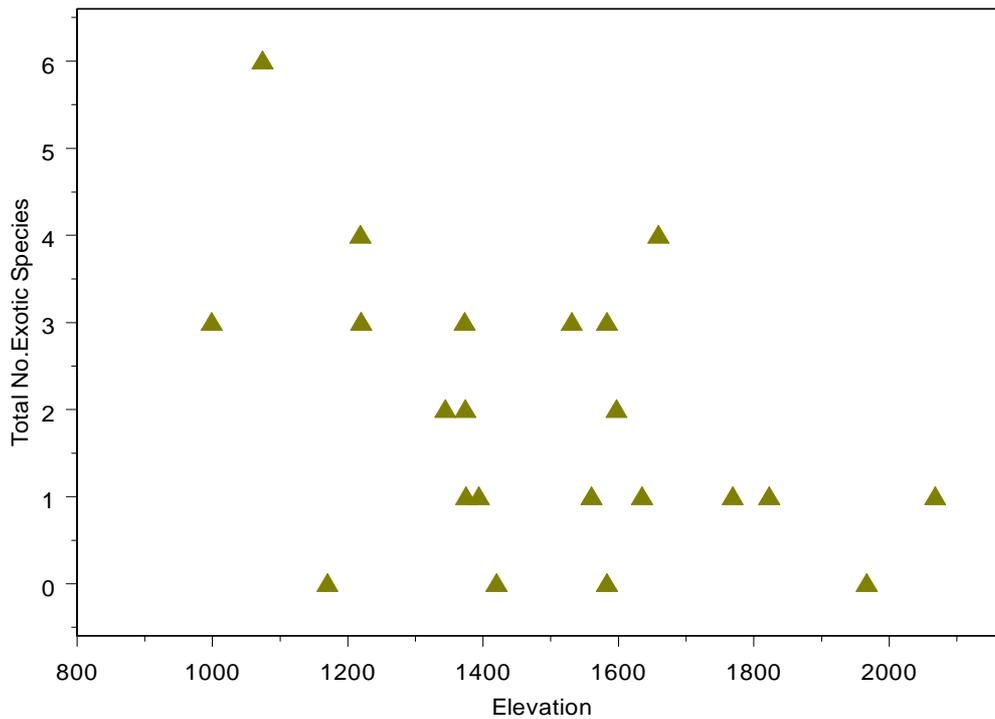


Figure 4.5. Relationship between total number of exotic species and elevation (m ASL) at natural areas > 50 m from roadsides in Kosciuszko National Park.

The GLM models for undisturbed areas beside roadsides, show that one model had $\Delta AICc \leq 2$ and a further four models had an $\Delta AICc \leq 3$. Model 1 indicated mean annual temperature was the main predictor variable for exotic species richness. This explained only 21% of the variation. The other models with an $\Delta AICc \leq 3$ included the variables phosphorus, sulphur, potassium and ammonium nitrate. Unexpectedly, all nutrients except potassium were negatively, not positively associated with exotic species richness.

Table 4.3. Comparison of models fitting exotic species richness with explanatory variables for natural areas in proximity to roadsides ($\Delta AICc \leq 3$)

Rank	Model	K	AICc	R2	$\Delta AICc$	wi
1	ESR~MAT	2	29.21	0.21	0.00	0.31
2	ESR~MAT+P	3	31.38	0.23	2.17	0.11
3	ESR~MAT+ExK	3	31.60	0.22	2.39	0.10
4	ESR~MAT+S	3	31.83	0.21	2.62	0.08
5	ESR~MAT+AmN	3	31.87	0.21	2.66	0.08

K, number of estimated parameters, AICc – Akaike’s Information Criterion corrected for small sample sizes, R2 – adjusted R², $\Delta AICc$ – difference in AIC, wi, Akaike weights- for each variable are summed across all candidate models in the set, ESR, exotic species richness, MAT, mean annual temperature, P, phosphorus, ExK, extractable potassium, S, sulphur, Amn, Amonium nitrate

Undisturbed human nodes

Exotic richness in undisturbed human nodes was significantly positively correlated with elevation ($P = 0.0002$) and negatively correlated with mean temperature ($P = 0.0001$).

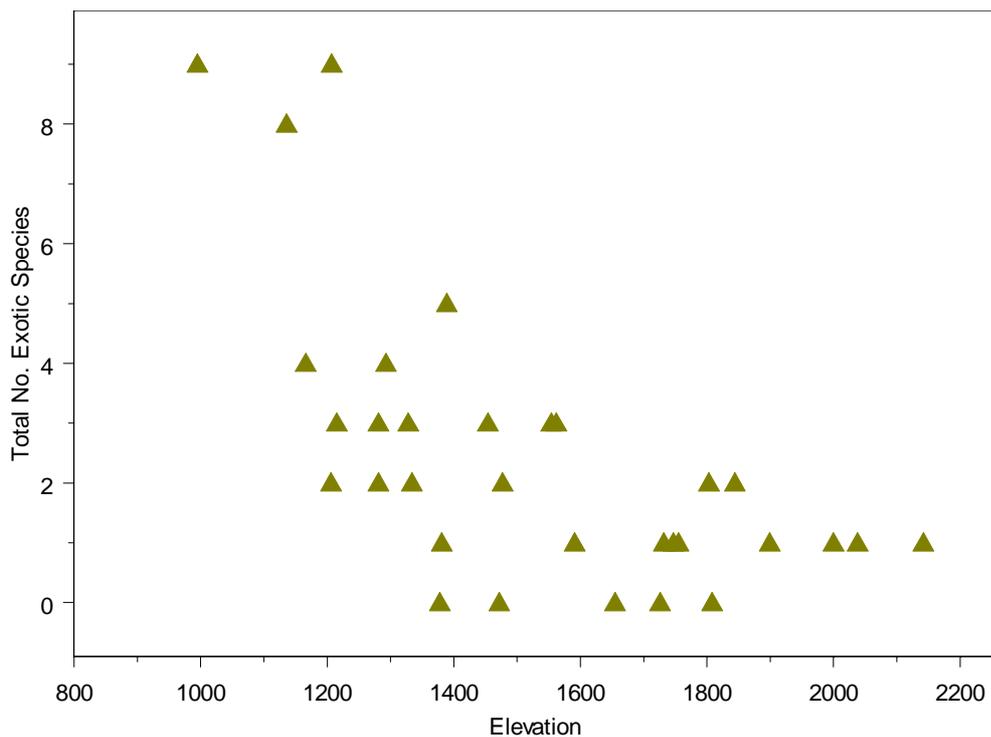


Figure 4.6. Relationship between total number of exotic species and elevation (m ASL) at natural areas > 50m from human nodes in Kosciuszko National Park.

Five models had $\Delta AICc \leq 2$ in the GLM analysis. This indicates a number of predictors are likely to contribute to the patterns associated with exotic species richness although Model 1

indicated mean annual temperature as the most significant factor which explained 51% of variation. Mean annual temperature was featured in every significant model. Because a number of models were equally valid, the importance of each variable was determined by summing the Akaike weights. Mean annual temperature had the highest summed Akaike weight ($\sum w_i=0.68$), followed by soil depth ($\sum w_i=0.22$), nitrate ($\sum w_i=0.21$) and phosphorus ($\sum w_i=0.09$).

Table 4.4. Comparison of models fitting exotic species richness with explanatory variables for natural areas in proximity to human nodes ($\Delta AICc \leq 2$)

Rank	Model	K	AICc	R2	$\Delta AICc$	wi
1	ESR~MAT	2	37.65	0.51	0.00	0.24
2	ESR~MAT+SD	3	38.94	0.53	1.29	0.13
3	ESR~MAT+NN	3	39.13	0.52	1.47	0.12
4	ESR~MAT+P	3	39.50	0.52	1.85	0.10
5	ESR~MAT+SD+NN	4	39.56	0.56	1.91	0.09

K, number of estimated parameters, AIC–Akaike’s Information Criterion corrected for small sample sizes, R2 – adjusted R², $\Delta AICc$ –difference in AIC, wi, Akaike weights-for each variable are summed across all candidate models in the set, ESR, exotic species richness, MAT, mean annual temperature, SD , soil depth, NN, nitrate nitrogen, P, phosphorus

4.6.4 Additional results

Due to collinearity pH was excluded from the final GLM model. However, when tested using Spearman rank correlation, pH correlated significantly with both elevation ($r = 0.82$, $P < 0.001$ negative) and total exotic species ($r = 0.73$, $P < 0.001$, positive).

4.7 Discussion

This study found the number of exotic species in undisturbed areas was smaller than in disturbed mountain systems (Chapter 3). These results are consistent with other global and regional mountain studies which have found natural areas to have fewer exotic species than adjacent disturbed areas (Daehler 2003, Godfree *et al.* 2004, McDougall *et al.* 2005, Chytry *et al.* 2008). Given the low number of exotic species this study supports other findings that natural areas can better resist invasion than disturbed areas (Hobbs and Huenneke 1992, Godfree *et al.* 2004, Lake and Leishman 2005).

This study found that elevation and mean annual temperature were both significant in explaining low exotic species richness in undisturbed areas. Given this finding elevation (climate), along with limited or no anthropogenic disturbance may provide an additional barrier in maintaining low exotic richness in high elevation areas. Patterns in richness at the same elevation did show variations (Figures 4.3 and 4.4) indicating other site factors may be influential (Mallen-Cooper and Pickering 2008).

At undisturbed plots near human nodes, this study found that whilst mean temperature was an important explanatory factor in GLM soil attributes also contributed to significant models. High exotic richness was associated with shallow soil depth and high phosphorus levels. Nitrate nitrogen demonstrated a similar pattern in undisturbed and disturbed human nodes, and increased with elevation, despite exotic species richness declining. The GLM results indicated soil attributes at undisturbed roadsides had no influence on exotic species richness overall however individual sites may vary.

Soil pH correlated significantly with exotic species richness and mean temperature but was not included in the final GLM due to collinearity with elevation and temperature. Low pH has been attributed to reduced exotic plant richness in other natural systems (Rose and Hermanutz 2004). A decreasing pH with elevation in undisturbed areas may reduce the availability of nutrients to plants (Dupré and Ehrlén 2002). However, the adaptation of native species to a more acidic pH through root adaptations such as arbuscular mycorrhizal fungi which assist the synthesis of nutrients may be advantageous for faster growth than exotic species. Johnston and Ryan (2004) found areas with a low cover of native species in alpine areas of the Australian Alps to have less diversity and extent of arbuscular mycorrhizal fungi.

Although my study did not investigate arbuscular mycorrhizal fungi it may be an important variable in the maintenance of biotic resistance in natural plant communities.

Mean annual temperature was the most parsimonious model for both disturbance types however in human nodes there were a number of models that included soil attributes. The difference in the GLM results between the two undisturbed habitat types may be explained by current and past land use history. Road construction and maintenance causes disturbance to soils and native vegetation communities (Hobbs 2006, Hobbs 2009, Jimenez *et al.* 2011) however, their disturbance is linear and often restricted to the depth of the road verge. Mallen-Cooper (2005) and Johnson and Johnson (2004) found exotic species largely absent five meters from road verge sites in KNP. Human nodes such as ski resorts may have the capacity to impact over a much broader area. In addition many of the human node localities were used as camps for summer grazing or the location of mining enterprises (Good 2002). Many of the sites in this study are still used today for recreation as overnight camps or horse riding camps (DEC 2006). Ongoing changes to the soil chemical properties, from animal manure or compaction may not be visually obvious in the vegetation community present.

In other studies (McIntyre and Lavorel 1994, Bashkin *et al.* 2003) the cover and richness of exotic species was influenced by geology. The types of geology in my study included basalt, limestone and granite and this may have influenced species richness at some sites. McDougall *et al.* (2005) study in the Australian Alps found increased species richness in areas with limestone and basalt geology.

Previous studies on mountain roadsides suggest that exotic species at higher elevations can be best described by directional elevation filtering, where species are dispersed along road corridors and those species with the widest climatic tolerance persist (Alexander *et al.* 2011). Those species found at the highest elevation are a subset (nested) of species from the lower elevations. Contrary to this I found differences in patterns of richness between roadsides and human nodes at disturbed sites (Chapter 3). These same patterns also occurred in the adjoining undisturbed areas. Based on the models developed in Chapter 3 (Figure 3.10, 3.11) and the results from this chapter, Figure 4.7 and 4.8 explain exotic species occurrence and richness in both disturbed and undisturbed habitats for roadsides and human nodes. Undisturbed roadside areas were nested and undisturbed human node sites un-nested

indicating that in roadsides patterns were best explained by indirect introductions and in undisturbed human nodes indirect and direct introductions. Despite these different patterns both shared the same two most common species, *Acetocella vulgaris* and *Hypochaeris radicata* (Table 4.2). Undisturbed human nodes varied in both the number of species and the type having ornamental species, including *Lynchis coronaria*. This is perhaps associated with the past and current land use of human nodes.

The results from this analysis suggest that different species patterns occur in undisturbed areas. Given these patterns undisturbed human nodes may have a greater capacity to contain different exotic species across the elevation gradient. Some of the sites also contained species that were not present in the adjoining disturbed sites, this may have been because they had been previously treated in exotic species control programs but left untreated in surrounding undisturbed areas. Therefore detection of new species should also be undertaken adjacent to human nodes.

This study highlights that, despite historic disturbances, exotic species numbers remain low in many of the undisturbed areas of Kosciuszko National Park. Disturbance and other factors, such as exotic seed dispersal, have not been sufficient over broad areas to disadvantage native vegetation communities. Natural or anthropogenic disturbance in the future could change this balance. Although not detected in this study there are natural areas in KNP that have had significant short term changes in the distribution of exotic species. The 2003 fires burnt 71% of the national park (Zystra 2006) which has led to an expansion in some exotic species distributions, such as *Hieracium aurantiacum* (Caldwell & Wright 2011) and *Leucanthemum vulgare* (OEH 2013).

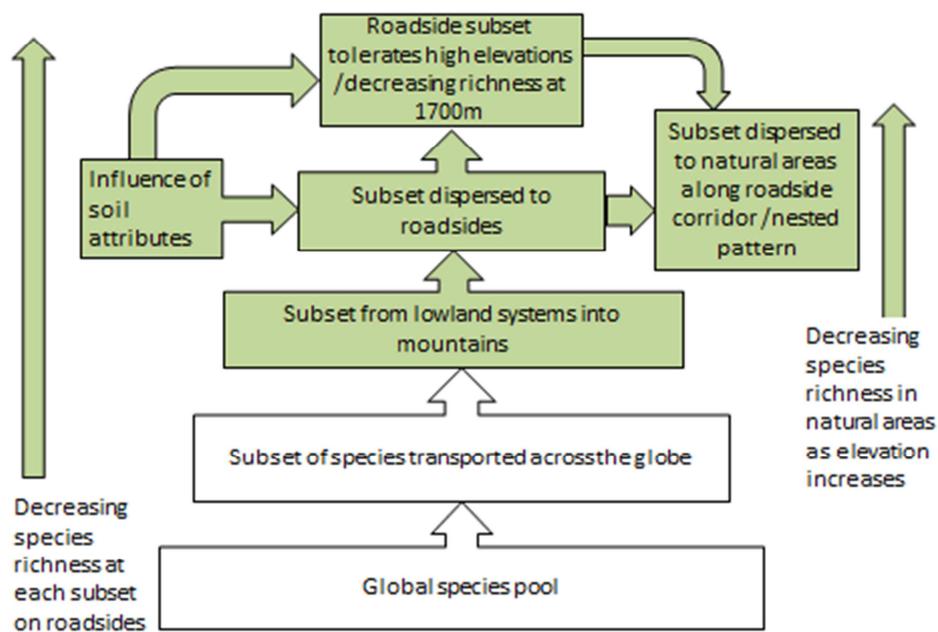


Figure 4.7. This model explains exotic plant species occurrence and richness in roadsides and undisturbed areas > 50 m from roadsides in the Australian Alps.

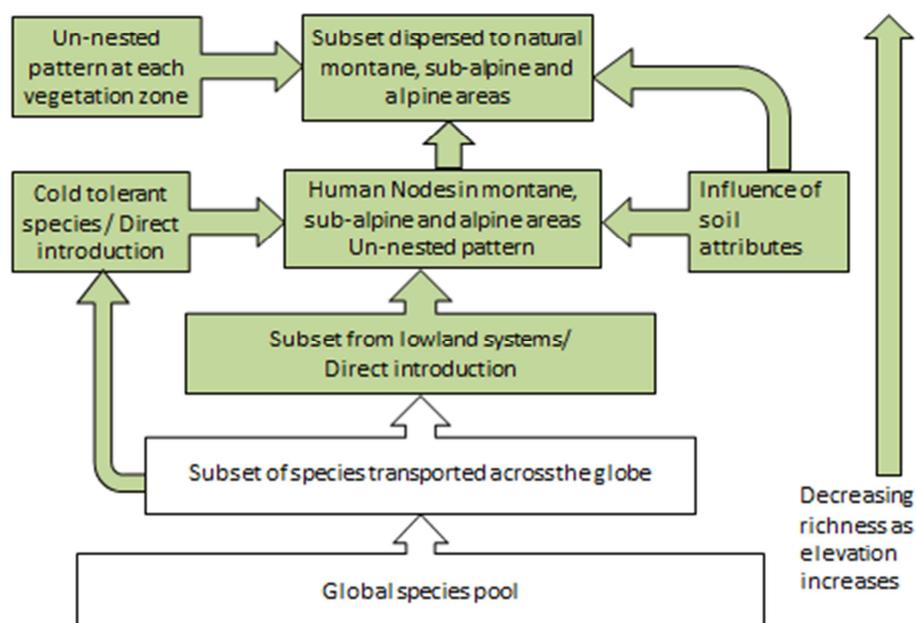


Figure 4.8. This model explains exotic plant species occurrence and richness in human nodes and undisturbed areas >50 m from human nodes in the Australian Alps.

This study indicated that mean temperature (climate) may help prevent the establishment of exotic species richness in undisturbed areas. The role of climate change for future management of exotic species in mountain systems is important as globally climate change has already been implicated in the increase in exotic species in mountain systems (Becker *et al.* 2005, Pauchard *et al.* 2009). The alpine areas of the Australian Alps have warmed at the rate of 0.2°C per decade over the past 35 years (Hennessy *et al.* 2003). The current snow line will rise and the level and duration of snow cover have already declined with earlier melt (Green and Osborne 2012). These increased temperatures, reduced snow cover and duration may provide conditions more suited for increased dispersal of existing exotic plants and for new species to establish (Pickering *et al.* 2004). Implications for existing naturalised exotic species in the Australian alps are largely unknown with the exception of modelling undertaken for *Hieracium* species (Beaumont *et al.* 2009) and *Achillea millefolium* (Johnston 2005).

4.8 Conclusion

Exotic species are present in undisturbed areas although in smaller numbers than disturbed areas. Protecting undisturbed vegetation communities in natural systems may be achieved by protecting areas from anthropogenic disturbance. Understanding the different patterns which influence exotic species in undisturbed areas in proximity to disturbed areas may assist in the detection of new incursions.

From the species which already occur in mountain systems only a small number will eventually have the potential to invade undisturbed vegetation communities (Pyšek *et al.* 2004, Rejmánek and Richardson 2006). There is an opportunity to identify from the pool of species already present which ones have the greatest capacity to expand. In Chapter 5 I will examine the abiotic and biotic attributes associated with differences in the composition of exotic plants in disturbed and undisturbed habitats.

CHAPTER 5 ARE ABIOTIC AND BIOTIC ATTRIBUTES ASSOCIATED WITH DIFFERENCES IN EXOTIC SPECIES COMPOSITION IN DISTURBED AND UNDISTURBED MOUNTAIN SYSTEMS?

5.1 Introduction

Changes in soil physical and chemical properties have been associated with increases in exotic plant species diversity and cover in lowland systems (Hester and Hobbs 1992, Burke and Grime 1996, Bashkin *et al.* 2003, Lake and Leishman 2004, Densmore 2008). By contrast, increasing elevation and associated climatic factors have been commonly used to explain exotic species richness and occurrence in mountain systems (Becker *et al.* 2005, McDougall *et al.* 2005, Mallen-Cooper and Pickering 2008, Haider *et al.* 2010).

Soils and vegetation have an integral relationship. Soils provide the essential requirements for plant growth including water, nutrients, oxygen, habitat for micro- and macro-organisms and temperature moderation. Vegetation provides protective cover, suppresses erosion and as a result of litter accumulation and decay helps maintain soil nutrients (Birkeland 1984). Various studies have explored how soil attributes influence natural vegetation communities and exotic species (Prober *et al.* 2002, Bashkin *et al.* 2003, Rose and Hermanutz 2004, Leishman and Thomson 2005).

Differences in available resources may lead to a range of conditions across a landscape which influence the types of exotic species present (Hobbs and Huenneke 1992, Burke and Grime 1996). Some natural systems may be more vulnerable to exotic species invasion due to their naturally fertile soils. Vegetation communities occurring in areas of high substrate fertility with naturally high levels of soil nutrients have been found to be most vulnerable to invasion and have been found to have the highest number of exotic species (McIntyre and Lavorel 1994, Bashkin *et al.* 2003, McDougall *et al.* 2005).

Changes to soil nutrients as a result of disturbance or nutrient addition through the application of fertilizer have been associated with exotic species establishment in disturbed environments (Burke and Grime 1996, Stohlgren *et al.* 1999). Altered resources as a result of

increased light, moisture or soil nutrients in disturbed areas can provide opportunities for exotic plant establishment (Hobbs 1989, Hobbs and Huenneke 1992, Davis *et al.* 2000). Some exotic plant species, especially nitrogen-fixing species, can alter soil nutrient levels (Waterhouse 1989, Ehrenfield *et al.* 2001, Turner *et al.* 2008).

The impact of roads in altering soil physical and chemical properties has been explored in lowland systems (Gelbard and Belnap 2003, Christen and Matlack 2005, Christen and Matlack 2009). The role of roads in providing a conduit for exotic species into mountain systems has been examined globally and regionally (Mallen-Cooper 1990, Pauchard and Alaback 2004, Kalwij *et al.* 2008, Kosaka *et al.* 2008). The influence on exotic species richness due to changes in soil nutrients along roadsides and other disturbed areas in mountain systems has received less attention (Johnson and Johnson 2004, Alexander *et al.* 2009).

Differences in soil attributes can contribute to the type of species present. High nutrients have been associated with species that have a high specific leaf area (SLA). This trait leads to rapid growth rates as plants can access resources more readily (Cornelissen *et al.* 2003). In low nutrient environments, species with the ability to fix nitrogen, such as *Cytisus scoparius*, can change soil chemistry to advantage themselves above native plants that grow in low nutrient soils (Waterhouse 1988).

Most exotic plant studies in mountain systems have focused on species richness. Studies focusing only on richness have been criticised as hindering our understanding of drivers of invasion and as a poor substitute for assessing impact on native communities (Seabloom *et al.* 2013). A site which may be low in exotic species richness may still have a high cover of exotic species which may impact on ecosystem function. Examining variation in plant composition may explain different effects on ecosystem processes (Richardson and Pyšek 2006). One species or a group of species with a similar plant functional type may have a greater impact on soil nutrient cycling (Hooper and Vitousek 1997).

Changes in soil attributes may favour particular plant species over others (Godefroid and Koedam 2004). Increased nutrients have been associated with the proliferation of exotic grasses (Hobbs and Huenneke 1992). High potassium levels have been linked to the increased growth of exotic herbs like *Taraxacum officinale* (Densmore 2008). Some species,

such as the exotic grass *Festuca rubra*, can tolerate low soil nutrient conditions and are used globally to stabilize roadside soils (Dyrness 1975, Hansen and Clevenger 2005, Akbar 2009).

5.1.1 Exotic plants in the Australian Alps

Most studies of exotic plants in the Australian Alps have compared the richness of species in disturbed and natural systems (Johnston and Pickering 2001, McDougall *et al.* 2005, Mallen-Cooper and Pickering 2008). A number of studies have documented an increase in exotic species since the 1950s, especially in disturbed areas (Costin 1954, Mallen-Cooper 1990, Johnston 2005).

Exotic species richness has been linked to a number of factors in Australian mountain systems. High elevation areas have lower temperatures and shorter growing periods that may impact on growth or seed production (Costin *et al.* 2000, McDougall *et al.* 2005, Johnston 2005). A steep elevation gradient may limit dispersal (Alexander *et al.* 2011). Competition with other plants in native vegetation communities (Godfree *et al.* 2004) may prevent the establishment or persistence of some species. The longer an exotic species has become naturalised the more likely it is to have a wider distribution and occur at higher elevations (Johnston 2005, Morgan and Carnegie 2009, Haider *et al.* 2010).

Soil nutrients have been important for explaining exotic species richness and cover in some low nutrient, lowland systems in Australia (Hobbs and Atkins 1991, Prober *et al.* 2002, Leishman and Thomson 2005, Turner *et al.* 2008). Two studies comparing exotic species richness between road verges and adjoining native vegetation communities in the Australian Alps found exotic species were largely confined to road edges (McDougall 2000, Johnston and Johnston 2004). Both studies found higher levels of calcium and phosphorus in the road verge. Johnston and Johnston (2004) found higher nitrogen and lower pH in adjoining native vegetation communities whereas McDougall (2001) found no differences in nitrogen or pH. These studies did not investigate the relationship of exotic species composition with the soil attributes.

No study in the Australian Alps has investigated differences in soil chemistry between different types of disturbance (human nodes and roadside) and undisturbed areas across an elevation gradient.

In Chapters 3 and 4 I investigated the role of elevation and soil attributes in explaining exotic plant richness in disturbed and undisturbed mountain systems. As expected, disturbed roadsides and human nodes had greater richness of exotic species than undisturbed sites. The undisturbed sites were located in native vegetation communities over 50 m away from the last obvious point of physical soil disturbance.

As patterns of species richness along the elevation gradient were different in disturbed roadsides and human nodes, two models were developed (Refer to Chapter 4, Figure 4.7, 4.8). Elevation filtering of exotic species was only obvious above 1700 m along disturbed roadsides. Soil attributes appeared to have the greatest effect on species richness, perhaps as the result of road construction and maintenance activities. Exotic species composition along roadsides was consistent with directional elevation filtering (Alexander *et al.* 2011), i.e. the species found at higher elevations were a subset of species found at lower elevations.

In human nodes a combination of mean temperature (elevation) and various soil attributes explained species richness. Exotic species richness in human nodes was interpreted by a combination of indirect and direct introductions. Both disturbance types shared many of the common exotic species but human nodes had more ornamental species associated with past horticultural use. In contrast, in natural areas >50 m from roadsides and human nodes exotic species richness was found to be influenced predominantly by mean annual temperature.

5.2 Chapter aims

This chapter will investigate associations between exotic species composition and soil attributes and temperature in disturbed and undisturbed mountain systems. Specifically I address the following questions:

1. How does the composition of exotic species vary between disturbed and undisturbed habitat types?
2. How do soil attributes vary between disturbed and undisturbed habitat types?
3. What is the relationship between exotic plant composition and soil attributes and temperature?
4. Does the influence of abiotic and biotic factors vary for different species?

5.3 Study area and field methods

The study area is described in the Introduction and Chapter 3. The methods for site data collection are included in Chapter 3 and Chapter 4. The number of plots surveyed was 46 for disturbed and undisturbed roadsides and 64 for disturbed and undisturbed human nodes. Percentage cover of all exotic species was visually estimated using the scale 0-1, >1-5, >5-10, >10-25, >25-50, >50-75, >75-94, >94-100. Analyses in this chapter are based on the cover of each exotic species at each plot.

A soil auger was used to remove ten random samples from the top 5 cm of soil (5 cm depth x 4 cm width) in each plot. The samples were bulked to obtain a representative sample and mixed well. Samples were chilled to prevent microbial activity and were sent to CSPB Soil Analysis & Plant Laboratory in Western Australia. Soil testing included Colwell phosphorus and potassium (Colwell 1965), nitrate and ammonium (Searl 1984, Rayment and Lyons 2011), pH and electrical conductivity (Rayment and Lyons 2011), organic carbon (Walkely and Blake 1934, Rayment and Lyons 2011), sulphur (Blair et al 1991), available phosphorus and exchangeable cations (aluminium, magnesium, calcium, potassium, sodium), total nitrogen and total phosphorus (Rayment and Lyons 2011). Soils were classified using the Australian Soil Classification System (Isbell 1996).

5.4 Statistical analysis

5.4.1 Exotic plant composition

The ordination analysis, non-metric multi-dimensional scaling (NMDS), was used to determine whether exotic species composition differed between the four habitat types: roadside, undisturbed roadside, human node and undisturbed human node. NMDS was undertaken using the PRIMER package, version 6 (Clarke and Gorley 2006). This analysis is commonly used to visualise dissimilarities in species composition data. Points on a NMDS graph that are close together display samples which are similar in community composition (Clarke 1993, Clarke *et al.* 2006). The closeness of fit of an NMDS plot is expressed in terms of stress level. A stress level of ≤ 0.1 corresponds to a good ordination, a stress level of ≤ 0.2 provides a potentially useful 2-dimensional picture and a stress level ≥ 0.2 indicates that an alternative analysis should be considered (Clarke and Warwick 2001). Data on exotic species

were square root transformed and a dissimilarity matrix was created using the zero-adjusted Bray-Curtis dissimilarity measure. The zero-adjusted Bray-Curtis coefficient (Clarke *et al.* 2006) allows plots with no exotic species to be included in the analysis. After initial analysis, two outliers (1121, 1187) were removed from the species composition and soil attribute data as both plots formed significant outliers, due to high levels of exchangeable sodium. Both sites occur adjacent to exposed localities on Kosciuszko Rd where snow accumulates and de-icing salts are used throughout the winter months to reduce snow. It is possible that there was some persistence of sodium in the soil.

For the analysis of multivariate data in response to categorical variables (factors) I used PERMANOVA (Anderson *et al.* 2008). PERMANOVA allows multivariate data to be simultaneously tested for one or more factors based on resemblance measures. A two-way crossed experimental design was used, the top level factor being roads and human nodes and second level factor being disturbed and undisturbed.

To understand which exotic species contributed to the separation of habitat types an analysis of similarities (SIMPER) procedure was undertaken. This exploratory analysis identifies the percentage that each exotic plant species contributes to overall dissimilarity in a Bray-Curtis dissimilarity matrix (Clarke 1993). This test used the same factors as the PERMANOVA test.

5.4.2 Soil data comparisons

To determine if soil variables differed between habitat types an NMDS was undertaken. To test for multi-collinearity amongst variables (Graham 2003) I first used Spearman's rank correlation (Tibco 2010) on all soil data and removed all variables with a >0.6 correlation. The final variables used were: soil depth, nitrate nitrogen, pH, sulphur, potassium, exchangeable sodium, phosphorus and organic carbon. The soil data were then $\log(x + 1)$ transformed and normalized. Dissimilarity matrices were then created using Euclidean distance.

For the analysis of soil data in response to categorical variables (factors) I used PERMANOVA (Anderson *et al.* 2008). I used a two-way crossed experimental design, the top level factor being roads versus human nodes and the second level factor being disturbed versus undisturbed.

The means and standard deviation of all soil attributes (not transformed) in each habitat type were calculated in S Plus (Tibco 2010).

5.4.3 Relationship of exotic species composition to abiotic factors

Based on findings in Chapter 3 and 4, mean temperature was included with soil attributes in the multivariate analysis. To understand the relationship of abiotic factors (temperature and soils) to the variability in exotic species composition, distance based linear models (DISTLM) were used (Anderson *et al.* 2008). This analysis modeled the relationship between multivariate data (species composition) and the predictor variables (soil attributes and temperature).

To undertake the DISTLM routine, the Bray-Curtis resemblance matrix of exotic species composition data was used (as in the MDS analysis above). The environmental variables used included soil attributes (as above) and mean annual temperature. The data were then $\log(x+1)$ transformed and normalized. DISTLM was then constructed using a stepwise selection procedure with adjusted R^2 to determine the influence of each environmental variable. Akaike Information Criterion (AIC) was also calculated to determine the overall best fitting model. Distance based redundancy analysis (dbRDA) was used to visually describe the models developed through DISTLM. The vectors on the dbRDA graph identify the gradients of individual variables across the plot axis. The length of the vector is proportional to the Pearson correlation co-efficient (Anderson *et al.* 2008).

5.5 Results

5.5.1 Exotic plant composition

The stress level for the 2-dimensional NMDS ordination analysis was 0.2 and for the 3-dimensional analysis was 0.14. A stress value of ≤ 0.1 corresponds to a 'good' ordination and values ≤ 0.2 provide a 'potentially useful' 2-dimensional picture (Clarke and Warwick 2001). Consequently, the 3-D analysis was used. The 3-dimensional NMDS graph of the four habitat types (Figure 5.1) clearly separated the disturbed and undisturbed plots. However there was no obvious separation between roadsides and human nodes for either the disturbed or undisturbed plots.

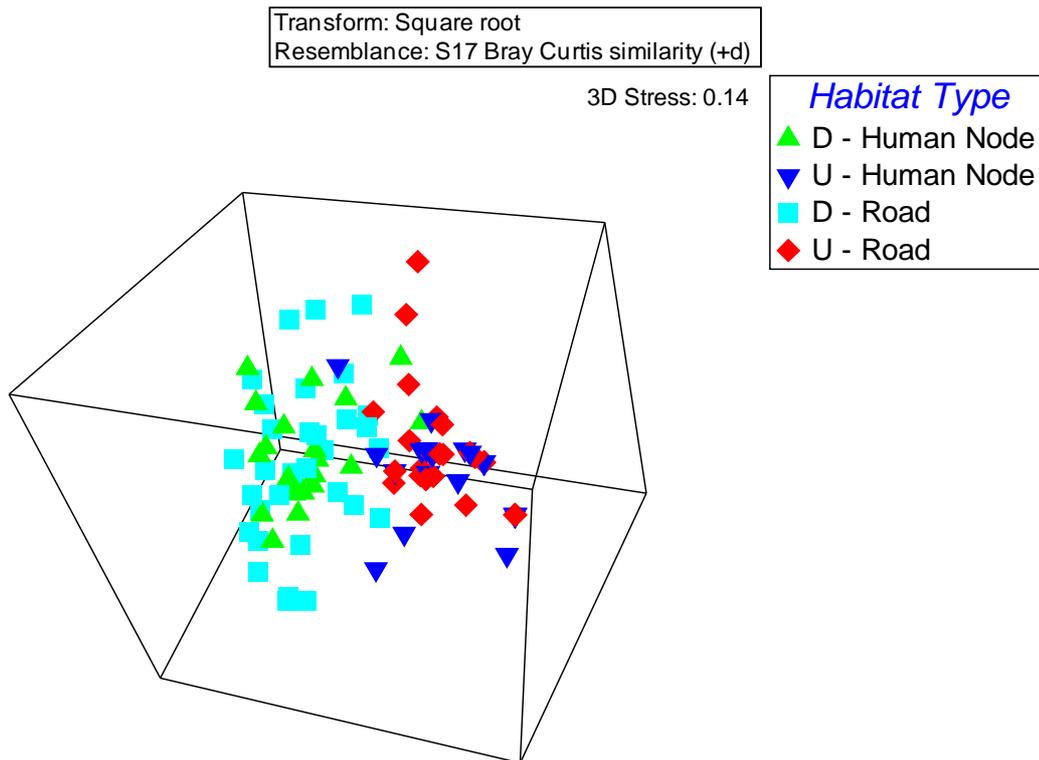


Figure 5.1. Three-dimensional NMDS of exotic plant species composition in four mountain habitat types. D = disturbed, U = undisturbed.

The visual interpretation of Figure 5.1 was supported by analysis of the exotic species composition data in a two-way crossed experimental design using PERMANOVA. The results (Table 5.1) demonstrated a significant difference in the composition of exotic species between disturbed and undisturbed plots ($P = 0.001$). Disturbed plots included data from both disturbed roadsides and human nodes, and ‘undisturbed’ plots included data from undisturbed plots > 50 m from roads or human nodes. There was no significant difference ($P = 0.759$) between the roadside plots and human nodes (note that ‘roadside’ and ‘nodes’ both include disturbed and undisturbed plots in this comparison). There was also no significant interaction ($P = 0.241$) between the top level factor, roads and human nodes, and the second level factor, disturbed versus undisturbed (Table 5.1).

Table 5.1. Two way fixed factor PERMANOVA table of results for exotic species composition

	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>Pseudo - F</i>	<i>P</i>
<i>Disturbed x Undisturbed</i>	1	62032	62032	34.729	0.001***
<i>Roadside x Human node</i>	1	1091.9	1091.9	0.6113	0.759
<i>Disturbed/Undisturbed x Roadside/Human node</i>	1	2343.4	2343.4	1.312	0.241

df = degrees of freedom, *MS*, mean squares, Significance levels * 0.05, ** 0.01, ***0.001, 999 permutations

The SIMPER analysis results showed that 12 exotic species contributed to 90% of the dissimilarity amongst the disturbed plots. Of these species, seven were grasses and five were forbs. The species with the greatest influence were *Festuca rubra*, *Trifolium repens*, *Hypochaeris radicata*, *Acetocella vulgaris*, *Anthoxanthum odoratum*, *Agrostis capillaris*, *Achillea millefolium* and *Poa pratensis* (Table 5.2). Only three species characterised the undisturbed plots (1 grass and 2 forbs): *Acetocella vulgaris*, *Hypochaeris radicata* and *Anthoxanthum odoratum*. These three species contributed to 96% of the dissimilarity amongst undisturbed samples.

Table 5.2. Species which best account for the independent variation in composition within disturbed and undisturbed plots based on the SIMPER analysis

Average similarity of disturbed (30.72) and undisturbed plots (24.03)

Species	Disturbed			Undisturbed		
	Average Abundance	Contribution %	Cumulative %	Average Abundance	Contribution %	Cumulative %
<i>Festuca rubra</i>	1.28	16.47	16.47			
<i>Trifolium repens</i>	1.04	14.58	31.05			
<i>Hypochaeris radicata</i>	0.80	10.82	41.87	0.50	27.94	76.38
<i>Acetosella vulgaris</i>	0.85	9.94	51.81	0.52	48.44	48.44
<i>Anthoxanthum odoratum</i>	0.98	9.09	60.89	0.57	19.64	96.02
<i>Agrostis capillaris</i>	0.85	8.60	69.49			
<i>Achillea millefolium</i>	0.65	5.40	74.89			
<i>Poa pratensis</i>	0.64	5.05	79.94			
<i>Dactylis glomerata</i>	0.59	4.08	84.03			
<i>Holcus lanatus</i>	0.53	2.84	86.87			
<i>Taraxacum sp.</i>	0.36	2.50	89.37			
<i>Poa annua</i>	0.38	2.06	91.43			

The SIMPER analysis showed that a large number of species contributed to the differences between disturbed and undisturbed plots, with 28 species accounting for 90% of the dissimilarity between the two groups. All 28 species were more abundant in disturbed plots,

and 14 of the 28 differentiating species were only recorded from disturbed plots. The top seven species that contributed to 50% of the dissimilarity between disturbed and undisturbed plots are shown in Table 5.3.

Table 5.3. SIMPER analysis of average dissimilarity between disturbed and undisturbed plots (A 50% cut off for low contributions was used).

Average dissimilarity = 86.92

Species	Disturbed Average Abundance	Undisturbed Average Abundance	Combined % Contribution	Combined Cumulative %
<i>Festuca rubra</i>	1.28	0.00	10.27	10.27
<i>Anthoxanthum odoratum</i>	0.98	0.57	7.87	18.14
<i>Trifolium repens</i>	1.04	0.18	7.61	25.75
<i>Agrostis capillaris</i>	0.85	0.00	6.84	32.58
<i>Acetosella vulgaris</i>	0.85	0.52	6.41	38.99
<i>Hypochaeris radicata</i>	0.80	0.50	5.51	44.50
<i>Achillea millefolium</i>	0.65	0.03	5.05	49.55
<i>Dactylis glomerata</i>	0.59	0.04	4.95	54.50

The percentage frequency occurrence of each species in each habitat type is shown in Table 5.5. The most frequently occurring species in disturbed roadsides and human nodes were *Hypochaeris radicata*, *Acetosella vulgaris*, *Trifolium repens*, *Anthoxanthum odoratum*, *Achillea millefolium*, *Festuca rubra* and *Agrostis capillaris*. In undisturbed areas the most frequently occurring species were *Acetosella vulgaris*, *Hypochaeris radicata* and *Anthoxanthum odoratum*.

Table 5.4. Percentage frequency of occurrence of species in the four habitat types. Species recorded only once are not shown. Species occurring in $\geq 50\%$ of plots within any habitat type are shown in bold.

Exotic Species	Roadside n=23	Human Node n=32	Undisturbed Roadside n=23	Undisturbed Human node natural n=32
<i>Hypochaeris radicata</i>	91	47	43	53
<i>Acetosella vulgaris</i>	74	47	43	31
<i>Trifolium repens</i>	70	62	22	13
<i>Anthoxanthum odoratum</i>	57	40	43	31
<i>Achillea millefolium</i>	57	38	4	
<i>Festuca rubra</i>	50	53		
<i>Agrostis capillaris</i>	48	44		
<i>Poa pratensis</i>	31	41		
<i>Holcus lanatus</i>	30	31	4	6
<i>Dactylis glomerata</i>	26	34	9	3
<i>Echium vulgare</i>	26	19		
<i>Plantago lanceolata</i>	26	5		
<i>Taraxacum</i> spp.	26	31	17	6
<i>Trifolium dubium</i>	26	9	9	10
<i>Trifolium arvense</i>	22	6		
<i>Sonchus oleraceus</i>	21	25	17	16
<i>Petrorhagia dubia</i>	17			
<i>Phleum pratense</i>	17	16		
<i>Viola arvensis</i>	13	3		
<i>Geranium molle</i>	13	13		
<i>Festuca arundinacea</i>	13	19		
<i>Juncus effusus</i>	13	3		
<i>Onopordium acanthium</i>	13	10	4	10
<i>Poa annua</i>	10	31		
<i>Hypericum perforatum</i>	9	3		
<i>Tragopogon dubius</i>	9	6		3
<i>Cerastium glomeratum</i>	4	13		10
<i>Cynodon dactylon</i>	4	3		
<i>Lagurus ovatus</i>	4	3		
<i>Potentilla recta</i>	4	10		3
<i>Prunella vulgaris</i>	4	10		3
<i>Polygonum aviculare</i>	1	3		
<i>Malus domestica</i>		10		3
<i>Rosa rubiginosa</i>				6
<i>Rumex crispus</i>		6		3
<i>Verbascum virgatum</i>		3		
<i>Vulpia bromoides</i>		19		

5.5.2 Soil data comparisons

The NMDS 2-dimensional stress level was 0.19 and the 3-dimensional stress level was 0.11. Consequently the 3-dimensional analysis was used (Figure 5.3). The NMDS graph of the 3-dimensional analysis of soil attributes clearly separated disturbed and undisturbed plots but disturbed human nodes and roads were poorly differentiated.

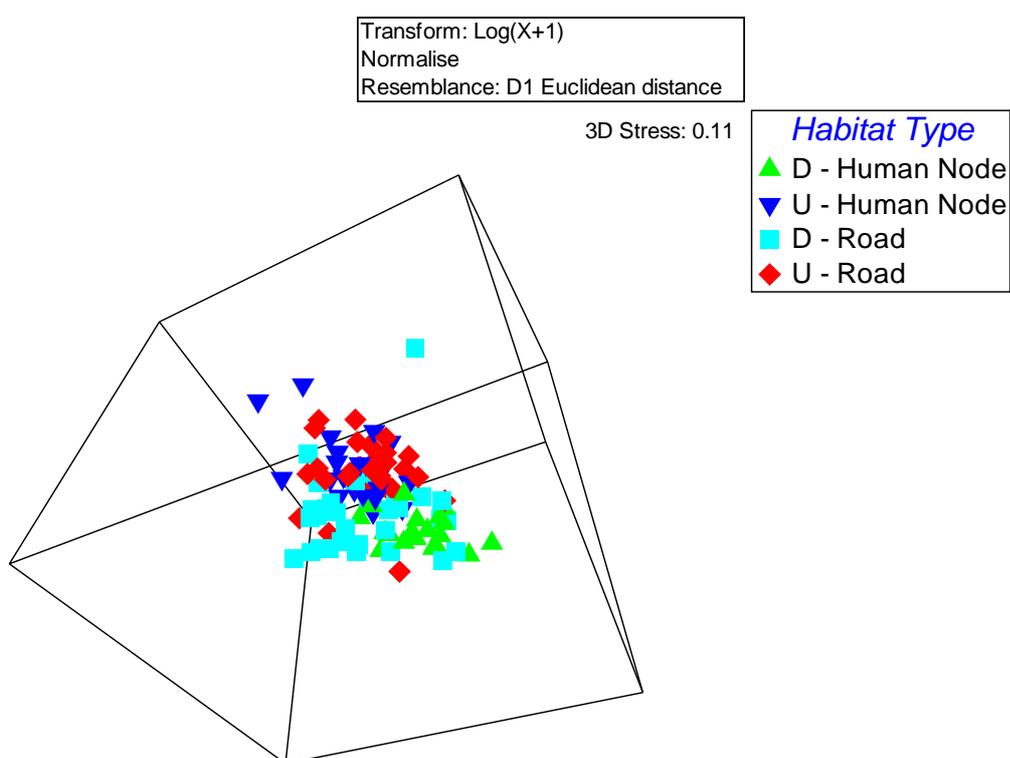


Figure 5.2. NMDS Variation in soil attribute data for four mountain habitat types. D = disturbed, U = undisturbed.

Differences in soil attributes among habitat types were analysed using PERMANOVA. The results (Table 5.5) demonstrated a significant interaction ($P = 0.002$) between the top level factor roads and human nodes and the second level factor, disturbed road and undisturbed human node. There was also a significant difference between disturbed and undisturbed plots ($P = 0.001$) and between roadside plots and human nodes ($P = 0.012$).

Table 5.5. Two way fixed factor PERMANOVA table of results for all soils data

	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>Pseudo - F</i>	<i>P</i>
<i>Disturbed x Undisturbed</i>	1	116.15	116.15	17.354	0.001***
<i>Roadside x Human node</i>	1	23.473	23.473	3.5072	0.012**
<i>Disturbed/Undisturbed x Roadside/Human node</i>	1	33.162	33.162	4.9548	0.002**

df = degrees of freedom, *MS*, mean squares, Significance levels * 0.05, ** 0.01, ***0.001, 999 permutations

The means and standard deviation of untransformed data of the chemical and physical properties of soils from roadside disturbed and undisturbed plots and human node disturbed and undisturbed plots are shown in Table 5.6. The results indicates that there are differences between disturbed and undisturbed habitat types and the different disturbance types have affected soils in different ways.

Table 5.6. A summary (means and standard deviation of untransformed data) of the chemical and physical properties of soils taken from roadside disturbed and undisturbed plots, human nodes disturbed and undisturbed plots.

Soil Property	Human Node		Roadside	
	Undisturbed	Disturbed	Undisturbed	Disturbed
Soil depth (cm)	21.6 ± 1.8	12.2 ± 2.2	23.9 ± 1.8	4.9 ± 2.2
Ammonium nitrate mg/k	26.2 ± 4.7	13.7 ± 1.6	21.6 ± 4.6	7.5 ± 1.6
Nitrate Nitrogen mg/k	6.7 ± 1.2	17.5 ± 3.1	6.9 ± 1.2	4.4 ± 0.7
Phosphorus mg/k	34.7 ± 4.8	56 ± 7.4	36.1 ± 2	23.1 ± 2
Potassium mg/k	293.5 ± 18.6	288.8 ± 2	317.6 ± 2	215.2 ± 13.1
Sulphur mg/kg	4.4 ± 0.6	3.5 ± 0.3	4.9 ± 1	3.1 ± 0.4
Organic carbon mg/kg	6.9 ± 0.3	5.12 ± 0.4	6.8 ± 0.4	2.8 ± 0.3
Conductivity dS/m	0.05 ± 0.01	0.1 ± .01	0.1 ± 0.01	0.04 ± 0.01
pH	4.5 ± 0.1	4.8 ± 0.8	4.6 ± 0.1	5.2 ± 0.1
Exchangeable aluminium meq/100g	2.4 ± 0.4	0.6 ± 0.1	1.7 ± 0.3	0.2 ± 0.1
Exchangeable calcium meq/100g	7.1 ± 1.6	7.6 ± 0.8	6.4 ± 0.95	5.5 ± 0.7
Exchangeable magnesium meq/100g	1.3 ± 0.1	1.1 ± 0.1	1.4 ± 0.1	1.1 ± 0.1
Exchangeable potassium meq /100g	0.7 ± 0.1	0.7 ± 0.1	0.7 ± 0.1	0.4 ± 0.03
Exchangeable sodium meq/100g	0.06 ± 0.007	0.1 ± 0.01	0.1 ± 0.02	0.02 ± 0.1
Total nitrogen %	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.05	0.3 ± 0.03
Total phosphorus mg/k	585.5 ± 35.7	631.8 ± 40	552 ± 41.3	482 ± 28.

5.5.3 Exotic species composition relationship to soil attributes and temperature

The DISTML test (Table 5.7) found four variables significantly contributed to exotic species composition: soil depth, mean annual temperature, pH and nitrate nitrogen. The adjusted R² for the model was 0.31, indicating that almost 70% of variation was unaccounted for.

The full model can be visualized in the dbRDA ordination plot (Figure 5.3). The first two dbRDA axes capture 86% of the fitted model and 32% of the total variability in the species composition data. The 1st axis, which explains 56% of the variation of the fitted model, is associated with disturbance, with the disturbed plots on the left and undisturbed plots on the right. Undisturbed plots have deeper soils, higher levels of organic carbon and extractable sodium than disturbed plot. Disturbed plots have higher pH levels than undisturbed plots. The 2nd axis explains an additional 30% of variation in the fitted model and is associated with mean annual temperature, which is strongly correlated with elevation ($r^2 = 0.86$). Plots at the top of the graph are from warmer lower elevation sites and those at the bottom from high elevation sites. The trends in soil potassium, nitrate nitrogen and phosphorus were associated with temperature (elevation) with higher levels of potassium at lower elevation and higher levels of phosphorus, nitrate nitrogen and sulphur at higher elevations.

To illustrate the associations of exotic species across habitat types and the influence of environmental variables bubble plots of the most common exotic species were superimposed on the dbRDA graph (Figure 5.4). Disturbed sites are on the left side of each chart and undisturbed sites on the right. Lower elevation warmer sites are on the top of the graphs and cooler high elevation sites on the bottom, as temperature and elevation were correlated. The size of the bubble corresponds with the cover of each species in each plot. The larger the bubble the greater the cover (refer to Figure 5.3). *Festuca rubra* and *Agrostis capillaris* were abundant across a range of elevations on disturbed sites with high pH levels, shallow soils and low organic carbon levels. *Anthoxanthum odoratum* was common at lower elevation sites with relatively high potassium, low nitrate nitrogen, phosphorus and sulfur. *Dactylis glomerata* is most abundant at disturbed mid elevation sites. *Acetocella vulgaris* and *Hypochaeris radicata* occurred in all habitat types.

Table 5.7. DISTLM Sequential results for fitting environmental variables, soil attributes and mean annual temperature to the exotic species composition data.

Environmental Variable	Adj R ²	Pseudo-F	P	Cumulative proportion	res.df
Soil depth	0.14	18.85	0.001	0.15	106
Mean annual temperature	0.23	13.71	0.001	0.25	105
pH	0.27	6.38	0.001	0.29	104
Nitrate Nitrogen	0.29	3.47	0.002	0.32	103
Organic carbon	0.29	1.82	0.068	0.33	102
Phosphorus	0.30	1.91	0.06	0.34	101
Potassium	0.30	1.55	0.136	0.35	100
Sulphur	0.31	1.88	0.062	0.36	99
Extractable Sodium	0.31	1.28	0.255	0.37	98

R², Adjusted R², P= Significance levels

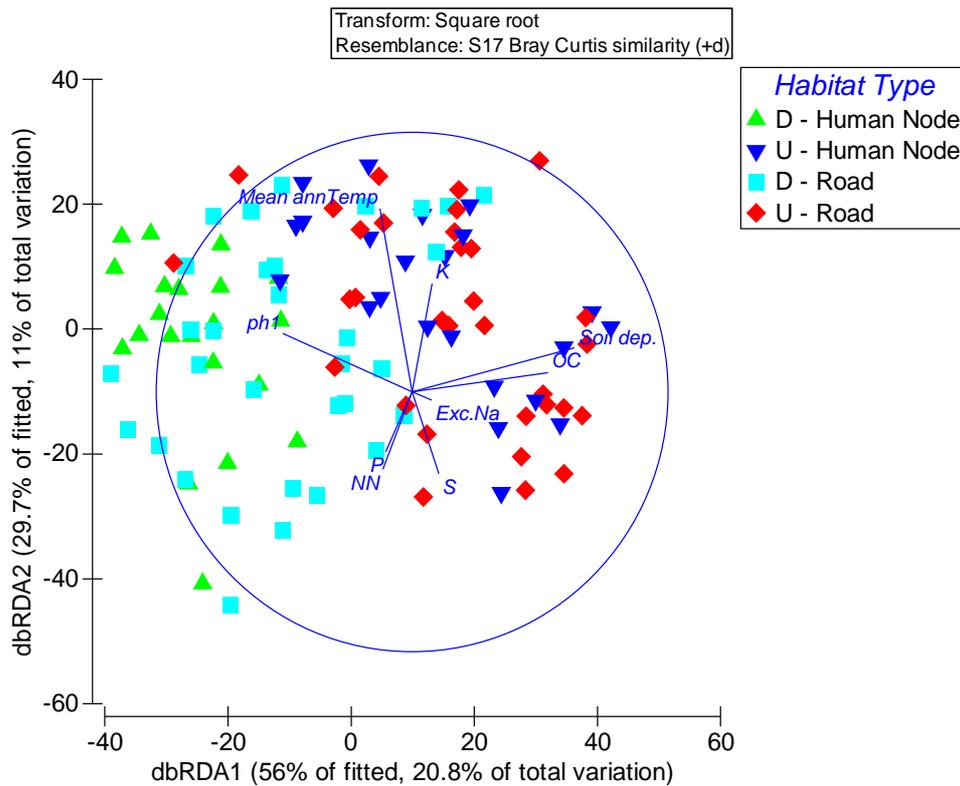


Figure 5.3. dbRDA ordination plot displays the relationship between soil attributes and temperature and how they explain the variation in exotic species composition in different habitat types.

The vectors within the circle show the degree of association of the predictor variables and exotic composition, the longer the vector from the center the larger the “effect”. Vectors with a correlation >0.2 are included. Undisturbed areas are represented by the blue triangle and red diamond. The vector overlay shows how the first dbRDA axis is strongly correlated with soil depth, pH and organic carbon. The second axis is strongly correlated with mean temperature.

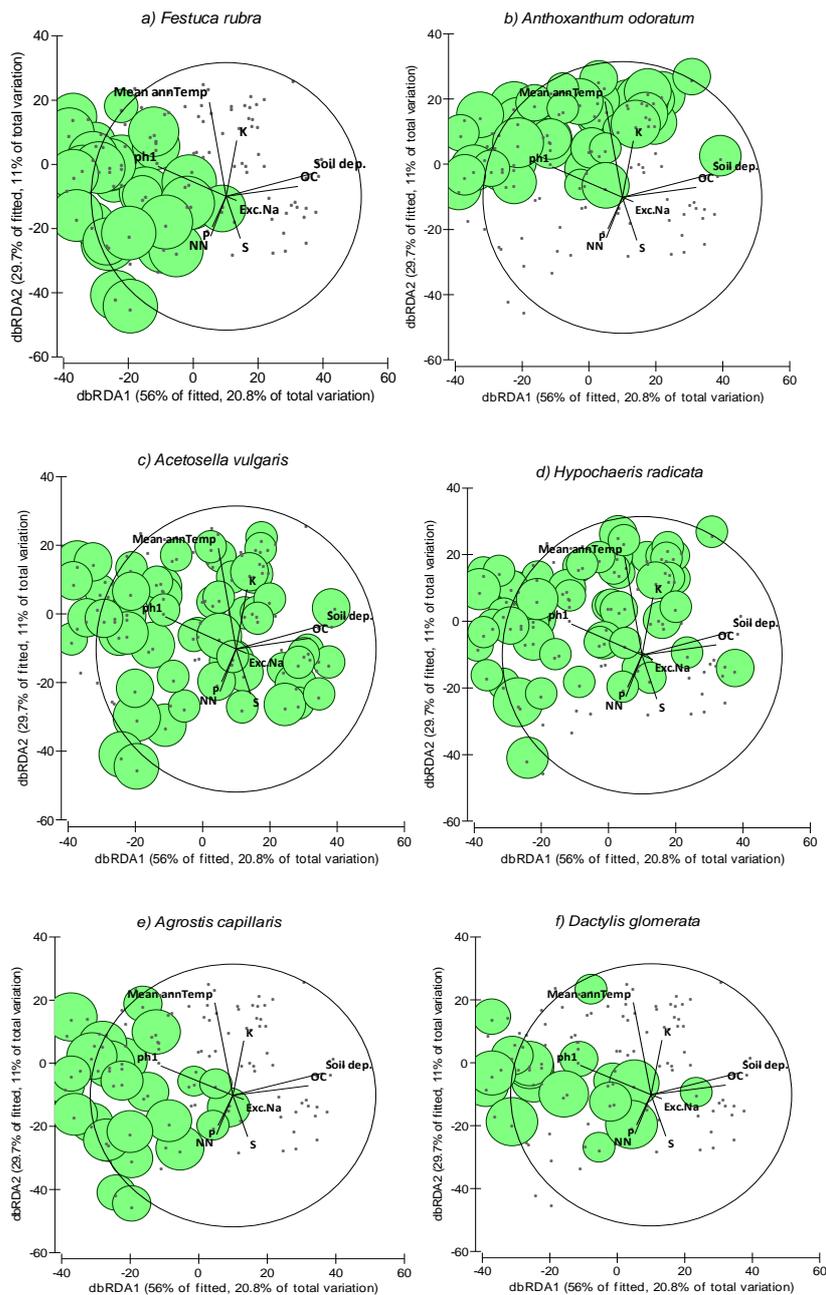


Figure 5.4 dbRDA bubble plots illustrating the associations of common exotic species across habitat types and the influence of environmental variables.

a) *Festuca rubra*, b) *Anthoxanthum odoratum*, c) *Acetosella vulgaris*, d) *Hypochaeris radicata*, e) *Agrostis capillaris* and f) *Dactylis glomerata*. The greater the size of the bubble indicates greater cover. Disturbed sites are on the left side of each chart and undisturbed sites on the right. All plots are shown by grey plots. Lower elevation warmer sites are on the top of the graphs and cooler high elevation sites on the bottom. The axis labels include the % variation of the DISTML fitted model and total variation. The environmental variables are shown as vectors their strength of correlation indicated by length.

5.6 Discussion

Does the composition of exotic species vary between disturbed and undisturbed habitat types?

As expected exotic species composition was significantly different between disturbed and undisturbed habitat types. In disturbed areas exotic species demonstrated a higher cover and richness than undisturbed areas. The species which most contributed to the differences in composition included *Festuca rubra*, *Trifolium repens*, *Hypochaeris radicata*, *Acetocella vulgaris*, *Anthoxanthum odoratum*, *Agrostis capillaris*, *Achillea millefolium* and *Poa pratensis*. Three of these were also the main contributors to species composition in undisturbed areas, *Acetocella vulgaris*, *Hypochaeris radicata* and *Anthoxanthum odoratum*. *Festuca rubra*, *Agrostis capillaris* and *Poa pratensis* were absent from undisturbed areas in this study. The species *Trifolium repens* and *Achillea millefolium* were common in disturbed areas but absent or at a low proportion of richness and cover in undisturbed plots.

The differences in exotic species composition and richness may be explained by land use changes, through road construction and village development which have removed native vegetation and altered soil physical and chemical properties. By contrast, I found there was no significant difference in exotic species composition between roadsides and human nodes. Other studies and anecdotal evidence suggests that some of the common species detected in disturbed areas also occur in less disturbed areas at both lower elevations and higher elevations in Australian mountain systems where they have been used in rehabilitation (McDougall *et al* 2005, Johnston 2005).

Three of the species which contributed to a large proportion of dissimilarity in disturbed habitat types (Table 5.3) were previously used in rehabilitation programs in the Australian Alps and this may help explain their persistence today. These three species are *Agrostis capillaris*, *Festuca rubra*, *Trifolium repens* (Clothier and Condon 1968). These species were originally chosen because of their adaptability in a range of climates and soil (Good 2006). Once these species establish they are competitive against native species (Akbar 2009).

Festuca rubra which was found to be the species with the greatest contribution to plot dissimilarity in disturbed areas can tolerate low soil nutrient conditions and compacted soils

and has been used globally as a stabilizer of roadsides and ski slopes (Dyrness 1975, Hansen and Clevenger 2005, Akbar 2009, Burt 2012). This species has also demonstrated allelopathy impacting on the germination and growth of other plant species (Boston *et al.* 2013). Other species common in disturbed sites include fast growing ruderal species, *Acetosella vulgaris* and *Hypochaeris radicata*. Both of these species were also common in undisturbed areas and have been considered to have little impact on native plant diversity in undisturbed communities (Godfree *et al.* 2004, McDougall *et al.* 2005). Both of these species have a long history of introduction (Maiden 1898) which may help explain their occurrence in natural areas. Exotic species with a longer introduction history have been found to have a wider distribution (Hamilton *et al.* 2005, Haider *et al.* 2010).

How do soil attributes vary between disturbed and undisturbed habitat types?

My results indicate soils in disturbed and undisturbed habitats were significantly different. Disturbed sites were characterized by shallower soil depth, lower levels of organic carbon and phosphorus and a more neutral pH than undisturbed sites. Undisturbed sites were characterised by deeper soils, higher levels of organic carbon and lower levels of phosphorus and more acidic soils than disturbed sites. These findings are consistent with previous studies that reported higher nutrients and lower pH in undisturbed areas in the Australian Alps (Johnston and Johnston 2004, McDougall 2001).

Soils along roadsides were also significantly different from those in human nodes with phosphorus, extractable sodium, sulphur and nitrate contributing most to these differences. The differences in soils between habitat types are likely to be the result of previous land use. Road construction and maintenance activities are known to alter soil properties such as reducing or increasing some nutrients and compacting soils (Cale and Hobbs 1989, Jimenez *et al.* 2011). My results suggest that past road works may have led to shallow soils and low levels of organic carbon along roadsides.

Human nodes may occur over a much broader area having a greater impact, such as ski slopes (Gros *et al.* 2004). These sites may also have a past land use history associated with

summer grazing and mining (Good 1992) or still be used for recreation activities including horse riding (DEC 2006).

Which attributes are associated most strongly with exotic plant composition?

Increasing elevation (temperature) is correlated with a low number of exotic plants in mountain systems (Becker *et al.* 2005, Mallen-Cooper and Pickering 2008, Alexander *et al.* 2011). In my study many of the higher elevation disturbed sites had low numbers of exotic species but had high cover, therefore examining only species richness may not address the factors contributing to exotic species occurrence. Seabloom *et al.* (2013) concluded in a global study of grassland communities that unless richness is very high it is difficult to predict the impacts or understand drivers of invasion without examining species composition.

The DISTML model (Table 5.7) helps explain the complexity of relationships between soil attributes, temperature and exotic species composition. These findings suggest that whilst mean temperature is an important factor in explaining exotic species richness in undisturbed areas (Chapter 4) exotic species composition patterns in disturbed and undisturbed habitat types can be explained by a combination of mean temperature and soil attributes. Mean annual temperature and the soil attributes soil depth, pH, and nitrate nitrogen all significantly contributed to species composition in different habitat types. All of these factors have been linked to explaining exotic species occurrence in other studies (Hobbs and Atkins 1988, Burke and Grime 1996, Rose and Hermanutz 2004, MacDougall 2005).

Greater soil depth was positively associated with a low cover of exotic species in undisturbed sites. This finding is supported by (Macdougall *et al.* 2006) who found that annual grasses and perennial forbs were more likely to occur in shallow soils where perennial grasses and shrubs dominated deeper soils. My findings also corroborate a study on exotic species at back country huts in the Australian Alps which found increased compaction leading to lower soil depths could explain exotic species occurrence (Morgan and Carnegie 2009).

My results showed that a more neutral pH was associated with a greater cover of exotic species in disturbed sites. Other studies have attributed a neutral pH to the invasion of other habitat types, including hardwood forests (Kourtev *et al.* 1998) by exotic plant species. Acidic soils have been attributed to reduced exotic plant richness in other natural systems (Rose

and Hermanutz 2004). A low pH in soils can affect the plant's ability to uptake nutrients (Dupré and Ehrlén 2002) and may favour native species with adaptations such as arbuscular mycorrhizal fungi (Johnston *et al.* 2004). These adaptations assist in the absorption of nutrients.

Interestingly I found that nitrogen, phosphorus and potassium were all more strongly associated with temperature than with disturbance. As temperature decreased, nitrogen, phosphorus and potassium levels increased. This could be because soil testing was undertaken following snow melt to maximize nutrients available for plant growth. Nutrients in alpine areas are at their highest concentration following snow melt largely from the accumulation of atmospheric dust on snow (Johnston 2001). In most lowland studies higher nutrient levels are associated with disturbance (Hobbs 1989, Leishman and Thompson 2005) and exotic plant occurrence (Burke and Grime 1996). The results suggest that the influence of low temperatures at higher elevations may limit the availability of nutrients for plant growth.

The influence of abiotic attributes on individual exotic plant species response

Different species demonstrated different patterns of occurrence and composition and this could be explained by soil attributes and mean temperature. *Festuca rubra* and *Agrostis capillaris* are more common in disturbed areas (Figure 5.4) at all elevations. In localities where these species have a high percentage cover soils had a high pH and low nutrients. Previous studies indicate that in its native range and where it has been introduced *Agrostis capillaris* is a competitive species (Burke and Grime 1996, Daehler 2005). Whilst it was not found to be common in undisturbed areas in this study it has been found to persist in rehabilitation sites in KNP (Johnston and Ryan 2004) and has been observed in wet areas (personal obs).

Anthoxanthum odoratum was found to be common in montane areas in disturbed and undisturbed habitat types (Figure 5.4b). Given this species is an invasive species of other high elevation areas (Daehler 2005) it may be it has not reached its full extent. It is also known to display phenotypic plasticity by being tolerant of a wide range of soils with the ability to flower and set seed earlier than other plant species (Platenkamp 1990).

Hypochaeris radicata was common in disturbed and undisturbed sites (Figure 5.4d). This species is a known primary colonizer with the ability to take advantage of nitrogen pulses, rapidly absorbing nitrogen and converting it into growth (Schoenfelder *et al.* 2010). The presence of *Acetosella vulgaris* in undisturbed areas which were categorized by low pH may be best explained by its ability to increase its cover with increasing soil acidity (Tyler 1996). It has also been found to produce more seed when there is loss of grass cover (Pickering *et al.* 2006). *Dactylis glomerata* another species which is associated with only disturbed areas in the Australian Alps is known to be invasive in other natural areas (Daehler 2003).

It must also be considered the important role that intact native vegetation communities play in preventing or slowing the spread of these species into natural or less disturbed habitats (Daehler 2003, Richardson and Pyšek 2006).

Implications for management

Maintaining soil physical and chemical properties in undisturbed areas could assist native vegetation communities to resist invasion from exotic species. New exotic plant species and species occurring at higher elevations continue to be recorded in KNP (Schroder 2010, McDougall 2012 unpublished data). Preventing disturbance and bare ground could prevent or delay exotic species incursions into native vegetation communities.

Increased temperatures associated with climate change in the Australian Alps (Steffen *et al.* 2009) may create conditions more suitable for exotic plant establishment at higher elevations. This has already been documented in other mountain systems (Becker *et al.* 2005, Pauchard *et al.* 2009). The ability of exotic plants to establish at higher elevations as temperatures increase could be compounded by the results from this study where I found a greater availability of nutrients at higher elevations compared with lower elevations. Higher nutrients have been associated with invasion in other disturbed and undisturbed habitats (Hester and Hobbs 1992, Burke and Grime 1996, Bashkin *et al.* 2003, Lake and Leishman 2004, Densmore 2008).

From the species which already occur in mountain systems only a small number will eventually become invasive and impact on natural vegetation communities (Pyšek *et al.* 2004, Rejmánek and Richardson 2006). Some species not currently considered invasive in

undisturbed communities may not have reached their full extent. Identifying species with the potential to spread particularly at higher elevations where vegetation communities have greater conservation value may be important (Costin *et al.* 2000, McDougall *et al.* 2011a, Kueffer *et al.* 2013). Identifying invasive species may be achieved by addressing the introduction history of a particular species and its behaviour in other mountains systems (Hamilton *et al.* 2005, Haider *et al.* 2010).

5.7 Conclusion

By examining the patterns between exotic species, temperature and soil attributes there is a greater understanding of the processes explaining exotic species composition in disturbed and undisturbed habitats. The results suggest a combination of factors contribute to exotic species composition and can differ from those which describe richness (Chapter 3 and 4).

A higher cover of exotic species may have a greater impact on natural communities than high exotic species richness. Richness studies can provide insight into the potential species pool which may become invasive – exotic plant composition studies help to understand the drivers of invasion. Therefore studying both richness and composition provides a greater understanding of the processes explaining exotic plant occurrence.

Understanding what factors contribute to exotic plant composition in the Australian Alps may assist in improving exotic plant management. In areas of high exotic plant cover it is likely that changes to soil chemical and physical properties caused by disturbance could reduce the success of exotic plant control and rehabilitation programs.

CHAPTER 6 SYNTHESIS AND GENERAL DISCUSSION

6.1 Introduction

Previous studies have identified the important role of elevation in explaining low exotic plant species richness at high elevations in mountain systems (Becker *et al.* 2005, McDougall *et al.* 2005, Haider *et al.* 2010, Alexander *et al.* 2011). Given the complexity of other factors which occur as part of disturbance, such as changes to resources (Hobbs 1989, Davis *et al.* 2000), it is likely that other abiotic and biotic factors play an important role which has not been considered. This study focussed on improving our understanding of the processes underlying exotic species occurrence in the Australian Alps. It had two main objectives:

1. Determine the degree to which elevation filtering can explain exotic plant occurrence in disturbed and undisturbed habitats.
2. Establish the degree to which biotic and abiotic factors (other than elevation and temperature) explain differences in exotic plant richness and composition between disturbed and undisturbed habitat types.

In this Chapter I summarise the main findings from the thesis and provide recommendations for exotic plant management and future research in the Australian Alps.

6.2 The role of elevation and soil attributes in explaining exotic plant richness in disturbed and undisturbed mountain systems

In Chapters 3 and 4 I sought to determine if species richness declines with increasing elevation in disturbed and undisturbed habitats. I also investigated the combined role of elevation and soil attributes in explaining exotic plant richness. As expected, disturbed roadsides and human nodes had greater richness of exotic species than undisturbed sites although patterns of species richness along the elevation gradient were different between disturbance types. Elevation was significantly negatively correlated with the richness of exotic plants in human nodes and natural habitats but not along roadsides. At roadsides a decline in exotic species was only evident above 1700 m although this was not reflected in the overall correlation analysis.

Along roadsides soil attributes appeared to have the greatest effect on species richness across the entire gradient, perhaps as the result of road construction and maintenance activities which alter soil physical and chemical properties (Cale and Hobbs 1991, Christen and Matlack 2006, Jimenez *et al.* 2007). Exotic species richness along roadsides was best explained by directional elevation filtering (Alexander *et al.* 2011); i.e. most species are dispersed along road corridors and only a subset of species with a wide climatic tolerance persist at higher elevations.

In human nodes a combination of mean temperature (which is negatively correlated with elevation) and soil attributes such as nitrate, soil depth, sulphur and pH best explained species richness. Exotic species richness patterns in human nodes were explained by a combination of directional elevation filtering and direct introductions through ornamental use. Human nodes had more ornamental species associated with past horticultural use and species found at disjoint localities.

In natural areas more than 50 m from roadsides and human nodes, exotic species richness was influenced predominantly by mean annual temperature. Species richness decreased with declining temperature at higher elevations (Chapter 4). In natural areas the occurrence patterns were influenced by the adjacent disturbance types. In natural areas more than 50 m from roadsides species occurrence could be explained by directional elevation filtering, and at natural areas greater than 50 m from human nodes exotic species richness could be explained by direct introductions and directional elevation filtering.

Other exotic plant studies in mountains have focused on the strong inverse correlation between elevation and exotic species richness at higher elevations (Pauchard and Alaback 2004, Becker *et al.* 2005, Daehler 2006, Haider *et al.* 2010, Alexander *et al.* 2011). My study is (to the best of my knowledge) the first study to investigate interactions between soil attributes and mean temperature along an elevation gradient to explain exotic species richness. My results suggest that the richness of exotic species in disturbed habitats can be explained by understanding interactions between elevation and soil attributes (Chapter 3). It would appear that elevation (climate) may not prevent exotic species establishment at higher elevations and areas where soil disturbance has occurred may be more vulnerable to exotic species establishment.

6.3 The abiotic and biotic attributes associated with differences in exotic species composition in disturbed and undisturbed mountain systems

In Chapter 5 I examined how temperature and soil attributes explained differences in exotic plant composition between disturbed and undisturbed habitat types. My results suggest that species composition and soil physical and chemical properties varied between disturbed and undisturbed habitats. Disturbed sites were characterised by shallow soil depth, low levels of organic carbon and phosphorus and a closer to neutral pH. Undisturbed sites were characterized by deeper soils, a higher organic carbon content, low phosphorus levels and acidic soil when compared with disturbed sites.

Whilst I found that soil properties were different in roads and human nodes, the most frequent species were similar in both zones. Three of these species (*Agrostis capillaris*, *Festuca rubra* and *Trifolium repens*) were previously used in rehabilitation programs (Clothier and Condon 1968) and this may help explain their presence at many disturbed sites. *Festuca rubra* continues to be used in ski slope and roadside stabilisation (DECC 2007). These species were chosen for their ability to colonise disturbed sites (Good 2006) and some have capacity to occur away from areas where they were originally used in rehabilitation (Johnston and Ryan 2001). Two of the species I found to have the greatest frequency in this study, *Hypochaeris radicata* and *Acetosella vulgaris* also have the longest history of introduction (Maiden 1898; Johnston 2005).

My results suggest that whilst mean temperature is important for explaining richness in undisturbed areas (Chapter 4), exotic species composition in undisturbed and disturbed habitats can be explained by a combination of mean temperature and soil attributes. I found that a combination of four variables contributed to explaining exotic species composition: mean temperature, soil depth, nitrogen and pH. All of these factors have been associated with exotic species composition in other studies (Hobbs and Atkins 1988, Huenneke *et al.* 1990, Rose and Hermanutz 2004, MacDougall 2005). Greater soil depth was associated with a low cover of exotic species in undisturbed habitats. A neutral pH was associated with a greater cover of exotic species in disturbed habitats and a higher mean temperature was associated with increased exotic species cover. Interestingly nitrogen was more strongly associated with temperature and increased with elevation, suggesting that low

temperatures at higher elevation may limit nitrogen availability to plants. This is in contrast with lowland studies where higher nutrients have been associated with increased exotic plant occurrence (Hobbs 1989, Burke and Grime 1996, Leishman and Thompson 2005).

6.4 Other considerations in understanding the processes of exotic plant occurrence

6.4.1 Linking soil attributes and the composition of exotic plant species

My study indicated that soil attributes were different between disturbed and undisturbed sites and between roads and human nodes (Chapter 5). Low soil nutrients and shallow soil depth in roadsides was likely to be more conducive for species capable of growing in these conditions, such as *Festuca rubra* (Hansen and Clevenger 2005, Akbar 2009, Burt 2012). In contrast many human nodes had high nutrient levels compared to adjacent natural habitats (Chapter 5). Although I did not find that species composition was different in roads and human nodes, I did find that human nodes had more ornamental species and forbs. Findings from other studies (Hedde and Specht 1975, Hobbs and Atkins 1992, Prober *et al.* 2002, Leishman and Thompson 2005) suggest that higher nutrients at human nodes may provide more favourable conditions and could lead to an increase in species richness and cover in the future.

Traditionally exotic plant control programs target the plant and not the management of abiotic and biotic factors (Downey and Sheppard 2006). Many factors cannot be 'managed' (e.g. elevation) but others can. Control of exotic species without considering the influence of soil factors could lead to the occurrence of new exotic plant species. This has occurred in lowland exotic plant programs where removal of exotic plant species such as *Chrysanthemoides monilifera* and *Asparagus asparagoides* has promoted other exotic plant species (Turner *et al.* 2008, King and Downey 2008). Control programs focused on integrating soil management may prove more successful in exotic plant management. For example the addition of a carbon supplement (sugar or sawdust) to the soil may temporarily reduce nutrients at high nutrient localities (Blumenthal *et al.* 2003, Prober *et al.* 2005) or the use of organic mulches may increase organic carbon and nutrients in habitats where topsoil has been lost (Chambers 1997).

6.4.2 Time since introduction

Residence time is an important factor in exotic species establishment (Hamilton 2005, Haider 2010). For many exotic species, the longer the time since naturalisation, the larger altitudinal distribution (Pyšek *et al.* 2011). Understanding the length of time it may have taken for a species to disperse from its original point of release may be very important for predicting future invaders.

In the Australian Alps, many exotic species have only become established in the past fifty years (Johnson 2005). This is recent compared with other mountains, where some species have been naturalised for longer periods (Daehler 2005, Haider 2010, Pyšek *et al.* 2011). A number of species found at low frequencies in disturbed sites in this study are considered invasive at higher elevations in other mountain regions and may not have reached their full extent, including *Anthoxanthum odoratum*, *Leucanthemum vulgare*, *Verbascum thapsus* and *Potentilla recta* (Whipple 2001, Clements *et al.* 2003, Conn *et al.* 2008, Ansari and Daehler 2010). I recommend that these species be considered in future research to determine their potential spread and impact on native communities.

6.4.3 Influence of climate change on the occurrence of exotic plant species

The alpine areas of the Australian Alps have warmed at the rate of 0.2°C per decade over the past 35 years and snow depth and duration of cover are declining (Hennessy *et al.* 2003, Green 2009). A range of secondary biophysical effects are likely to occur as climate change intensifies, including increased solar radiation and erratic weather events, such as high intensity storms (Howden *et al.* 2003, Garnaut 2008). Given these predictions, the Australian Alps has been identified as a hot spot for future potential invasions from species already naturalised in disturbed habitats or lowland areas (Hughes *et al.* 2013, Duursma *et al.* 2013). Climate change implications for existing naturalised exotic species in the Australian alps are still largely unknown with the exception of modelling undertaken for *Hieracium* species (Beaumont *et al.* 2009) and *Achillea millefolium* (Johnston 2005).

With predicted changes to climate, elevation filtering in natural habitats may become less effective in preventing exotic species establishment at higher elevations (Pickering *et al.* 2004, Pauchard *et al.* 2009, Steffen *et al.* 2009, Chapter 4). Other studies in mountain

systems have found increases in the elevation range of exotic and endemic species attributed to warming (Becker *et al.* 2005, Pyšek 2009, Jump *et al.* 2011).

In this study I found that nitrate nitrogen levels in human nodes were greatest at high elevations. Despite this, exotic richness remained low at these sites (Chapter 3), but with predicted increases in temperature this may affect nitrogen availability and lead to increased exotic species richness in the future.

Although not detected in this study, there are natural areas in KNP that have had significant short term changes in exotic species following fire. Fires in 2003 burnt 71% of Kosciuszko National Park (Zystra 2006) which has led to an expansion in some exotic species distributions, such as *Hieracium aurantiacum* (Caldwell and Wright 2011) and *Leucanthemum vulgare* (OEH 2012). This has also occurred in other parts of the Australian Alps with the expansion of *Cytisus scoparius* (Wearne and Morgan 2004) and *Salix* spp. in the Bogong High Plains (Moore 2011). Increased fire frequency is predicted as a result of climate change (Steffen *et al.* 2009) and may facilitate expansion of exotic species.

An increase in herbivore grazing by native and exotic species at higher elevations, including deer, feral horse, hare and rabbits, as a result of climate change (Green and Osborne 2012) could increase impacts on soils and further promote the introduction and spread of exotic plant species. The presence of introduced herbivores has been associated with a decrease in palatable exotic plant species in Australian mountain systems (Leigh *et al.* 1987, Bridle and Kirkpatrick 1999).

My findings indicate that elevation contributes to maintaining low species numbers of exotic species in undisturbed habitats at higher elevations but increased temperatures predicted as part of climate change may reduce the effectiveness of this filter and allow conditions for more species to establish, especially in nutrient-rich areas at high elevation.

6.4.4 The role of plant traits in predicting invasive plant species

Plant traits have been used as a tool to identify successful invaders (Grotkopp and Rejmánek 2007, Pyšek and Richardson 2007, Ordonez *et al.* 2010). Some successful invaders possess traits which include high specific leaf area, early and longer phenology, leaf area and shoot allocation (Lake and Leishman 2004, Grotkopp and Rejmánek 2007, Pyšek and Richardson

2007, Ordonez *et al.* 2010, Tecco *et al.* 2010, Van Kluennen *et al.* 2010). Cold tolerant adaptations such as perennial underground storage may assist species in mountain systems, e.g. *Acetosella vulgaris* (Tyler 1996). Early flowering times may be important at higher elevations when seasons are short.

I found that some species were affected differently by abiotic and biotic factors in different habitat types, and specific traits could contribute to this (Chapter 5). I have not examined the role of traits in this thesis but recommend that it be considered in the future to further improve our ability to predict which species are most capable of growing at higher elevations or spreading into natural areas.

6.5 Management recommendations

The movement of exotic species along road corridors or through direct introductions into mountains is likely to continue (McDougall *et al.* 2005, Alexander *et al.* 2011, Chapter 3) and may increase with climate change and as human populations expand (Pauchard 2009, Hughes *et al.* 2013, Duursma *et al.* 2013). The Australian Alps are recognised internationally for their high species endemism (Costin 2000, DEC 2006). Building on the results of my thesis, I recommend that preventative management of exotic species in sub-alpine and alpine habitats should be a priority. This can be achieved through programs designed to predict future invaders and to detect and treat new incursions of these species.

The exotic plant species of most concern for future management of natural mountain systems are those which pose the greatest threat to biodiversity by competing with native species and transforming vegetation communities (McDougall *et al.* 2011). There are predictive tools available to assess the invasiveness of an exotic species (e.g. Virtue 2004, Johnson 2009, Hughes *et al.* 2013) and there has been some attempt to prioritise exotic plant species already present in the Australian Alps (DECC 2009, OEH 2012, DPI 2013). Some of these species are already widespread, especially in agricultural areas (e.g. *Echium vulgare*, *Xanthium pungens*, *Sonchus* spp). Many latent species – i.e. those species which have not yet reached their full extent but have been identified in this thesis or other surveys (Mallen-Cooper 1995, Johnston 2001) and known to be invasive in natural habitats – are not considered in current management strategies for Kosciuszko National Park (DECC 2009, OEH

2012). These include *Juncus effusus*, *Bromus tectorum* and *Melilotus albus* (Belnap and Phillips 2001, Larson *et al.* 2001, Daehler 2005, McDougall *et al.* 2005).

Developing selective management strategies for different disturbance types

Land managers have little control over the influence of elevation or climate. However they have a capacity to manage soil disturbance. Changes to soil physical and chemical properties as a result of disturbance can explain greater exotic plant species richness and cover (Chapter 3 and 5). Consequently, soil disturbance should be minimised where possible. It is recommended that the use of road materials be free of exotic plant seed and consistent with the local geology may help reduce impacts as will rehabilitation programs which favour the use or promotion of native species (Gelbard and Belnap 2001).

Changes to roadside construction and maintenance practices may also reduce the spread of exotic species. Cleaning of all machinery and vehicles (including firefighting appliances) before and during construction activities or entering remote areas may prevent propagule movement (Moerkerk 2006). The introduction of hygiene protocols for machinery, such as wash down facilities may help prevent the movement of seed into the National Park.

I found that the patterns of occurrence vary between roadsides and human nodes and management may need to be approached differently in the two areas. All landscaping in ski resort gardens in Kosciuszko National Park should continue to use endemic plant species (DEC 2006, DECC 2007). It is recommended that rehabilitation programs use sterilized mulch to prevent exotic plant introductions (Kruse *et al.* 2004) and promote the use of local native species, particularly at higher elevations (Chambers 1997, DECC 2007). Increased community awareness may reduce species transported on clothing or equipment through recreational pursuits such as bushwalking or mountain bike riding (Mount and Pickering 2009, Morgan and Carnegie 2009).

Review the use of exotic species in rehabilitation programs

One of the most common species found in disturbed habitats in Kosciuszko National Park *Festuca rubra* (Chapter 5) is still widely used in rehabilitation programs in ski resorts and road corridor upgrades (DECC 2007). The species continues to be used as it grows rapidly from seed, and can tolerate low soil nutrient conditions and steep slopes (Dyrness 1975,

Hansen and Clevenger 2005, Akbar 2009, Burt 2012). Dominance of this species in disturbed areas may prevent the long term re-establishment of native species particularly as it has been found to have allelopathic effects (Boston *et al.* 2013). Rehabilitation manuals written specifically for the Australian Alps and for the NSW Ski Resorts document additional measures which use native species in disturbed sites, such as half mixes of fescue and poa as initial cover crops (Good 2006, DECC 2007). It is recommended that future research be undertaken to identify alternative native species for rehabilitation in mountain systems to move away from the use of exotic species such as Fescue..

Below is a summary of principles to guide management based on the results from this thesis:

- Species already present in lower elevations should be screened to identify climate generalists. A species considered a climate generalist is likely to have the greatest chance of spreading from lower elevations into mountain systems.
- At roadsides, species richness and composition may be explained by low nutrient levels and shallow soil depth (Chapter 3). Therefore the species which occur in these localities have a greater capacity to tolerate these conditions and spread into other disturbed sites..
- Patterns of distribution between disturbance types vary and therefore management (prevention and control) for these areas should be approached differently. For example, exotic plants along roadsides may be spread by road works in gravel and by machinery, and human nodes may receive plants through direct planting of ornamentals or through discarding vegetable and fruit material in ski resorts.
- A variety of exotic species is likely to occur in natural areas surrounding human nodes and therefore these are important areas for detection of new exotic plant species.
- In human nodes, soil nutrients are often higher than surrounding natural areas and therefore nodes may provide opportunities for a greater range of species to occur.
- Exotic species composition in natural areas could be explained by greater soil depth and more acidic soil. Therefore when establishing predictive tools, exotic species capable of growing in these conditions could have an advantage.

- Species with a high frequency and cover at low elevations (e.g. *Anthoxanthum odoratum*) should be examined for their introduction history and their potential to spread based on traits and invasive history in other mountain systems.
- Changes in climate may lead to acceleration in species capable of colonising higher elevations, particular human nodes where nutrients are high.

To develop informed lists for early detection of exotic plants in undisturbed areas, the principles above are presented in Table 6.1 with other important factors including time since introduction (Johnston and Pickering 2001, Haider 2010 , Pyšek *et al.* 2011), competitive ability in other mountain systems (Haider 2010, McDougall *et al.* 2011a). A summary of management considerations are also included.

Table 6.1. Summary of factors explaining exotic plant occurrence in disturbed and undisturbed habitats, and management considerations that may assist in the prevention, early detection and control of exotic plant species in Australian mountain systems. The ticks identify which habitat type each factor or management consideration applies to.

Factors explaining occurrence (thesis results)	Human		
	Roadside	Node	Undisturbed
A species with a high frequency in disturbed and undisturbed habitats is likely to be a climate generalist occurring from the montane to the alpine, e.g. <i>Actosella vulgaris</i> , <i>Trifolium repens</i>	✓	✓	✓
A species which has been directly introduced for ornamental plantings and may prefer higher nutrient levels and deeper soil depth may have a greater capacity to spread into undisturbed areas.e.g. <i>Leucanthmum spp.</i>		✓	✓
A species which can grow in soils with low levels of nutrients and shallow soil depth. This species may be restricted to disturbed road edges or ski runs.	✓		
A species which is capable of growing in acidic soils, higher nutrient levels and greater soil depth. eg. <i>Juncus sp.</i> , <i>Anthoxanthum odoratum</i>			✓
Other factors explaining occurrence (literature review)			
Plant traits which assist growth in a high elevation environment, e.g. geophyte, early flowering, wind and animal dispersal (Körner 2003, Daehler 2003, Pyšek and Richardson 2007)	✓	✓	✓
Examine the competitive ability of a species in other natural mountain systems (Haider 2010, McDougall <i>et al.</i> 2011a)			✓
Consider the time since a species has been introduced (Johnston and Pickering 2001, Haider 2010 , Pyšek <i>et al.</i> 2011) and compare this with its occurrence in other mountain systems.			✓

Management Considerations	Roadside	Human node	Undisturbed
Minimise all soil disturbance and where possible use local materials in roadside construction and maintenance (Gelbard and Belnap 2001, Good 2006, DEC 2007, McDougall <i>et. al</i> 2011)	✓	✓	✓
Implement hygiene protocols for machinery or vehicles using remote areas, especially during fire events (Moerkerk 2006, Mount and Pickering 2009, Morgan and Carnegie 2009)			✓
Use of sterilized (exotic plant free) mulch in rehabilitation projects (Kruse <i>et al.</i> 2004, DECC 2007)	✓	✓	✓
Prevent non-endemic plant species and encourage the use of local native plant species in ornamental gardens (Chambers 1997, DECC 2007).		✓	✓
Replace exotic plants used in any rehabilitation programs with local native plant alternatives (Good 2006, DECC 2007).	✓	✓	
Develop an Australian Alps exotic plant risk assessment system to identify future invaders of natural habitats—screen any new species detected and species occurring at lower elevations	✓	✓	✓

6.6 Conclusion

The results from this thesis improve our understanding of the drivers of exotic plant richness and composition in Australian mountain systems, and may benefit management in guiding strategies to control and predict invasive species.

At present undisturbed Australian mountain systems, particularly at higher elevations, have low species richness and abundance. To reduce the potential for increases in exotic species richness and cover anthropogenic disturbances must be minimised. This is even more important in light of predicted changes to climate. Future management should focus on predicting and targeting species which may pose the greatest threat to biodiversity. This may be achieved by incorporating results from this study and information on time since introduction, invasiveness in natural habitats and specific plant traits to develop an exotic plant risk assessment system specifically for Australian mountain systems.

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