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Untangling spatial distribution patterns of the invasive herb *Hieracium lepidulum* Stenstr. (Asteraceae) in a New Zealand mountain landscape

A thesis
submitted in partial fulfilment
of the requirements for the Degree of
Doctor of Philosophy

At
Lincoln University
By
A.L. Miller

Lincoln University
2006
Earth, dear one, I will! Oh, believe it needs not one more of your springtimes to win me over. One, just one, is already too much for my blood.

-excerpt from the Ninth Elegy by Rainer Maria Rilke

the trees which enchanted me; vistas vast and nearly touchable; meadows of a vernal cast and every wondrous joy my heart could claim.

-excerpt from The Sonnets to Orpheus by Rainer Maria Rilke

When that exists, that comes to be; on the arising of that, this arises. When that does not exist, this does not come to be; on the cessation of that, this ceases.

-From *The Middle Length Discourses of the Buddha* translated by Bhikkhu Ñanamoli and Bhikkhu Bodhi
Abstract of a thesis submitted in partial fulfilment of the requirements for the Degree of Ph.D.

Untangling spatial distribution patterns of the invasive herb *Hieracium lepidulum* Stenstr. (Asteraceae) in a New Zealand mountain landscape

by A.L. Miller

The invasive herb *Hieracium lepidulum* Stenstr. (Asteraceae) has been observed increasing in a range of indigenous ecosystems in New Zealand in recent years. The ability of this species to occupy and potentially to dominate a wide range of indigenous ecosystems at the expense of native biota triggered alarm among conservation managers, and set the stage for this research. The overall aim of this thesis was to identify and explain patterns of *H. lepidulum* invasion on a national and landscape scale, and to provide the data necessary to model the future spread of *H. lepidulum* throughout the landscape.

A reconstruction of spatiotemporal spread patterns of *H. lepidulum* in New Zealand showed that spread has been focussed around three centres in the eastern South Island ranges where *H. lepidulum* was recorded relatively early. More recently, *H. lepidulum* has spread to West Coast and Fiordland ranges, areas of high rainfall that are potentially favourable for *H. lepidulum*, and which potentially provide a new ‘frontier’ for spread.

A survey of the spatial distribution of *H. lepidulum* among habitats in an upland mid-Canterbury landscape showed that high population abundances of *H. lepidulum* in forest creek habitats appear to act as sources for spread of *H. lepidulum* into adjacent beech forest and alpine habitats. These results served as the framework with which to generate hypotheses about how habitat variation in habitat resistance to invasion, propagule supply, plant performance in established populations and dispersal patterns might have generated the observed spatial distribution patterns.
A seed-sowing experiment measured among habitat resistance to invasion by quantifying how the interaction between habitat resistance to establishment and seed supply determined seedling establishment. Tussock grassland and alpine creek habitat were least resistant to *H. lepidulum* establishment. Forest creek and canopy gap habitat were less resistant than forest interior habitat. Variation in habitat resistant to establishment thus appeared to at least partially explain the variable pattern of distribution of *H. lepidulum* among forest habitats, while a lack of seed reaching alpine habitats appeared to explain the low abundance of *H. lepidulum* in the alpine.

Monitoring of plant performance in natural populations supported this, with plant size and reproductive output highest in tussock grassland and alpine creek habitats, and higher in forest creek and canopy gap populations than in forest interior populations.

Among habitat variation in dispersal patterns was examined by measuring dispersal curves in five habitats under different wind conditions. Wind conditions best explained variation in the number of seed dispersing, and the rate of decline of seeds dispersing with distance from source. However, there was a trend for greater seed dispersal (in terms of distance dispersed and number of seeds) in forest creek habitat relative to forest interior and canopy gap habitat, suggesting that facilitation of dispersal in forest creeks may contribute to high abundances in forest creek populations relative to the forest interior.

The uneven spatial distribution of *H. lepidulum* among habitats in the mid-Canterbury landscape is predominately a function of variation in habitat resistance to invasion, subsequent population growth due to variation in plant performance among habitats, and variation in propagule supply rates.

**Keywords:** biological invasion, *Hieracium lepidulum*, dose-response curve, propagule supply, resistance to invasion, invasibility, habitat, landscape spread, historical spread, establishment, dispersal, demography.
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$$\lambda = \frac{N_t}{N_{(t-1)}}$$

$N_{(t-1)}$ is taken as a population of 40 individuals of *H. lepidulum*. $N_t$ is the estimated size of this population after one year, resulting from recruitment (R) and mortality (M):

$$N_t = N + R - M$$

R = number of new recruits into the population, estimated as per population seed production (estimated as $N_{(t-1)}$ x the proportion of individuals in a population seeding x the mean number of seed heads produced per seeding individual x the mean number of seeds/seed head (Chapter 5, Table 2b)) x the rate of seedling establishment (estimated from the dose-response curve (Chapter 4, Table 3c)).

M = number of adult plants dying over the study period (estimated as $N_{(t-1)}$ x the proportion of individuals dying (Chapter 5, Table 2)).
Chapter 1.

General introduction: making sense of spatial distribution patterns to predict future spread of invasive species

Introduction

Biological invasions and the changes they bring about are second only to direct habitat destruction in terms of threats to indigenous biodiversity (Mack et al. 2000). The ecological consequences of invasions are many, ranging from competitive displacement of indigenous biota, changes in community structure and ecosystem processes, to alteration of entire ecosystems (Vitousek 1986, MacDonald et al. 1989, D'Antonio and Vitousek 1992, Vitousek et al. 1997, Mack et al. 2000, Hierro et al. 2005).

The best way to manage invasions is to prevent them from occurring in the first instance, or to eradicate them when colonising populations are still small and few (Simberloff 2003). If an invader has already become established however, the ability to predict future patterns of how that invader will spread throughout the landscape is important for appropriate management action (Kolar and Lodge 2001, Heger and Trepl 2003, Volin et al. 2004). Predicting future spread requires a comprehensive understanding of current patterns of distribution: what they are and how they have developed (Lambrinos 2001). This requires documenting patterns of distribution firstly on large scales (e.g. nationally or regionally) to gauge the extent of the problem and to identify broad scale factors contributing to spread. Secondly, distribution patterns must be documented on a landscape scale, and the components that underlie landscape level distribution, i.e., the factors contributing to the establishment, population growth and spread of the invader must be dissected. Once these factors have been properly understood, then predictions of future spread dynamics can be made.

The Process of Invasion

Invasion occurs as a progression of stages, beginning with the introduction of propagules into a new location, establishment, population growth following establishment, and finally spread into new locations (Figure 1) (e.g., Bazzaz 1986, Mooney and Drake 1989, Williamson 1996, Mack et al. 2000, Kolar and Lodge 2001, With 2002). The initial
introduction to a new location is typically largely determined by association with humans, and to a lesser extent, dispersal ability (Mooney and Drake 1989, Mack 1995, Mack et al. 2000).

**Establishment**

Following introduction to a new location, the probability of establishment is determined by both environmental resistance to invasion, or the abiotic and biotic factors that determine the availability of safe sites (*sensu* Grubb 1977, Harper 1977) for establishment, and propagule pressure, or the number of colonising individuals and the frequency of introductions (Williamson 1996, D'Antonio et al. 2001, Rouget and Richardson 2003, Foxcroft et al. 2004, Richardson 2004).

**Propagule pressure**

Propagule pressure has emerged as the most robust determinant of establishment success of species introduced to new regions (Kolar and Lodge 2001, Lockwood et al. 2005). Species introduced in greater numbers and more often are more likely to establish, as shown by retrospective analyses of introductions of birds (Duncan 1997, Green 1997, Duncan et al. 1999, Duncan et al. 2001a, Forsyth and Duncan 2001, Duncan et al. 2003), mammals (Forsyth et al. 2004), fish (Marchetti et al. 2004), and plants (Mulvaney 2001, Gravuer 2004). Experimental studies that have manipulated propagule supply (number of colonising individuals) have also shown that establishment success increases with propagule supply (Ebenhard 1989, Memmot et al. 1998, Grevstad 1999, Hee et al. 2000, Ahlroth et al. 2003, Memmot et al. 2005). Additionally, propagule supply, measured as distance to source populations, was shown to be a better predictor of the distribution of several plant invaders in a South African landscape than environmental factors (Rouget and Richardson 2003, Foxcroft et al. 2004).

The increased likelihood of establishment success with increased propagule pressure is an important and intuitive concept: a founder population is more likely to withstand environmental stochasticity to establish and persist when the colonising pool is large than when it is small (MacArthur and Wilson 1967, Schoener and Schoener 1983, Roughgarden 1986, Ebenhard 1989, Mack 1995, 2000, Forsyth and Duncan 2001, Ahlroth et al. 2003, Lockwood et al. 2005). Similarly, a founder population has a greater chance of encountering favourable conditions for establishment if it is introduced more times
A larger colonising pool is more likely to contain individuals genetically suited to the invaded environment, and individuals are more likely to find suitable microsites to establish and grow in (Roughgarden 1986, Mack 1995, 2000, Ahlroth et al. 2003). Further, the potential negative effects of existence in low densities (Allee effects) are reduced with a larger propagule supply (Ahlroth et al. 2003, Lockwood et al. 2005).

**Habitat resistance to invasion**


The successful establishment of invasive exotic plants is often correlated with an abundance of abiotic resources such as light, soil nutrients and moisture (e.g., Huenneke et al. 1990, Davis et al. 2000, Davis and Pelsor 2001, Denslow 2003). Community characteristics influencing ground cover composition and intensity of competition for space and abiotic resources are also important determinants of invasive plant establishment. Competition with resident species can contribute to invasion resistance, but is rarely effective at completely preventing establishment (Levine et al. 2004). The availability of bare ground where an invader can establish free from competition with resident species is often correlated with establishment success; thus disturbances that create bare ground are thought to be important for invasive species establishment (Crawley 1986, Rejmánek 1989, Burke and Grime 1996, Turnbull et al. 2000, Zobel et al. 2000). However, sheltering microsites that ameliorate harsh climatic conditions such as extreme aridity or cold, which can be provided by litter or resident vegetative cover, may be more important than bare ground availability (Hunter and Aarssen 1988, Greenlee and Calloway 1996, Smith et al. 2004). The relative importance of competition or facilitation in determining establishment often shifts along environmental gradients (Hunter and Aarssen 1988, Greenlee and Calloway 1996, Callaway and Walker 1997, Choler et al. 2001).
Habitats differ in resistance to invasion because of differences in abiotic resource availability, climate, biotic interactions and disturbance regimes that influence safe site availability. Habitats will therefore differ in the propagule supply rate required for establishment to succeed, in the rate of establishment for a given propagule supply, and in the level at which they are saturated, i.e., when further propagule addition ceases to result in further establishment. Thus, understanding how the relationship between establishment success and propagule supply changes with resistance to invasion is key to making sense of spatial patterns of invasive species distribution and predicting future spread (D'Antonio et al. 2001, Kolar and Lodge 2001, Ruiz and Carlton 2003, Lockwood et al. 2005). Yet, the interaction between propagule pressure and resistance to invasion remains poorly studied (Kolar and Lodge 2001, Ruiz and Carlton 2003, Lockwood et al. 2005).

**Population growth**

Following introduction and establishment, the next stage of the invasion process is population growth. Habitat resistance may not prevent establishment of an invading species, but may limit population growth following establishment (D'Antonio et al. 2001, Levine et al. 2004). Species may successfully establish in abiotically unsuitable habitats due to high propagule supply rates into those habitats, but have such low fecundity levels that net population growth is negative (Keddy 1982, Pulliam 1988, Dias 1996, Holway 2005). There are many examples of species from open habitats invading forest edges where they can survive but not reproduce (e.g., Pierson and Mack 1990, Brothers and Spingarn 1992, Parendes and Jones 2000). Similarly, seedlings may successfully establish in communities with high cover of resident species, but then fail to grow due to competition (Levine et al. 2004 and references therein).

**Spread**

The final stage of invasion is spread; spread rates are determined by vital rates (birth, survival, and reproductive rates) within established populations, and dispersal rates (Clark 1998) (Figure 1). Variation in population vital rates, as well as seed dispersal patterns among habitats can lead to variation in spread rates among habitats, thus contributing to variable patterns of distribution.
Summary

Predicting the future spread dynamics of an established invasive species requires documenting how that invader is spatially distributed both at broad (e.g. national) and landscape scales to set the context for the problem, and to generate hypotheses about the factors underlying the spatial distribution patterns. Landscape level distribution patterns may be determined by 1. interactions between propagule pressure and environmental resistance to invasion that determine the probability of the invader establishing; 2. by variations in population vital rates among components of the landscape; and 3. by variation in dispersal patterns among components of the landscape. Understanding the relative contribution of each of these three components to invasive spread allows for the development of models of spatial spread over the landscape, and allows for management strategies to be aimed at specific components (Parker 2000).

This Ph.D. dissertation uses the above framework to disentangle the spread dynamics of the invasive herb *Hieracium lepidulum* Stenstr. (Asteraceae) in New Zealand in order to a) understand the factors that underlie the current distribution of this species, and b) to predict the likely future patterns of spread of this species.

*Hieracium lepidulum* invasion in New Zealand

While invasion is a global problem, New Zealand is at the extreme end of the invasion scale, with naturalised exotic species accounting for approximately half of New Zealand’s vascular plant flora (Heywood 1989, Owen 1998). Exotic plant species are considered a threat to the persistence of 59% of New Zealand’s threatened flora (Dopson et al. 1999).

Notorious among New Zealand’s exotic plant invaders are species in the genus *Hieracium* (Asteraceae). The ‘*Hieracium* problem’ has predominately been considered a tussock grassland problem, with the invasion of *Hieracium* species into New Zealand tussock grassland communities receiving much attention from ecologists, conservationists and land managers over the past 30 years (e.g., Scott 1984, Scott et al. 1990, Hunter 1991, Treskonova 1991, Scott 1993, McIntosh et al. 1995, Rose et al. 1995, Duncan et al. 1997, Rose et al. 1998, Johnstone et al. 1999, Rose and Frampton 1999, Svavardsdóttir et al. 1999, Scott et al. 2001). Most of this research has focused either on *H. pilosella* (mouse-eared hawkweed) or on *Hieracium* species in general. *Hieracium lepidulum* (tussock hawkweed),
although it is considered one of the four ‘problem’ *Hieracium* species in New Zealand (Scott 1984, Hunter 1991, Duncan et al. 1997, Rose et al. 1998, Espie 2001), has received relatively little attention. This is probably because it is not as widespread and abundant as *H. pilosella* (Hunter 1991), does not dominate short tussock pastoral grasslands to the degree that *H. pilosella* does, and since it is a palatable and nutritious source of food for stock, it does not lower pastoral production values to the same extent.

Over the last 50 years however, *H. lepidulum* has been steadily increasing in frequency and abundance in a wide range of indigenous plant communities, from montane short tussock grasslands to high altitude tall tussock grasslands, mountain and silver beech forest, and subalpine scrub and herb fields throughout the South Island of New Zealand (Rose et al. 1995, Duncan et al. 1997, Wiser et al. 1998, Mark et al. 1999, Wiser and Allen 2000, Duncan et al. 2001b). In some areas, such as the Rob Roy catchment in central Otago, parts of mid-Canterbury, and the Borland Mire in Southland, *H. lepidulum* is present at close to 100% cover. *Hieracium lepidulum* is capable of establishing under the shade of dense tall tussock canopy, unlike *H. pilosella* and *H. praealtum* (Rose and Frampton 1999), enabling it to invade a wider range of indigenous communities. This spread into, and consequent dominance of indigenous communities with high conservation values, triggered alarm among conservationists and land managers, and set the stage for the current research.

**Biology**

*Hieracium lepidulum* is a member of a very large, taxonomically complex genus. It is a broad-leaved, tap rooted rosette-forming perennial herb (Figure 2). Leaves are basal and cauline (cauline leaves reduced up flowering stems), and are toothed, often with purple undersides. *Hieracium lepidulum* reproduces solely by apomictic seed production (Chapman et al. 2004). While not stoloniferous, *H. lepidulum* does form multiple rosettes via rhizomes. Seed are achenes, c. 3 x 0.5 mm, with pappus 6–7 mm (Webb et al. 1988), and are predominately wind-dispersed, but humans and animals may aid dispersal. Flowering and fruiting occurs from November to May (Webb et al. 1988). Leaves die back in fall (May), and plants overwinter as a rhizome with new leaves budding around September (pers. obs.).
Ecology

Native and naturalised distribution

*Hieracium lepidulum*, also known as *H. lachenalii*, is native to Europe, where it is mainly a forest herb though occurs in a variety of habitats except for wetlands and very acidic soils (Wiser and Allen 2000). *Hieracium lepidulum* is naturalised in the United States, Canada, and Australia as well as New Zealand.

Factors affecting invasion resistance to *H. lepidulum*

A comprehensive examination of historical, environmental and community factors associated with *H. lepidulum* invasion over 23 years in mountain beech forest in the Craigieburn area of mid-Canterbury showed that soil fertility, community diversity and composition were important in explaining patterns of invasion, with *H. lepidulum* more likely to invade fertile, species rich sites with a higher percentage of species in the same guild (Wiser et al. 1998). Disturbance, measured as change in stand biomass between measurement years, was found to have only weak associations with *H. lepidulum* invasion (Wiser et al. 1998). However, field observations indicate that *H. lepidulum* can be abundant in naturally disturbed areas such as creek sides and landslide scars (Wiser and Allen 2000).

Grazing may favour invasion of *H. lepidulum* into grasslands. Vegetation changes in short-tussock grassland in the Harper-Avoca catchment were measured at 5 to 10 year intervals over 25 years (Rose et al. 1995). Sites with different grazing histories were compared to assess the affects of sheep grazing on *Hieracium* invasion. *Hieracium lepidulum* was initially present at higher frequencies on grazed transects and remained so; however, the rate of increase was similar on both grazed and ungrazed transects (Rose et al. 1995).

Summary

In summary, little is known about the invasion ecology of *H. lepidulum* in New Zealand ecosystems. The species is capable of invading a range of indigenous habitat types, and it has the potential to dominate these habitats. High soil fertility and more species rich sites are more favourable for *H. lepidulum* invasion in mountain beech forests (Wiser et al. 1998). Anecdotal evidence indicates that some forms of natural disturbance promote invasion, and disturbance by grazing may also promote invasion.
Overall Aim

The overall aim of this thesis is to identify and explain patterns of *Hieracium lepidulum* invasion in New Zealand on a national and landscape scale, and to provide the data necessary to model the future spread of *H. lepidulum* throughout the landscape.

Specific Objectives:
To document the spatial distribution of *H. lepidulum* at

1. A national scale.

2. A landscape scale, and to test the hypothesis that creeks act as source habitats for the spread of *H. lepidulum* throughout the landscape.

I then examine how landscape level distribution patterns might be explained by the three components contributing to invasive spread over the landscape (see page 5):

3. The interaction between propagule supply rate and invasion resistance among habitats.

4. Variation in population vital rates among habitats.

5. Variation in dispersal patterns among habitats.

Thesis Structure
Besides the general introduction (Chapter 1) and general conclusions (Chapter 7), this thesis is structured as a series of papers.

Chapter 2 provides the broad context for the spread of *H. lepidulum* in New Zealand. I describe the spatiotemporal patterns of spread using historical and present distribution records of *H. lepidulum* that I collated from herbaria, the National Vegetation Survey database, miscellaneous datasets and personal communications and observations. I examine how patterns of spread have been associated with geographic regions and habitat types.
Chapter 3 presents the results of a survey of the landscape-level distribution of *H. lepidulum* within the Harper-Avoca/Craigieburn area of mid-Canterbury that was designed to determine whether creek habitats serve as sources for spread into the surrounding landscape. The observed spatial distribution patterns serve as the framework with which to generate hypotheses about how differences in propagule supply, habitat resistance to invasion, plant performance in established populations and dispersal patterns determine patterns of distribution, and the likely future spread of the species. These hypotheses were then tested in the following chapters.

Chapter 4 describes a seed-sowing experiment in which I investigate the relationship between rates of propagule supply and rates of seedling establishment (the dose-response curve), and how this varies among habitats, as a measure of habitat resistance to establishment. I then correlate measures of resistance derived from the dose–response curve with environmental variables to explore whether these can explain differences in resistance to invasion among habitats.

Chapter 5 describes the results of demographic monitoring of plant performance in natural established populations of *H. lepidulum* in seven different habitats, to determine whether variation in plant performance (plant size, reproductive output and survival) could partly explain the uneven distribution of *H. lepidulum* among habitats.

Chapter 6 presents an experiment in which I quantified dispersal curves of *H. lepidulum* in five habitats under different wind conditions to determine whether variation in dispersal patterns among habitats could partly explain the uneven distribution of *H. lepidulum* among habitats.

Chapter 7 General conclusions. This chapter summarises the results from the previous four chapters and uses the data from these chapters to determine rates of population increase among habitats.

References


staphylinus) released against gorse (Ulex europaeus) in New Zealand. Biocontrol Science and Technology 8:103-115.


Invasive plant spread and spatial patterns of distribution

1. Introduction to new location
   - Human association
   - Dispersal ability
   - Proximity to source

2. Seedling establishment
   - Propagule pressure
     - propagule supply
     - frequency of introductions
   - Environmental resistance: Safe site availability

3. Population growth
   - resources
     - soil fertility
     - moisture
     - light
   - biotic interactions
     - competitors
     - mutualists
     - nathorens
   - microsite
     - litter
     - bare ground
     - moss

4. Spread
   - Population vital rates (establishment, reproduction, mortality)
   - Dispersal

Figure 1.1. The process of a biological invasion, including how variability in the factors contributing to each stage of the process may lead to a variable pattern of abundance in the landscape.
Figure 1.2. *Hieracium lepidulum* growing in mountain beech forest, Craigieburn Ranges, New Zealand.
Chapter 2.

The spatiotemporal patterns of spread of Hieracium lepidulum in New Zealand

Introduction


Historical patterns of distribution and rates of spread are traditionally traced with herbarium records which may be supplemented with regional plant lists, questionnaires, aerial photography, scientific and grey literature, and general or specific botanical surveys (e.g., Mack 1981, Forcella and Harvey 1983, Forcella 1985, Pyšek and Prach 1995, Weber 1998, Stansbury and Scott 1999, Lambrinos 2001, Novak and Mack 2001, Delisle et al. 2003). Spatial patterns of spread can be mapped by plotting occurrence records as points on maps, or more commonly, by plotting occurrence records onto grid squares overlaying regional maps (Perrins et al. 1993, Pyšek and Prach 1995, Weber 1998), or by occurrence in geographical areas such as counties in a state (e.g., Lambrinos 2001). Rates of spread are frequently determined as some function of the cumulative number of grid squares occupied, or cumulative number of occurrence records, over time (e.g., Forcella and Harvey 1983, Forcella 1985, Pyšek and Prach 1995, Weber 1998, Lambrinos 2001, Delisle et al. 2003).

Here, I traced the spatiotemporal spread patterns of H. lepidulum in New Zealand from the earliest records of occurrence up to the present distribution, using data collected from herbarium records, vegetation plot records archived by the National Vegetation Survey database (NVS), and miscellaneous other datasets, personal observations and personal
communications. I calculated an overall rate of spread, and examined how patterns of spread have been associated with regions and habitats. The purpose of this chapter is to provide an overall context for *H. lepidulum* invasion in New Zealand, not to exhaustively document the factors underlying the historical spread of *H. lepidulum* in New Zealand.

**Methods**

**Data collection**

Records of *H. lepidulum* occurrence within New Zealand were obtained from all New Zealand herbaria (139 records), the National Vegetation Survey (NVS) database (1262 records), miscellaneous datasets held by individual researchers, and personal communications and observations (414 records). These records were collated into a database where each record included a NZMS260 topographic map series (Anonymous 2004) grid reference, date of observation, and when possible, a habitat category.

I recorded habitat categories, where present, from herbarium labels and survey plot sheets, and after examining all records, grouped records into the following categories: 1. Tussock grassland. This included grassland dominated by indigenous tussock forming grass species from low altitude short tussock grassland up to high altitude snow tussock grassland. 2. Scrub. This included low altitude seral scrub vegetation (e.g. kanuka/manuka) up to subalpine scrub. 3. Scrub-tussock. This was vegetation composed of a mix of both scrub and tussock grassland. Observations were assigned to this category when I could not judge from the plot or herbarium labels which of the two vegetation types dominated. 4. Forest. This encompassed indigenous forest vegetation from monospecific beech forest (*Nothofagus* sp.) to mixed forest comprising a range of compositional types. 5. Wetland. This included riparian margins, lake margins and swamps. 6. Herbfield. This included herb-dominated subalpine and alpine vegetation. 7. Rock. This included bluff systems, boulder and scree fields. 8. Ruderal. Ruderal habitat included tracks, roads and road margins, huts and clearings. 9. Exotic. This habitat included pastures dominated by exotic grasses and herbs, and exotic forestry plantations. Exotic forestry plantations were included with exotic pasture because there were only two forestry records.
Analysis

Visualising spread
Spatiotemporal patterns of *H. lepidulum* spread within New Zealand were visualised using ARCVIEW GIS. Using ARCVIEW, I extracted the earliest date of occurrence of *H. lepidulum* in each cell of 1-km grid squares overlaying a map of New Zealand. I then mapped the dates of first occurrence onto a map of New Zealand and colour-coded these by date.

I examined how occurrence records were distributed among habitat categories by calculating the number of records per habitat per decade, and using Chi-Square contingency tests to test whether particular habitats were invaded at earlier stages of invasion.

Spread rates
I calculated the national rate of spread of *H. lepidulum* as the slope of the linear regression of the log of the cumulative 1-km grid squares occupied as a function of year (e.g. Pyšek and Prach 1995, Weber 1998, Lambrinos 2001). I informally compared spread among South Island Conservancies (political regions managed by the Department of Conservation) by plotting the cumulative number of occurrence records in each of the four conservancies in which *H. lepidulum* occurred in sufficient numbers, as a function of year. I compared spread rates among the five dominant habitat categories invaded by *H. lepidulum* in the same manner.

Historical reconstructions of spread may be biased due to variable collection intensity among regions or time periods (e.g. Mihulka and Pyšek 2001, Delisle et al. 2003, Gravuer 2004). I do not formally account for potential biases in analysis as these authors did. Here, I address potential spatial bias by also mapping grid references for all vegetation plots held by NVS where *H. lepidulum* did not occur; this allowed me to identify true distribution gaps from gaps that represented unsurveyed areas. To address potential temporal bias in collection, I examined how the number of records from each data source was distributed over time, and plotted the cumulative number of records of *H. lepidulum* from the three source categories of data source (NVS, Herbarium records, Miscellaneous) per decade.
Results

The earliest record of *H. lepidulum* occurrence in New Zealand is from 1941 in creek margin habitat in the Craigieburn ranges in mid-Canterbury (CHR 301081). In 1950, *H. lepidulum* was first noted in Central Otago at Lake Wanaka (CHR 77071). In 1964, *H. lepidulum* was first observed in Nelson/Marlborough in a 'fescue swamp' (CHR 152221). These three early records are from areas that appear to have acted as centres of spread for *H. lepidulum* (Figure 1, Table 1). Although *H. lepidulum* was observed as early as 1964 on the North Island beside a road on the slopes of Mt Egmont (CHR 159569), and was still there in 2001 (C.C. Ogle, National Weeds Database record), it has not spread there to a significant degree (Figure 1). During the last four years that I have occurrence records for (2000–2004), *H. lepidulum* has spread into the headwaters of the West Coast ranges and into Southland (Figure 1).

The large distribution gaps apparent between the three focal distribution centres on the map appear to be real, or at least were when the data were collected, as collection intensity in these areas was not consistently different from areas from which *H. lepidulum* is recorded (Figure 1).

Habitats invaded

The highest number of *H. lepidulum* occurrences was reported from tussock grassland habitat, followed by scrub (Table 2). Indigenous forests have the next greatest number of reported occurrences, followed by wetland habitats, and rock habitats (Table 2). Herbfields and ruderal habitats each had a small number of records, and exotic habitats had the fewest (Table 2). There were no significant associations of *H. lepidulum* occurrence records with habitat type over time (Table 3, Chi-square test of independence, P > 0.05).

Rates of spread

The plot of cumulative number of 1-km grid squares occupied by *H. lepidulum* over time demonstrates a 40-year lag phase following the first recorded occurrence of *H. lepidulum* in New Zealand, a period of rapid exponential growth beginning in the 1980s, followed by an apparent slowing down of spread in the early 1990s (Figure 2). The overall rate of spread calculated was 1.18 1-km grid squares occupied per year.
Rates of spread in Canterbury and Otago have been roughly equal, while they were slower in Marlborough (Figure 3).

It is very difficult to determine whether the temporal spread patterns described by the occurrence records are real, or reflect temporal variation in collection effort. When the cumulative number of occurrence records were mapped by source, the rate of spread indicated by herbarium records was linear, and did not show a lag phase or period of rapid increase, while the NVS records showed a steep rate of increase from when these records began in the 1970s (Figure 4). The miscellaneous records reflect more recent spread; this is because these records have not yet been archived with NVS, and they include personal observations and communications. The period of rapid spread of *H. lepidulum* indicated in Figure 2 coincides with the Protected Natural Areas surveys instigated by the Department of Industrial Research (DSIR) in the 1980s.

Tussock habitats have been overrepresented in terms of *H. lepidulum* presence throughout the invasion process (Figure 5). Rapid spread began in tussock, scrub, forest, riparian and rock habitat at roughly the same time (early 1980s), and the rate of spread was exponential and not different among the first four habitats, while it was slower and linear in rock habitats. All five habitats show a decline in spread rates in the early 1990s (Figure 5). Again, I have to be careful in interpreting differences both in rates of spread, and the distribution of *H. lepidulum* occurrence records among habitats, without accounting for differences in collection effort among habitats.

**Discussion**

The spatial pattern of spread of *H. lepidulum* in New Zealand has been centred around three main foci that correspond to early occurrence records in the eastern ranges of the South Island: mid-Canterbury, Central Otago and inland Marlborough. Although *H. lepidulum* was also recorded relatively early on the North Island, it has persisted there but has not spread. Similarly, *H. lepidulum* has not spread from an early occurrence record from the Canterbury plains, indicating that the lowland, highly modified landscape of the eastern South Island lowlands is not suitable for *H. lepidulum*. While historically, spread has radiated outwards from these three focal points, *H. lepidulum* has recently spread to
subalpine areas west of the Main Divide, and to ranges in Southland, including Fiordland National Park.

The West Coast and Southland may provide a new ‘frontier’ for the spread of *H. lepidulum*, especially as *H. lepidulum* appears to thrive in areas with higher rainfall (Rose et al. 1995, Mark et al. 1999, Wiser and Allen 2000). Spread rates have apparently slowed for Canterbury, Otago and Nelson-Marlborough, but there are still significant gaps in the distribution of *H. lepidulum* within the eastern ranges. There is no obvious biological explanation for why *H. lepidulum* would be excluded from these areas (for example, in terms of climate, habitat types, abiotic factors). The lack *H. lepidulum* occurrence in these areas therefore likely reflects dispersal and propagule supply limitations, and amalgamation of the range of *H. lepidulum* throughout the eastern ranges can probably be expected.

*Hieracium lepidulum* has most frequently been recorded in tussock and scrub habitats. However, *H. lepidulum* has historically occurred in a range of habitats, unlike some invaders which dominate disturbed or ruderal habitats early in the invasion process (Pyšek and Prach 1993, Pyšek and Pyšek 1995, Pyšek et al. 1998). Here I found no statistical evidence for changes in *H. lepidulum* association with habitats over time.

The temporal spread of *H. lepidulum* in New Zealand demonstrates a pattern typical of biological invasions, with a lag phase following introduction, a period of exponential growth and the beginning of a saturation phase when spread rates slow (Hengeveld 1989, Kowarik 1995, Shigesada and Kawasaki 1997, Lambrinos 2001). However, I can not distinguish here whether the pattern implied by the occurrence records of *H. lepidulum* is an artefact of temporal bias in collection intensity or accurately reflects spread dynamics (Mihulka and Pyšek 2001, Delisle et al. 2003). The herbarium data indicate a linear rate of spread; however, rates of spread calculated from herbarium data may be underestimated because once species are commonly encountered, collection intensity may decline.

Workers involved in vegetation surveys of New Zealand during the PNA years and before, feel that *H. lepidulum* did in fact ‘take off’ in the 1980s (Susan Wiser, pers. comm.). A long-term dataset from mid-Canterbury subalpine tussock grasslands does provide evidence for a period of rapid increase in the frequency of *H. lepidulum* on grassland plots occurring between 1980 and 1990, while frequency increased much more slowly from
1960 to 1980 (Rose et al. 1995). A dataset from forest systems in the same area showed a rapid increase in frequency of *H. lepidulum* on forest plots between 1970 and 1985, with a slower rate of increase between 1985 and 1993 (Wiser et al. 1998). I suspect that there was a period of rapid spread of *H. lepidulum* during the 1980s, but perhaps not as steep as the occurrence records indicate. With the data available however, I can not show that this is the case.

**Summary**

*Hieracium lepidulum* occurs in nearly half of the NZMS 260 series grid squares on the South Island. Spatial distribution is centred in Canterbury, Otago and inland Marlborough, all locations where *H. lepidulum* was recorded relatively early. Spread rates and frequency of occurrence have been highest in Canterbury and Otago, although recent arrival of *H. lepidulum* on the West Coast and in Southland may see an increase in the spread of *H. lepidulum* in these regions in the near future. *Hieracium lepidulum* has been recorded most frequently in tussock grassland and scrub habitat, but has occurred in a range of habitats since it was first recorded in New Zealand, including indigenous forest, riparian and rock habitats, herb fields, ruderal habitats and exotic dominated habitats.

**References**


Table 2.1. A breakdown of the number of records of *H. lepidulum* by New Zealand Conservancy (with the North Island); the number of records for each Conservancy is listed.

<table>
<thead>
<tr>
<th>Conservancy</th>
<th>Number of records</th>
<th>Earliest record</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canterbury</td>
<td>692</td>
<td>1941</td>
</tr>
<tr>
<td>Otago</td>
<td>630</td>
<td>1950</td>
</tr>
<tr>
<td>Southland</td>
<td>299</td>
<td>1998</td>
</tr>
<tr>
<td>Nelson/Marlborough</td>
<td>177</td>
<td>1965</td>
</tr>
<tr>
<td>Westland</td>
<td>9</td>
<td>1996</td>
</tr>
<tr>
<td>North Island</td>
<td>5</td>
<td>1964</td>
</tr>
<tr>
<td>location not available</td>
<td>4</td>
<td></td>
</tr>
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</table>

Table 2.2. Habitats invaded by *H. lepidulum*. The number of records of *H. lepidulum* occurrence in each habitat type is listed for the 1231 records for which information was available. Habitats were identified from herbarium labels and vegetation survey plot sheets.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Number of records</th>
</tr>
</thead>
<tbody>
<tr>
<td>tussock grassland</td>
<td>485</td>
</tr>
<tr>
<td>scrub</td>
<td>346</td>
</tr>
<tr>
<td>scrub-tussock</td>
<td>74</td>
</tr>
<tr>
<td>indigenous forest</td>
<td>126</td>
</tr>
<tr>
<td>wetland</td>
<td>87</td>
</tr>
<tr>
<td>rock</td>
<td>47</td>
</tr>
<tr>
<td>herb field</td>
<td>25</td>
</tr>
<tr>
<td>ruderal</td>
<td>28</td>
</tr>
<tr>
<td>exotic</td>
<td>11</td>
</tr>
<tr>
<td>habitat data not available</td>
<td>585</td>
</tr>
</tbody>
</table>
Table 2.3. Breakdown of habitats invaded by *H. lepidulum* by decade. The percentage of the number of records per decade occurring in each habitat category is listed for the 1231 records for which this information was available. There was no significant decade by habitat association (Chi-square test of independence \( P > 0.05 \)).

<table>
<thead>
<tr>
<th></th>
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<th></th>
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<tbody>
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<td>.</td>
<td>12</td>
<td>30</td>
<td>23</td>
<td>53</td>
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<tr>
<td>tussock grassland</td>
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<td>54</td>
<td>15</td>
<td>40</td>
<td>46</td>
<td>.</td>
</tr>
<tr>
<td>scrub-tussock</td>
<td>14</td>
<td>4</td>
<td>.</td>
<td>7</td>
<td>5</td>
<td>.</td>
</tr>
<tr>
<td>forest</td>
<td>.</td>
<td>8</td>
<td>12</td>
<td>10</td>
<td>7</td>
<td>22</td>
</tr>
<tr>
<td>riparian</td>
<td>.</td>
<td>8</td>
<td>27</td>
<td>7</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>herb field</td>
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<td>.</td>
<td>2</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td>rock</td>
<td>14</td>
<td>.</td>
<td>.</td>
<td>3</td>
<td>13</td>
<td>6</td>
</tr>
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<td>.</td>
<td>19</td>
<td>23</td>
<td>1</td>
<td>3</td>
<td>13</td>
</tr>
<tr>
<td>exotic</td>
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<td>12</td>
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<td>1</td>
<td>3</td>
</tr>
<tr>
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<td>26</td>
<td>26</td>
<td>992</td>
<td>145</td>
<td>32</td>
</tr>
</tbody>
</table>
Figure 2.1. The spatiotemporal spread of *H. lepidulum* in New Zealand. Points are the earliest occurrence records in 1-km grid squares (records are colour-coded for the date of earliest occurrence in a 1-km grid square (see legend). Spatial collection intensity is illustrated in the smaller map, with NZMS 260 grid squares shaded by number of National Vegetation Survey database (NVS) records occurring in them as of 2004 (see legend).
Figure 2.2. The cumulative rate of increase of *H. lepidulum* in New Zealand as the cumulative number of 1-km grid squares occupied versus year. The rate of spread, calculated as the slope of the linear regression of log(cumulative grid squares occupied) as a function of year for the period 1947 to 1990 was an increase of 1.18 grid/squares per year.
Figure 2.3. The cumulative rate of increase of *H. lepidulum* by South Island, New Zealand Conservancy as the cumulative number of records versus year.
Figure 2.4. The cumulative rate of increase of *H. lepidulum* as the cumulative number of records versus year depicted by three different data sources.
Figure 2.5. The cumulative rate of increase of *H. lepidulum* by habitat as the cumulative number of records present in five habitat types versus year.
Chapter 3.

Creeks as source habitats for the spread of an invasive herb: dynamic front or ‘spatial mass’?

Introduction

The spread of invasive species in natural landscapes is an accelerating concern for conservation managers throughout the world (e.g., Mack et al. 2000). Understanding the forces determining the spread of invasive species within the landscape is a practical necessity for managing the spread of invasive species. The first phase of managing invasions is to document how they are spatially distributed in the landscape, as this spatial distribution provides a framework for generating hypotheses explaining the forces underlying the pattern (Weins 1997, Parendes and Jones 2000, With 2002). Further, the spatial distribution of invaders among habitats has implications for ongoing spread dynamics (Weins 1997, With 2002). Habitats that are highly invaded, i.e., in which invader abundance is high, can serve as demographic sources for spread into the surrounding landscape (Pulliam 1988, Mooney and Drake 1989, Pulliam and Danielson 1991, Dias 1996). Identification of source habitats for invasive spread, and how these sources function throughout the landscape in terms of spread dynamics, is necessary for the allocation of management resources to most efficiently control spread.

The role of source habitats in invasive spread dynamics has been empirically demonstrated in many studies. It has been inferred from the historical association of invaders with specific source habitats followed by subsequent spread into a wider range of habitats (Pyšek and Prach 1993, Pyšek and Pyšek 1995, Ernst 1998, Pyšek et al. 1998), and by field measurements of the degree of invasion in putative source relative to adjacent habitat (Brothers and Spingarn 1992, Tyser and Worley 1992, DeFerrari and Naiman 1994, Harrison 1999, Gelbard and Belnap 2003, Watkins et al. 2003, Holway 2005). Habitats that have a high frequency of disturbance, and/or in which dispersal is facilitated (riparian habitats, roadsides, railways), are especially prevalent as source habitats (Rejmanek 1989, Pyšek and Prach 1993, Planty-Tabacchi 1996, Collingham et al. 1997, Stohlgren et al. 1999, Parendes and Jones 2000, Wadsworth et al. 2000, Holway 2005). While the
occurrence of source habitats for invasive spread has been widely demonstrated, documentation of the role of these sources across a diverse landscape is rare.

Variation in the spatial distribution of invasive species, and in particular, the existence of source habitats with high invader abundances, may arise from differences in habitat resistance to invasion or from variation in propagule supply rates among habitats (Williamson 1996, Lonsdale 1999, D'Antonio et al. 2001). Differences in propagule supply rates or differences in habitat resistance to invasion have different implications for spread dynamics. Differences in rates of spread driven by differences in propagule supply imply a dynamic invasion front. Differences in habitat resistance imply either a dynamic front where more resistant habitats are invaded at a slower rate relative to less resistant source habitats, or, if recipient habitats are highly resistant to invasion, a static spatial mass effect where invasion into recipient habitats is entirely dependent on their proximity to source habitat (Pulliam 1988, Pulliam and Danielson 1991, Dias 1996, Kunin 1998).

Here, I quantified the spatial distribution of the invasive exotic herb *H. lepidulum* among habitats in the mid-Canterbury region of New Zealand’s Southern Alps, specifically asking whether high densities of *H. lepidulum* in creek habitats drive spread of *H. lepidulum* into adjacent forest and alpine habitats. I then used the observed spatial distribution patterns to generate a series of hypotheses concerning the processes underlying these patterns.

During the last several decades, *H. lepidulum* has been steadily increasing in frequency and abundance throughout the South Island of New Zealand, and is now present in a wide range of habitats, from modified short tussock grassland to intact beech forest to high alpine herb fields (Chapter 2, Rose et al. 1995, Duncan et al. 1997, Rose et al. 1998, Wiser et al. 1998, Wiser and Allen 2000). Field observations indicate that *H. lepidulum* might be over represented in naturally disturbed habitats like creeks and rock outcrop systems (Wiser and Allen 2000), suggesting that such habitats may play an important role in the spread of *H. lepidulum* throughout the landscape. *Hieracium lepidulum* is recorded most frequently from lowland tussock grassland habitats (Chapter 2), thus creeks may act as sources for the spread of *H. lepidulum* from high density populations in anthropogenically induced lowland tussock grasslands into adjacent forest and up into alpine vegetation (Figure 1).
If creeks act as source habitats for spread into adjacent forest and alpine habitats, then I can make three predictions:

1. **Hieracium lepidulum** abundance will decline with increasing distance from creek into adjacent habitats. This prediction assumes that creek habitats are less resistant to *H. lepidulum* invasion and/or function as a dispersal corridor to transport *H. lepidulum* from high abundance populations in lower altitude tussock grasslands through the forest and up into the alpine (Figure 1), leading to higher *H. lepidulum* abundance in creek habitat than in adjacent forest and alpine habitat (e.g., Dias 1996, Kunin 1998). If creeks are source habitats for spread into adjacent vegetation, diffusive spread away from a source will result in a pattern of decreasing abundance with distance from source.

2. The pattern of decline in abundance from creek into adjacent forest and alpine habitat will depend on the underlying processes. *A priori* I do not know how these habitats differ in invasion resistance. However, if propagule supply rate is important then I predict a steeper decline in abundance moving from creek into forest habitat than from creek into alpine habitat because forest vegetation poses a greater barrier to dispersal (e.g., Cadenasso & Pickett, 2001).

3. There will be a positive relationship between *H. lepidulum* abundance in creek habitat and *H. lepidulum* abundance in adjacent habitat. Higher population densities in creeks will result in more seed dispersing into adjacent habitats, and thus a greater likelihood that some plants will establish (Kunin 1998, Rouget and Richardson 2003, Foxcroft et al. 2004).

To test these predictions, I quantified the abundance of *H. lepidulum* in transects extending from creek habitat into adjacent forest and alpine habitats in the mid-Canterbury region of the Southern Alps, New Zealand. A decline in abundance with distance from creek (prediction 1) could also be explained by a gradient in habitat resistance to invasion with distance from creek, while a positive relationship between *H. lepidulum* abundance in creeks and abundance in surrounding habitat (prediction 3) could be a consequence of differences among entire transects. I controlled for the effects of differences in creek, transect and local environmental variables that might explain *H. lepidulum* distribution in my statistical models. Since the purpose of my study was to document the spatial
distribution of *H. lepidulum* among habitats, and not to exhaustively document the site conditions under which *H. lepidulum* invades (see Wiser et al. 1998), I only included environmental variables that were likely to be relevant to *H. lepidulum* invasion, and that I could measure relatively quickly, allowing me to survey a larger number of creeks. I measured ground cover composition, macrosite features (slope, altitude, aspect), and overhead canopy cover.

**Methods**

**Field Site**

My study comprised two locations (‘Avoca’ and ‘Craigieburn’) on the eastern side of the Southern Alps, Canterbury, New Zealand (Figure 1). These locations were chosen because they have a long history of *H. lepidulum* invasion (Rose et al. 1995, Wiser et al. 1998), and I could be sure that *H. lepidulum* was sufficiently common to quantify its spatial distribution. Both locations are in Craigieburn Forest Park, which is managed for recreation (walking tracks, skiing) and conservation. The landscape is mountainous with elevations spanning 800 m to 2000 m. The mean annual temperature is 8.0°C and mean annual precipitation is 1447 mm (Wiser et al. 1998). Soils are recent or high-country yellow brown earths (Anonymous 1968). Mountain beech forest (*Nothofagus solandri* var. *cliffortiodes*) dominates from ~ 650 m to 1400 m elevation, and gives way to subalpine scrub, tussock grasslands (*Chionochloa* spp.) and alpine herb fields at higher elevations.

The Avoca area encompasses a main catchment (the Avoca river) fed by many smaller subcatchments, while the Craigieburn area consists of only small subcatchments. Subcatchments are typically steep and drained by creeks confined to narrow beds that experience rapid rising and lowering of water levels in response to heavy rain. Below treeline, larger creeks typically increase gradually in elevation, with forested slopes rising steeply from the valley bottom, although creeks are sometimes bordered by terraces. Smaller creeks typically increase steeply in elevation. Above tree line, creeks may retain a valley characteristic, may become small seepages, or may disappear beneath a channel of rubble. I defined the creek habitat as the area from the water or rubble edge (or if regularly flooded, unvegetated shingle was present, at the edge of the shingle) to the edge of continuous forest or alpine vegetation. Where there was not a distinct creek habitat, I
considered creek habitat as the 3-metre strip immediately adjacent to the water, or rubble edge on either side of the creek.

**Creek Selection**

I quantified the abundance of *H. lepidulum* in creeks and at increasing distances into adjacent forest and alpine habitats in seventeen creeks during January to May 2003 (Figure 1). In Avoca, creeks were stratified by distance up the main Avoca Valley, and ten creeks were randomly chosen for survey from NZ260 topographical maps such that creeks were sampled along the length of the Avoca. Only creeks longer than one kilometre, and that extended into the alpine, were included for selection. The lower reaches of the Avoca have been extensively burned and grazed, and were excluded from sampling. In Craigieburn, all seven creeks longer than one kilometre, and that were not excessively influenced by anthropogenic activities (ski fields, roads), were surveyed.

**Survey Design**

For each creek, transects running perpendicularly from the creek to 100 m into the adjacent vegetation were placed at 100 m intervals up the creek, beginning at a random point 0 to 50 m from the creek mouth, until either the creek habitat was no longer distinguishable from the surrounding alpine habitat, or the terrain became inaccessible. Each transect was placed on a random side of the creek. *Hieracium lepidulum* abundance and environmental variables were quantified in five plots along each transect located at: 1. a random point along the width of the creek bed (creek), 2. in the adjacent habitat, immediately on the edge of the creek bed boundary (edge), 3. at 10 m, 4. at 30 m, and 5. at 100 m into the adjacent habitat (Figure 3).

Plots were 2 m x 3 m (this size was chosen after a pilot study using different plot sizes showed that this size gave accurate estimate of mean abundance while being logistically manageable). Each 2 m x 3 m plot was subdivided into six 1 m x 1 m quadrats, and the number of *H. lepidulum* plants within each quadrat was counted. For the 2 m x 3 m plot, slope (°), aspect (°), altitude (m), percent overhead canopy cover, groundcover composition (vascular vegetation, bryophyte, litter, rock, and bare ground), and NZMS260 series topographical map grid coordinates were recorded. Canopy cover was visually assessed as a class (1. 0-25%, 2. 26-50%, 3. 51-75%, 4. 76-100%). Groundcover composition was recorded using a modified Braun-Blanquet cover scale (1. 0-1%, 2. 2-5%,
3. 6-25%, 4. 26-50%, 5. 51-75%, 6. 76-100%; (Payton and Moss 2001)). I also recorded the presence of disturbance on the plot (disturbances included treefall gaps, uproot mounds, landslips, or frost heaves).

Analysis

The Avoca and Craigieburn data were analysed independently because observations indicated that invasion was much more extensive in the Avoca.

1. **Does abundance of *H. lepidulum* decline with distance from creek?**

I first examined the spatial distribution of *H. lepidulum* by habitat, plotting mean density (number of plants/m²) of *H. lepidulum* versus distance from creek. I examined forest and alpine habitats separately, since I expected a stronger relationship between abundance and distance in forest than alpine habitats. I used Generalised Estimating Equations (GEEs) (Liang and Zeger 1986) to model the main effects of distance from creek, forest or alpine habitat, and an interaction between distance and forest or alpine habitat, on the abundance of *H. lepidulum* (expressed as the number of *H. lepidulum* per plot), fit with a negative binomial distribution. If prediction one is true, then this model will show a significant negative effect of distance from creek on *H. lepidulum* abundance. Generalised Estimating Equations were used because the data were clustered by transect, and therefore violated assumptions of independence; a negative binomial distribution was used to account for overdispersion (i.e., variance greater than the mean). Ideally, creek would also have been included as a random effect in the model to account for clustering by creek, however GEEs can only account for one clustering variable, so transect was the clustering variable and creek was added as an additional fixed effect.

To account for environmental gradients that could also potentially explain gradients in abundance of *H. lepidulum* with distance from creek, I tested for differences in plot environmental characteristics between creek plots and plots at each distance into the forest and alpine with ANOVA and Tukey's HSD tests when significant differences were found.

2. **Is the gradient in abundance of *H. lepidulum* with distance from creeks less steep in alpine habitat than in forest habitat?**
If prediction two is true, then the interaction term between distance and forest or alpine habitat in the above model will be significant, with a less negative estimate for the alpine habitat term than for the forest habitat term.

3. Is there a positive relationship between *H. lepidulum* abundance in creek habitat and *H. lepidulum* abundance in adjacent habitat?

I first examined the relationship between *H. lepidulum* abundance in creek habitats (expressed as the sum of the number of *H. lepidulum* in creek and edge plots) and abundance at 10 m, 30 m and 100 m into the forest and alpine along each transect using Spearman rank correlations. I then used a strength of evidence, model selection approach (Anderson and Burnham 2002, Burnham and Anderson 2002, Johnson and Kristian 2004) to determine whether *H. lepidulum* abundance at each distance into the forest or alpine was best explained by *H. lepidulum* abundance in adjacent creeks, by plot variables (overhead canopy, ground cover, slope, elevation and aspect relative to north), and/or by creek. This method assesses the strength of evidence provided by the data for each candidate model, rather than assessing arbitrary statistical significance as with null-hypothesis testing (Burnham and Anderson 2002). I first describe the set of candidate models I tested for the forest and alpine habitats, and then the procedures for model fitting and model selection.

**Models tested**

For the forest habitats I compared the fit of three models to the data. 1. Full model. This model tested the hypothesis that abundance of *H. lepidulum* at each distance into the forest was determined by both the abundance of *H. lepidulum* in the adjacent creek and by local plot variables. 2. Creek abundance. This model tested the hypothesis that the abundance of *H. lepidulum* in adjacent creek habitats alone best explained the abundance of *H. lepidulum* in the surrounding forest. 3. Local environment. This model tested the hypothesis that local plot variables best explained the abundance of *H. lepidulum* in the forest. Each of these three models was applied with and without creek included as a fixed effect. For the alpine habitats I tested four models. Because densities of *H. lepidulum* were higher in the forest, and thus forest populations might serve as a source of spread into the alpine zone, I included distance from tree line as an explanatory variable. 1. Full model. Same as above, but including distance from tree line. 2. Creek abundance. Same as above. 3. Local environment. Same as above. 4. Distance from tree line. This model tested the hypothesis
that distance from tree line alone best explained the abundance of *H. lepidulum* in alpine habitats.

**Model fitting**

In the forest, *H. lepidulum* abundances tended to be zero, low, or sometimes very high. I therefore used proportional odds regression (McCullagh 1980) with the number of *H. lepidulum* in a plot expressed as one of three categories (0, 1-25, > 25 plants/m²) as the response variable. In the alpine zone, where *H. lepidulum* was relatively rare, I used logistic regression to model the presence or absence of *H. lepidulum* in a plot. All statistical analyses used SAS version 8.0 (SAS Institute 1999).

**Model Selection**

Within the forest and alpine habitats, I used strength of evidence model selection criteria to select the model best supported by the data (Burnham and Anderson 2002, Johnson and Kristian 2004). I used AIC<sub>c</sub> values as the strength of evidence criteria for each hypothesis. AIC<sub>c</sub> is a small-sample bias correction for Akaike's Information Criterion (AIC), and should be used when the ratio of estimated model parameters to the number of observations is greater than 40 (Burnham and Anderson 2002). Models with the smallest AIC<sub>c</sub> have the most support (Burnham and Anderson 2002). I ranked models according to Akaike weights (w<sub>i</sub>):

(Eq. 1) \[ w_i = -\exp(\Delta AIC_i)/(\Sigma \Delta AIC) \]

Akaike weights provide an estimate of probability that a given model is the best fitting model of the candidate set (Burnham and Anderson 2002, Hobbs et al. 2003). When w<sub>i</sub> > 0.90, the model can be considered strongly supported by the data.

**Results**

**Prediction 1. Abundance declines with distance from creek**

As predicted, the abundance of *H. lepidulum* declined with distance from creek into adjacent habitat in both Avoca and Craigieburn (Figure 4). There was a significant negative slope parameter for the effect of distance on *H. lepidulum* abundance in the GEE model testing the main effects of distance from creek, forest or alpine habitat, and an
interaction between distance and forest or alpine habitat for both Avoca and Craigieburn (Table 1).

There was no gradient in plot characteristics with increasing distance into the forest; instead the main differences in plot characteristics were between creek and forest habitats (Tukey’s HSD tests, \( P < 0.05 \)). Creek plots had lower overhead canopy cover, lower moss and litter cover, and more rock and vascular plant ground cover than forest interiors in both Avoca and Craigieburn (Tukey’s HSD tests, \( P < 0.05 \)). There was a trend for more bare ground in creek than forest plots, but it was not significant (Tukey’s HSD tests, \( P > 0.05 \)).

In the alpine, there also was no gradient in plot characteristics beyond the creek, and the distinction between creek and alpine habitats was not as strong. In Avoca, creek plots had lower moss and greater rock cover than non-creek plots (Tukey’s HSD tests, \( P < 0.05 \)), but there were no consistent differences in vascular or bare ground cover between creek and non-creek plots (Tukey’s HSD tests, \( P > 0.05 \)). There were no differences between creek and non-creek plots in Craigieburn (Tukey’s HSD tests, \( P > 0.05 \)).

**Prediction 2. Abundance gradient less steep in alpine**

The GEE model showed a significant interaction between distance and forest or alpine habitat, indicating that the effect of distance on *H. lepidulum* abundance differs between the forest and alpine (Figure 4, Table 1). The slope estimate for this interaction term was not positive for the alpine, but was negative for the forest habitat, thus prediction two, that the decline in *H. lepidulum* abundance with distance from creek would be less steep in the alpine, was supported.

**Prediction 3. Abundance in creeks predicts *H. lepidulum* abundance in adjacent forest and alpine habitats**

As predicted, the abundance of *H. lepidulum* in combined creek and edge plots was positively correlated with abundance in both forest and alpine habitats in Avoca and Craigieburn, with the strength of that correlation declining with increasing distance away from the creek (Table 2). These results are consistent with the hypothesis that creek populations are acting as sources for spread of *H. lepidulum* into adjacent habitats.
The model selection results supported these trends. Models that included creek abundance as a variable explaining of *H. lepidulum* abundance in the forest or *H. lepidulum* presence in the alpine zone were either best-supported by the data, or when they were not, it was at 30 or 100 m into the adjacent habitat (Table 3, 5) where creek abundance would be expected to have less of an effect. In Avoca forests, *H. lepidulum* abundance was explained by both the abundance of *H. lepidulum* in the creek and local plot variables, with the full model strongly supported for all distances (Tables 3, 4). In Craigieburn forests, the abundance of *H. lepidulum* at 10 m away from the creek was explained by *H. lepidulum* abundance in the creek only, while at 30 m, local plot variables best explained abundance and *H. lepidulum* abundance in the creek had no effect (Tables 3, 4). Models would not converge at the 100 m distance in Craigieburn forests; only eight out of 93 plots were invaded at this distance.

In Avoca alpine habitat, the presence of *H. lepidulum* on plots at 10 m and 30 m away from the creek was best predicted by *H. lepidulum* abundance in the creek only, while at 100 m away, local plot variables best explained *H. lepidulum* presence (Table 5). In Craigieburn alpine habitats, I could fit the model only at 10 m because there were so few invaded plots at 30 m or 100 m (4 out of 24 in each). Here, the presence of *H. lepidulum* was best predicted by the distance from tree line model (Table 5), with *H. lepidulum* more likely to occur on plots closer to tree line (though this effect was weak) (Table 6). I tested for correlations between distance from tree line and plot variables in the alpine to test whether there were consistent changes in plot variables with distance from tree line. Bare ground increased with increasing distance from tree line (r = 0.29, P < 0.05), but there were no other significant gradients in plot variables (Spearman rank correlations, P < 0.05).

When local plot variables were included in models predicting *H. lepidulum* abundance in the forest, plots with less overhead canopy cover, more bare ground and rock, and less litter on the ground, and that were on steeper slopes, consistently had higher abundances of *H. lepidulum* (Table 4). An open canopy, high bare ground and low litter cover suggest a preference for disturbed sites; this was supported by a significant association of *H. lepidulum* presence with disturbed sites like canopy gaps and slips within the forest (Avoca $X^2_1 = 64.97, P < 0.0001$); Craigieburn $X^2_1 = 31.21, P < 0.0001$). In contrast, alpine plots with more moss cover and less bare ground were more likely to be invaded by *H.
*lepidulum* (Table 6), indicating that perhaps a requirement for shelter rather than disturbance is important for *H. lepidulum* spread in the alpine.

**Discussion**

I tested the hypothesis that creek habitats function as source habitats for the spread of *H. lepidulum* into surrounding habitats in the mid-Canterbury, Southern Alps landscape by testing three predictions about the relative abundance of *H. lepidulum* in creek and adjacent habitats. As predicted, *H. lepidulum* abundance declined in a pattern of decay from creeks into adjacent forest; and the abundance of *H. lepidulum* in creeks predicted abundance of *H. lepidulum* in adjacent forest. In the alpine zone, abundance of *H. lepidulum* in creek habitats was not higher than in adjacent alpine habitats; rather, *H. lepidulum* was sparsely distributed among all alpine habitats. I predicted that there would be less of a gradient in *H. lepidulum* abundance in the alpine due to the lack of a dispersal barrier; however, given the low abundance of *H. lepidulum* measured in the alpine, I cannot say whether the data is reflecting the lack of a source habitat in creeks, or the lack of a dispersal barrier. *Hieracium lepidulum* was more likely to be present on alpine plots at 10 and 30 m away from creeks when abundance in creek populations was higher, suggesting that creeks may act as sources for spread.

My results are consistent with the hypothesis that creek habitats function as sources for *H. lepidulum* invasion throughout the wider landscape. They are also consistent with results of other studies that show creeks acting as source habitats for invasive spread (e.g., Gregory et al. 1991, Pyšek and Prach 1993, DeFerrari and Naiman 1994, Lesica and Miles 2001).

By itself, this knowledge is important, as it provides a management focus for controlling *H. lepidulum* spread. However, more could be gleaned from an understanding of how the components contributing to establishment, population growth and spread of *H. lepidulum* underlie the spatial distribution patterns that I observed. In particular, do the spatial patterns reflect differences in the resistance of habitats to invasion by *H. lepidulum*, and/or differences in the rate at which *H. lepidulum* disperses into those habitats?

**Resistance to invasion**

Forest creeks appear to be less resistant to *H. lepidulum* invasion than the forest interior. Forest creek plots had an open canopy cover, less litter, and more bare ground, variables
that also predicted higher abundances of *H. lepidulum* within the forest. Light levels and disturbance were correlated with higher levels of exotic plant invasion among creeks in an Oregon forest system (Parendes and Jones 2000); higher light and higher levels of soil disturbance could likewise explain why forest creek habitat is more suitable than forest interior habitat for *H. lepidulum*. If present, this difference in habitat resistance to invasion would set up a source-sink relationship between forest creeks and forest interior that would result in a decline in abundance of *H. lepidulum* with distance from creek.

In the alpine zone, plot differences between creek and alpine interior habitats were less pronounced, and the lack of higher abundance of *H. lepidulum* in alpine creek relative to adjacent alpine habitat suggests that alpine creeks do not differ in resistance to invasion by *H. lepidulum* from the alpine interior. Therefore, in the alpine, the absence of a source-sink relationship driven by differences in resistance to invasion, could explain the even distribution of *H. lepidulum* in the alpine.

*Hieracium lepidulum* in Craigieburn alpine vegetation was more frequent closer to tree line, suggesting spread from forest populations; however, differences in resistance to invasion could also explain the scarcity of *H. lepidulum* in the alpine relative to the forest with the alpine perhaps relatively inhospitable habitat for *H. lepidulum*.

**Dispersal**

Differences in dispersal could also explain the patterns observed. In forests, creeks may act as a tunnel for wind (and thus wind dispersed seeds), while dispersal into the forest can be inhibited by the physical barrier of the forest edge, and further dispersal within the forest inhibited by low wind speeds under the forest canopy (Willson and Crome 1989, Brothers and Spingarn 1992, Parendes and Jones 2000, Cadenasso and Pickett 2001). Thus, the steep decline in abundance of *H. lepidulum* with distance into the forest could reflect a paucity of seeds dispersing into the forest, and low dispersal from established forest populations relative to dispersal rates in creeks.

In the alpine zone, the open structure of the vegetation means that creeks may not function as a dispersal corridor as they do in the forest, with seeds free to disperse throughout the alpine zone. This could also explain the even distribution of *H. lepidulum* among alpine habitats.
Spread dynamics

Thus, the uneven distribution of *H. lepidulum* among habitats could equally be explained as 1. A static, ‘spatial mass’ effect driven by high abundance of *H. lepidulum* in forest creeks (Levine and Rees 2002, Brown and Fridley 2003, Holway 2005). This would be the case if habitat resistance to invasion by *H. lepidulum* in forest and/or alpine habitats was high enough that population growth of *H. lepidulum* in these habitats could not be maintained without propagule addition from creek populations. For management, this would be the best case scenario, as forest creeks could be the major target for *H. lepidulum* control. 2. A dynamic front of *H. lepidulum* moving into the forest and into the alpine zone driven by propagule supply from the creek. This would arise if dispersal limitation rather than habitat resistance was responsible for the low abundance of *H. lepidulum* in forest and alpine habitats, and with time, populations of *H. lepidulum* would build and spread. 3. A dynamic front of *H. lepidulum* moving into the forest and into the alpine zone driven by variable habitat resistance, where higher resistance to *H. lepidulum* invasion in forests and/or alpine habitats leads to slower rates of spread in those habitats relative to creeks, but they are still capable of sustaining stable populations. 4. A combination of the three scenarios, where both differences in habitat resistance and differences in dispersal patterns underlie the spatial distribution patterns. This is the most likely explanation, as differences in vegetation structure among habitats in this landscape would very likely give rise to variation in dispersal and thus spread patterns (Greene and Calogeropoulos 2002, Nathan et al. 2002, Bullock et al. 2003, Tackenberg 2003, Nuttle and Haefner 2005); and, because of likely differences in abiotic resources and biotic interactions, resistance to invasion is also bound to vary with habitat (Elton 1958, Rejmánek 1989, Richardson et al. 2000).

To better understand how creek habitats function as sources for the spread of *H. lepidulum* across this landscape, a key step is to determine the extent to which habitat resistance to *H. lepidulum* invasion and dispersal limitation underlie the uneven distribution of *H. lepidulum* among creek, forest and alpine habitats. This would determine the extent to which the current patterns reflect a static situation, or a dynamic front. In the next chapter, I use seed-addition experiments to overcome dispersal limitation and test how habitat resistance determines establishment of *H. lepidulum*. Differences in plant performance following establishment could also partly explain the uneven distribution of *H. lepidulum* among habitats; in chapter five I determine how plant performance in established
populations varies among habitats. In Chapter six I compare within habitat dispersal patterns among habitats.

References


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Table 3.1. Results of Generalised Estimating Equations fit with a negative binomial error distribution, showing the significance of distance from creek, forest or alpine habitat, and a distance*habitat interaction on the abundance of *H. lepidulum*, with transect included as a clustering variable. Negative parameter estimates indicate a negative effect on abundance. Creek was included as an additional fixed effect, and was significant in both locations (results not shown).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Avoca</th>
<th>Craigieburn</th>
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<td>Estimate Z P</td>
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<tr>
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Table 3.2. Spearman correlation coefficients between the mean log of the sum of the number of *H. lepidulum* in the combined creek and edge plots, and at 10 m, 30 m, and 100 m into the adjacent forest and alpine habitats.

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<th>Distance (m)</th>
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Table 3.3. Akaike weights (*w_i*) for models predicting the abundance of *H. lepidulum* at 10 m, 30 m and 100 m into the forest in Avoca and Craigieburn. All models were fit with and without creek added as a fixed effect, and since all were improved by the addition of this effect, only models that include this effect are reported. Best-fitting models (highest *w_i*), are in bold.

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<thead>
<tr>
<th>Distance</th>
<th>Model</th>
<th>Avoca</th>
<th>Craigieburn</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>Full</td>
<td>0.9999</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>Creek abundance</td>
<td>0</td>
<td>0.98</td>
</tr>
<tr>
<td></td>
<td>Local environment</td>
<td>0.0001</td>
<td>0.01</td>
</tr>
<tr>
<td>30</td>
<td>Full</td>
<td>0.96</td>
<td>0.27</td>
</tr>
<tr>
<td></td>
<td>Creek abundance</td>
<td>0.00</td>
<td>0.26</td>
</tr>
<tr>
<td></td>
<td>Local environment</td>
<td>0.04</td>
<td>0.47</td>
</tr>
<tr>
<td>100</td>
<td>Full</td>
<td>0.91</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Creek abundance</td>
<td>0.00</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Local environment</td>
<td>0.09</td>
<td>convergence</td>
</tr>
</tbody>
</table>
Table 3.4. Parameter estimates (1 SE) from the best-fitting proportional odds model describing *H. lepidulum* abundance at 10 m, 30 m and 100 m into the forest in Avoca and Craigieburn. The response variable was categorical: 0, 1-25, >25 plants/m$^2$. (.) = the variable was not present in the best-fitting model. Positive parameter estimates indicate a positive effect on *H. lepidulum* abundance, while negative parameter estimates indicate a negative effect on *H. lepidulum* abundance.

<table>
<thead>
<tr>
<th>Location</th>
<th>Parameter</th>
<th>Parameter Estimate (1 SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avoca</td>
<td>Creek abundance</td>
<td>1.13 (0.36) 0.045 (0.18) 0.55 (0.26)</td>
</tr>
<tr>
<td></td>
<td>Overhead canopy</td>
<td>-0.69 (0.4) -0.81 (0.33) -0.93 (0.42)</td>
</tr>
<tr>
<td></td>
<td>Moss</td>
<td>-1.24 (0.4) 0.12 (0.40) 0.09 (0.41)</td>
</tr>
<tr>
<td></td>
<td>Litter</td>
<td>-1.49 (0.53) -0.47 (0.29) -0.45 (0.37)</td>
</tr>
<tr>
<td></td>
<td>Bare ground</td>
<td>0.27 (0.61) 0.60 (0.40) 0.57 (0.43)</td>
</tr>
<tr>
<td></td>
<td>Rock</td>
<td>0.49 (0.38) 0.23 (0.33) 0.54 (0.48)</td>
</tr>
<tr>
<td></td>
<td>Slope</td>
<td>0.037 (0.03) 0.041 (0.027) 0.058 (0.06)</td>
</tr>
<tr>
<td>Craigieburn</td>
<td>Creek abundance</td>
<td>0.22 (0.11) . . no convergence</td>
</tr>
<tr>
<td></td>
<td>Overhead canopy</td>
<td>. -0.50 (0.24) .</td>
</tr>
<tr>
<td></td>
<td>Moss</td>
<td>. -0.42 (0.40) .</td>
</tr>
<tr>
<td></td>
<td>Litter</td>
<td>. -0.73 (0.47) .</td>
</tr>
<tr>
<td></td>
<td>Bare ground</td>
<td>. -0.14 (0.35) .</td>
</tr>
<tr>
<td></td>
<td>Rock</td>
<td>. 0.007 (0.28) .</td>
</tr>
<tr>
<td></td>
<td>Slope</td>
<td>. 0.016 (0.026) .</td>
</tr>
</tbody>
</table>
Table 3.5. Akaike weights ($w_i$) for models predicting the presence of *H. lepidulum* at 10 m, 30 m and 100 m into the alpine in Avoca and Craigieburn. All models were fit with and without creek added as a fixed effect, and since all were improved by the addition of this effect, only models that include this effect are reported. Best-fitting models (highest $w_i$), are in bold.

<table>
<thead>
<tr>
<th>Distance</th>
<th>Model</th>
<th>Avoca</th>
<th>Craigieburn</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>Full</td>
<td>0.27</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Creek abundance</td>
<td>0.60</td>
<td>0.15</td>
</tr>
<tr>
<td></td>
<td>Local environment</td>
<td>0.02</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Distance from treeline</td>
<td>0.10</td>
<td>0.84</td>
</tr>
<tr>
<td>30</td>
<td>Full</td>
<td>0</td>
<td>no convergence</td>
</tr>
<tr>
<td></td>
<td>Creek abundance</td>
<td>0.63</td>
<td>0.79</td>
</tr>
<tr>
<td></td>
<td>Local environment</td>
<td>0.02</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>Distance from treeline</td>
<td>0.35</td>
<td>0.20</td>
</tr>
<tr>
<td>100</td>
<td>Full</td>
<td>0.05</td>
<td>no convergence</td>
</tr>
<tr>
<td></td>
<td>Creek abundance</td>
<td>0.04</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Local environment</td>
<td>0.88</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Distance from treeline</td>
<td>0.03</td>
<td></td>
</tr>
</tbody>
</table>

Table 3.6. Parameter estimates (1 SE) from the best-fitting logistic regression model explaining *H. lepidulum* presence at 10 m, 30 m and 100 m into the alpine. (.) = the variable was not present in the best-fitting model. Positive parameter estimates indicate a positive effect on the presence of *H. lepidulum* on a plot, while negative parameter estimates indicate a negative effect on *H. lepidulum* presence.

<table>
<thead>
<tr>
<th>Location</th>
<th>Parameter</th>
<th>Parameter Estimate (1 SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avoca</td>
<td>Creek abundance</td>
<td>0.50 (0.22)</td>
</tr>
<tr>
<td></td>
<td>Moss</td>
<td>.</td>
</tr>
<tr>
<td></td>
<td>Litter</td>
<td>.</td>
</tr>
<tr>
<td></td>
<td>Bare ground</td>
<td>.</td>
</tr>
<tr>
<td></td>
<td>Rock</td>
<td>.</td>
</tr>
<tr>
<td></td>
<td>Slope</td>
<td>.</td>
</tr>
<tr>
<td>Craigieburn</td>
<td>Creek abundance</td>
<td>-0.071 (0.49)</td>
</tr>
<tr>
<td></td>
<td>Distance up creek</td>
<td>-0.006 (0.0032)</td>
</tr>
</tbody>
</table>

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Figure 3.1. Proposed model of the spread of *H. lepidulum* through the study area landscape, with creek habitats acting as sources for the spread of *H. lepidulum* from induced lowland tussock grasslands into adjacent beech forest and up into alpine habitats.
Figure 3.2. Location of study area (Avoca and Craigieburn), with the seventeen surveyed creeks in bold and indicated by an asterisk.
Figure 3.3. Survey design. Transects were placed at 100 m up each surveyed creek. Transects extended perpendicularly from the creek 100 m into adjacent forest or alpine habitat. Five 2 m x 3 m plots were placed along each transect (1. creek bed, 2. edge, 3. 10 m, 4. 30 m, and 5. 100 m into the adjacent habitat).
Figure 3.4. The relationship between distance from creek habitat and the density of *H. lepidulatum* in adjacent forest and alpine habitats in Avoca and Craigieburn. Mean density of *H. lepidulatum* on a plot (plants/m²) ± 1 SE is plotted at 0 m, 5 m, 10 m, 30 m, and 100 m distances into the forest or alpine habitat. 0 m is in the creek habitat, 5 m is on the edge of the creek habitat, and 10, 30 and 100 m are in the adjacent forest or alpine habitat (n = number of transects).
Chapter 4.

Using dose-response curves to quantify habitat resistance to the establishment of an invasive herb: an experimental test

Introduction


Understanding why and how habitats differ in resistance to the establishment of invasive species requires controlling for the confounding effect of variation in propagule supply rate. This has been done using multivariate statistical techniques (e.g., Hutchinson and Vankat 1997, Wiser et al. 1998, Rouget and Richardson 2003, Foxcroft et al. 2004), or experimentally, by measuring relative establishment success in different habitats at some constant rate of propagule supply (e.g., D'Antonio 1993, Levine 2001, Meekins and McCarthy 2001, Lambrinos 2002). Alternatively, a more thorough understanding of invasion resistance could derive from understanding how propagule supply rate interacts with invasion resistance to determine successful establishment. This is because the establishment response is likely to vary with invasion resistance as some function of propagule supply rate (D'Antonio et al. 2001, Ruiz and Carlton 2003, Lockwood et al. 2005). For example, high propagule supply rates may overcome invasion resistance so that all habitats have a high probability of an invader establishing, with differences in resistance among habitats more evident at lower supply rates. Conversely, high propagule supply rates may have a strong affect on invasion outcomes in some habitats but little affect in others (D'Antonio et al. 2001).

The relationship between propagule supply rate and establishment success is described by a dose-response curve (Ruiz and Carlton 2003, Lockwood et al. 2005) (Figure 1). A comparative dose-response approach, for example, comparing how curves differ among habitats, allows us to describe how propagule supply interacts with invasion resistance to determine establishment success (Ruiz and Carlton 2003, Lockwood et al. 2005). Thus, this approach provides the means to quantify differences in invasion resistance to establishment among habitats.

The interaction between propagule supply rate and habitat resistance to establishment can be described by differences in the functional shape of the dose-response curve and/or changes in curve parameters (Figure 1). Habitats might exhibit one of two functional shapes that represent different mechanisms of limitation: a linear shape (seed limitation) and a saturating shape (seed then safe site limitation). A linear shape indicates that establishment is proportional to propagule supply, i.e., that ‘seed limitation’ regulates the number of individuals that establish (Eriksson and Ehrlen 1992, Turnbull et al. 2000). A saturating shape indicates that a threshold has been passed, beyond which additional seeds
do not lead to further establishment, implying that safe site limitation \textit{(sensu} Grubb 1977, Harper 1977\textit{)} also regulates the number of individuals that establish.

The parameters of the dose-response curve include the slope, or rate of establishment for a given propagule supply, and the asymptote, or propagule supply rate beyond which additional propagule addition ceases to result in additional establishment (saturation density). The magnitude of these parameters reflects the degree of habitat resistance to establishment. For example, a shallow slope indicates that high rates of propagule supply are required for a given level of establishment, implying high resistance. For invasive plants high resistance could reflect low abiotic resource availability (e.g., Huenneke et al. 1990, Davis et al. 2000, Davis and Pelsor 2001, Denslow 2003), low relative availability of suitable microsites for establishment (Fowler 1986, Eriksson and Ehrlen 1992, Coulson et al. 2001, Boyd and Van Acker 2004, Manning et al. 2004), high levels of competition or natural enemies, or low mutualist abundance (Richardson et al. 2000, Levine et al. 2004). A low saturation density implies that safe site limitation of establishment is high (e.g., Edwards and Crawley 1999b). For plants, safe site limitation is predicted to be stronger in communities where resident species biomass or species richness is high because of more intense competition for suitable sites for establishment (Crawley 1986, Rejmanek 1989, Burke and Grime 1996, Turnbull et al. 2000, Zobel et al. 2000, Foster et al. 2004, Smith et al. 2004). However, sheltering microsites that ameliorate harsh climatic conditions such as extreme aridity or cold, may be provided by resident vegetation (Hunter and Aarssen 1988, Greenlee and Calloway 1996, Smith et al. 2004), and greater species richness may provide a more diverse range of suitable microsites (Wiser et al. 1998, Lortie and Turkington 2002). Safe site limitation could result from the groundcover characteristics that contribute to safe site availability. For example, a ground cover dominated by rocks will potentially limit establishment more effectively than resident vegetation.

In addition to providing a means to quantify habitat resistance to establishment of invasive species, the dose-response curve provides a means to evaluate the relative contribution of potential mechanisms of resistance. For example, correlation of the parameters of the dose-response curve with environmental variables can indicate how abiotic resource availability or competition with resident species determines overall resistance to establishment or safe site availability. Or, a documentation of how the dose-response curve changes over time can indicate the relative importance of processes acting on different stages of establishment.
(e.g., seed germination versus seedling mortality). Quantitative data describing how the dose-response relationship changes with habitat to determine invasion outcomes are nonexistent (Ruiz and Carlton 2003, Lockwood et al. 2005). This is despite the singular ability of the dose-response relationship to disentangle how invasion resistance and propagule supply determines establishment of invasive species, and the wealth of practical information that the dose-response relationship offers.

*Hieracium lepidulum* (Asteraceae) is an invasive exotic plant in the South Island, New Zealand high country. My previous work has shown that *H. lepidulum* is unevenly distributed among upland habitats: abundance in forest creeks and forest canopy gaps is high relative to intact forest, and abundance in forest habitats is higher than in alpine habitats (tussock grasslands, alpine creeks and subalpine scrub) (Chapter 3). One explanation for these differences is that habitats differ in their invasion resistance. Here, I test the hypothesis that the dose-response relationship between seed sowing density and seedling establishment varies among six habitats (forest creek, intact forest, canopy gap, alpine creek, tussock grassland, subalpine scrub), and, because this variation implies differences in habitat resistance, that this could explain the uneven distribution of *H. lepidulum* across habitats. More specifically, I test five competing hypotheses concerning how habitats might differ in resistance to establishment based on the current spatial distribution of *H. lepidulum*: 1. There is no difference among the six habitats in their resistance to establishment, and the current uneven distribution of *H. lepidulum* among habitats presumably then results from variation in propagule supply rate. 2. Each of the six habitats differs from all others in resistance to establishment. 3. Forest habitats (forest creek, intact forest and canopy gap) are less resistant to establishment of *H. lepidulum* than alpine habitats (alpine creek, tussock grassland and subalpine scrub). 4. Forest habitats do not differ in resistance to *H. lepidulum* establishment, implying that the uneven distribution among forest habitats results from variation in propagule supply rate. 5. Forest creeks and canopy gaps are less resistant to *H. lepidulum* establishment than intact forest.

I use the following framework to test these hypotheses: First, I construct dose-response curves by sowing different densities of seed into each of the six habitat types and recording the number of seedlings that establish. Second, I quantify the dose-response relationships by fitting a general recruitment model to the data that allows the dose-response curve to take a linear or saturating shape. Third, I test how the shape and/or model parameters differ
among habitats using a model selection process. Fourth, I correlate parameters of the dose-response curve with environmental variables to explore how environmental factors may explain differences in establishment resistance among habitats.

**Methods**

**Field Site**

This study was carried out in the upper reaches of Craigieburn Stream, in Craigieburn Forest Park, in the mid-Canterbury region of the Southern Alps, New Zealand (43°10'S, 172°45'E). This park is managed for recreation and conservation. The landscape is mountainous with elevations spanning 800 m to 2000 m. The mean annual temperature is 8.2°C and mean annual precipitation is 1532.7 mm (1964–2005 MetStation records, unpub. data, Landcare Research Inc.). Soils are recent or high-country yellow brown earths (Anonymous 1968). Mountain beech forest (*Nothofagus solandri* var. *cliffortiodes*) dominates from ~ 650 m to 1400 m elevation, and gives way to subalpine scrub, tussock grasslands (grasslands dominated by long-lived, bunch-forming *Chionochloa* spp.) and alpine herb fields at higher elevations.

**Experimental Design**

**Seed density manipulation**

I used seven seed density treatments to construct dose-response curves: control with no seed addition and no initial wetting, procedural control with no seed addition but with wetting, and seed addition at rates of 25, 125, 625, 3125 and 15625 seeds per 30 by 30 cm plot with wetting. (These seed addition rates translate to 278, 1389, 6944, 34722, and 173611 seeds/m²). Wetting was used to prevent the seeds from blowing away during seed addition. These seed addition levels were chosen because, at the lower end, they encompass seed output densities likely to occur in the wild given the observed number of seeds produced per plant and the average densities of wild plants (unpublished data). Densities at the upper end were probably much higher than would normally be encountered in the wild, but allowed me to quantify the saturation density. The number of seeds used in the lower seed density treatments were counted (25 and 125), while the higher seed density treatments (625, 3125 and 15625) were based on mean weights taken from twenty replicates of 100 seeds. The control treatments rarely had seedlings establish, and were not included in the analysis.
Seed was collected in field during the same season as seeds were sown, from the lower reaches of the Avoca River, close to the study area. I used a single location to minimise potential variation in seed viability.

**Experimental lay-out**

To determine if and how the functional shape and/or parameters of the dose-response curve varied among habitats, the seed density treatments were applied to each of six habitats (forest creek, intact forest, canopy gap (treefall gaps), alpine creek, tussock grassland, subalpine scrub). To test the generality of the results, I conducted the seed-sowing experiment in two consecutive years (termed the ‘2003 cohort’ and ‘2004 cohort’). Both experiments were set out using the same randomised block design (the second experiment was sown adjacent to the first), with six replicate blocks in each of the six habitat types.

For forest creek and alpine creek habitat, blocks were located a random distance up Craigieburn Stream, with the forest creek blocks below tree line and the alpine creek blocks in a tussock grassland basin above tree line. For intact forest and tussock grassland habitat, blocks were located a random distance up Craigieburn Stream and a random distance into the forest or tussock habitat, with the latter distance no less than 20 m (to ensure the habitat was not strongly influenced by the creek) and no more than 200 m (for logistical reasons). Canopy gap blocks were located at the nearest gap greater than 25 m² a random distance up the creek and a random distance into the forest, as above. Scrub habitat blocks were randomly selected from all scrub patches within the study catchment, thus avoiding bias due to a non-uniform distribution of small and large scrub patches.

Each block comprised three replicate plots (30 cm x 30 cm) of each of the seven seed density treatments, randomly positioned in a 16-m² area such that there was at least a 30 cm buffer between each plot. Seed density treatments were randomly assigned to each plot following plot placement. Plots were permanently marked with two labelled corner pegs. Any *H. lepidulum* plants naturally occurring in, or within 20 m of the edge of the block were removed to minimise natural seed dispersal onto the plots. The 2003 cohort was sown in March 2003, and the 2004 cohort in March 2004.
Establishment response

To quantify the establishment response to seed-sowing density, the number of seedlings present per plot was censused at monthly intervals from December 2003 to April 2004 and from December 2004 to April 2005. For plots with very high seedling densities, a quadrat divided into a 1-cm x 1-cm grid was used and 20 1-cm cells were randomly selected for counting. No attempt was made to tag individual seedlings. In the second spring for the 2003 cohort, newly emerged seedlings could be separated from the first years surviving seedlings, and the number of these new recruits was recorded. Otherwise, counts represent both new recruitment and seedling survival.

Environmental data

To identify environmental factors that might account for differences in the shape and/or parameters of the dose-response curve among habitats, I measured light (% PPFD), soil fertility (pH, C:N ratio, nitrogen, phosphorous, % base saturation), soil moisture, ground cover and species composition. Soil fertility and moisture were measured at the block level, while light, ground cover and species composition were measured at the plot level.

Light was measured using the percentage of photosynthetic photon flux density reaching the site (% PPFD) under overcast skies. Fifteen instantaneous light measurements \( Q_i \) were taken at 1 cm above ground level over the centre of each plot using point quantum sensors (LI-190SA, LICOR, Lincoln, NE, USA). Outside (i.e., open) light conditions \( Q_o \) were logged continuously throughout the measurement period using two quantum sensors linked to a datalogger (LI-1400, LICOR) that recorded one-minute averages. Light conditions within each plot (%PPFD) were then calculated as \( Q_i/Q_o \times 100 \) by matching the time at which data were recorded.

Four soil samples were collected from just outside the corner of each block using a 10-cm soil corer. The four samples from each block were bulked, a 5 g sample was removed to calculate gravimetric soil moisture content, and the remainder was air-dried, sieved and analysed for pH, Olsen-soluble phosphorous, base saturation (%), and total carbon and total nitrogen. Total carbon and nitrogen were measured using a Leco CNS-2000 Analyser. Soil moisture content (smc) was measured using gravimetric analysis:
Within each plot, ground cover (vascular, bryophyte, litter, bare ground, and rock) was recorded using a modified Braun-Blanquet cover scale (1. 0-1% 2. 2-5% 3. 6-25% 4. 26-50% 5. 51-75% 6. 76-100% (Payton and Moss 2001)). Plot vascular plant cover was recorded at the understorey level (i.e., all vascular cover below 2.5 m), and did not include overhead canopy cover. All vascular plant species present in each plot were recorded.

**Analysis**

**Describing the dose-response curve: Beverton-Holt recruitment model**

I used a two-parameter Beverton-Holt recruitment model to describe the dose-response relationship between seed sowing density and seedling establishment of *H. lepidulum*.

(Eq. 2) \[ E = \frac{aS}{1 + aS/b} \]

Where \( E \) is the number of seedlings establishing from a seed sowing density of \( S \). The parameter \( a \) describes the slope, or the rate of seedling establishment given a supply of seeds, and \( b \) describes the asymptote, or the saturation density at which seed addition ceases to result in additional seedling establishment. This model has been used extensively in fisheries science to determine recruitment rates given spawning abundance, and to estimate carrying capacity (saturation density) (Myers 1983, 2001, Myers et al. 2001, Barrowman et al. 2003, Gibson and Myers 2003). It has also been used to investigate the importance of density-independent and density-dependent regulation of coral reef fish recruitment (Wilson and Osenberg 2002, Schmitt et al. 2003, Shima and Osenberg 2003).

The Beverton-Holt model is flexible enough to allow the functional shape of the dose-response curve to be linear (by setting \( b \to \infty \)) or saturating. Thus, it can be used where there are differences in the functional shape among habitats. Additionally, by testing
whether a linear shape (i.e., setting $b \to \infty$) or a saturating shape best describes the dose-response relationship, I could determine whether establishment was seed limited (linear shape) or seed and safe site limited (saturating shape). I expected that a saturating shape would best describe the establishment response, as I purposely sowed seed at densities high enough to force saturation; however, given that I did not a priori know what saturation densities were, I was not guaranteed of finding saturation.

**Habitat Resistance Hypotheses**

I tested five hypotheses (Table 1) about how resistance to *H. lepidulum* establishment might vary among habitats, based on the observed spatial distribution of *H. lepidulum* in the study landscape (Chapter 3). 1. *Uniform (U)*. There is no difference among habitats in their resistance to establishment, implying that the current uneven distribution of *H. lepidulum* results from limited dispersal into some habitats. If this is the case, I expect the same dose-response relationship in all habitats, and seedling establishment should vary as a function of seed density only. The remaining hypotheses test for differences among habitats in establishment resistance. 2. *Habitat (H)*. Each habitat differs from the others in resistance to *H. lepidulum* establishment and the current uneven distribution of *H. lepidulum* among habitats results at least in part from these differences. I therefore expect each habitat to differ uniquely in the magnitude of dose-response curve parameters and/or in the functional shape of the curve, and I test this by including a variable coding for the six different habitat types as a determinant of the dose-response curve parameters (see Table 1). 3. *Forest-Alpine (FA)*. Alpine habitats are more resistant to *H. lepidulum* establishment than forest habitats, and this broad-scale difference between forest and alpine habitats explains the relatively low density of *H. lepidulum* in alpine habitats. If this is true, I expect the parameters of the dose-response curve to be lower in alpine habitats than forest habitats, and within alpine and within forest differences among habitats will be small. I test this by including a variable coding for a ‘forest’ habitat (forest creek, forest and canopy gap) and an ‘alpine’ habitat (alpine creek, tussock grassland and scrub) as a determinant of the dose-response curve parameters as above. 4. *Forest equivalent (F)*. Forest habitats do not differ in resistance to *H. lepidulum* establishment, thus the uneven distribution among forest habitats reflects dispersal limitation into intact forest relative to canopy gaps and forest creeks. I therefore expect the same dose-response relationship among the three forest habitats, and I test this by including a variable coding for ‘forest’ (forest creek, forest and canopy gap), and for each of the three alpine habitats (the spatial
distribution of *H. lepidulum* among alpine habitats provides no *a priori* reason for assuming differences in resistance to invasion in the alpine habitats), as a determinant of the dose-response curve parameters as above. 5. *Disturbed forest* (D). Forest creeks and canopy gaps are less resistant to *H. lepidulum* establishment than intact forests, and this at least partially explains the uneven distribution among forest habitats. If this is the case, I expect similar dose-response curve parameters between forest creek and canopy gap habitats, and for these ‘disturbed’ forest habitats to differ from intact forest. I test this last hypothesis by including a variable coding for ‘disturbed forest’ (forest creek and canopy gap), intact forest and each alpine habitat as a determinant of the dose-response curve parameters.

**Model fitting and selection**

*Model fitting*

I used a mixed-modelling approach (e.g., Pinheiro and Bates 2000) with block included as a random effect to account for non-independence of block level data (Hurlbert 1984). This approach allows model parameters to vary around an overall mean with a separate intercept for each block, and thus has the added benefit of accounting for unexplained block-level variation without losing statistical power by including block as a fixed effect (Millar and Anderson 2004).

To test if and how the functional shape (linear or saturating) and parameters controlling the slope (*a*, establishment rate) and asymptote (*b*, saturation density) of the dose-response curve vary with habitat, I fit each of the above five models to each of the two functional shapes (linear and saturating) of the Beverton-Holt model. For the linear functional shape, the slope parameter (*a*) could vary with habitat or block, thus I vary the slope (*a*) according to the habitat resistance hypothesis being tested (Table 1). For the saturating functional shape, the slope (*a*), the asymptote (*b*), or both could vary with habitat or block. Therefore, for each habitat resistance hypothesis, I vary either the slope (*a*), the asymptote (*b*) or both together. Since I could include only one random effect in each model, I first compared models with the random block effect added to either the slope or asymptote. Because models with the random effect included in the asymptote were not well supported (see Results), I include the random block effect in the slope when both the slope and asymptote vary.
I defined three establishment phases: 1. Initial seedling emergence, 2. Seedling survival after one summer’s growth, and 3. Final seedling establishment two years after seed was sown. I did this to allow detection of differences in the relative importance of mechanisms limiting establishment among habitats (e.g., differences in initial germination rates versus differences in seedling mortality rates). For each establishment phase, I fit each resistance model, each functional shape, and each curve parameter variation \((a, b, \text{or both varying})\). For this chapter, data were collected only up to survival after one summer for the 2004 cohort.

The response variable, number of seedlings, was a count, which is appropriately modelled using either a Poisson or negative binomial distribution. The data were highly overdispersed (variance much greater than the mean), so I used a negative binomial error distribution for all models. All models were fit using PROC NLMIXED in SAS Version 8.0 (SAS Institute, 1999), providing maximum-likelihood estimates of model parameters, confidence intervals and AIC values using the Newton-Raphson optimisation technique and the Gauss-Hermite quadrature integration to estimate random effects.

**Model Selection**

To evaluate which hypothesis, functional shape and parameter variation best described the dose-response relationship, I used strength of evidence model selection criteria to select the model best supported by the data for each establishment phase (Burnham and Anderson 2002b, Johnson and Kristian 2004). I used AIC\(_c\) values as the strength of evidence criteria for each hypothesis. AIC\(_c\) is a small-sample bias correction for AIC, and should be used when the ratio of estimated model parameters to the number of observations is greater than 40 (Burnham and Anderson 2002a). Models with the smallest AIC\(_c\) have the most support (Burnham and Anderson 2002a). I ranked models according to difference in AIC\(_c\) (\(\Delta\text{AIC}_c\)) from the best-fitting model (the best-fitting model thus has \(\Delta\text{AIC}_c = 0\)). For each model with \(\Delta\text{AIC}_c \leq 10\), I calculated an Akaike weight \(w_i\):

\[
\text{Eq. 5) } \quad w_i = \frac{-\exp(\Delta\text{AIC}_c)}{\sum \Delta\text{AIC}_c}
\]
Akaike weights provide an estimate of probability that a given model is the best fitting model of the candidate set (Burnham and Anderson 2002b, Hobbs et al. 2003). When $w_i > 0.90$, the model can be considered strongly supported by the data, when $w_i < 0.90$, the inferences resulting from each supported model ($w_i > 0$) should be considered (Burnham and Anderson 2002a). When using parameter estimates from models to make inferences about the study system, and parameter estimates from alternative models are markedly different, model averaging or model uncertainty estimates should be considered (Burnham and Anderson 2002a). If inferences based on the set of reasonably fitting models are similar, then sound inferences on the general result predicted by the model can be made using the best-fitting model of the set; however the implication is that the hypothesis defined by that particular model is not strong (Burnham and Anderson 2002a). Here, when several candidate models were supported by the data (i.e., $w_i < 0.90$ for the best fitting model) I examined parameter estimates of each model to determine whether model inferences changed appreciably. I assessed model fit by fitting the predicted values from the best-fitting model to the raw data.

**Environmental correlates of resistance**

To explore how environmental differences among habitats may explain differences in the dose-response relationship, I tested how environmental variables were correlated with the slope ($a$) and asymptote ($b$) parameters of the best-fitting dose-response curve for the final establishment phase, using Spearman rank correlations at the block level. I used the Best Unbiased Linear Predictors (BLUPS) from the best-fitting models identified from the model selection process (see above) to estimate the slope of the dose-response curve for each block. Since the best-fitting model for the dose-response curve did not include a random effect for the asymptote, I could not estimate the asymptote for each block using this approach. Instead, I used the mean number of seedlings established in the two highest density seed sowing treatments as an estimate of the saturation level. Having correlated the slope and the saturation levels with environmental variables at the block level, I then examined how differences in environmental variables among habitats could explain these correlations by testing for habitat differences with one-way ANOVA and Tukeys HSD tests when differences were present.
**Results**

**Dose-response relationship**

In three of the five cases, the dose-response relationship between *H. lepidulum* seed sowing density and seedling establishment was best described by the disturbed forest hypothesis, \( D \), fit with a saturating functional shape where both rate of establishment (slope \( a \)) and saturation density (asymptote \( b \)) varied among habitats (Table 2). Although initial emergence for the 2003 cohort was described by a linear functional shape that differed between forest and alpine habitats (hypothesis \( FA \)), convergence on hypothesis \( D \) was consistent across establishment phase and seed cohort (Table 2). Thus, the data provided strong support for the hypothesis that habitat resistance to *H. lepidulum* establishment is equivalent in forest creeks and gaps, which are less resistant to establishment than intact forest, and that resistance to establishment differs between forest and alpine habitats.

Other models were supported by the data (Table 2), but a comparison of parameter estimates for these models showed that inferences were similar. For example, two saturating models (\( H \) and \( FA \)) received support in describing the initial emergence response of the 2003 cohort (Table 2); parameter estimates for these models showed that they were essentially still fitting a linear function to the data by estimating a very high saturation density, and that establishment rates were unchanged (results not shown). Support for these models was thus a consequence of the flexibility of the Beverton-Holt model, and did not reflect an improvement in model fit by allowing for saturation. For final seedling establishment for the 2003 cohort, the alternative hypothesis to \( D \), hypothesis \( F \), which predicted that all forest habitats were equivalent was the second best-fitting model (Table 2). Parameter estimates from the two models were virtually identical, and support for \( F \) arose because saturation densities among the three forest habitats were similar (Table 3c). Since there were differences in establishment rates among the three forest habitats, model \( D \) does in fact describe the data best, this was supported by a graphical fit of model predictions to the data (Figure 2).

Variations in the dose-response relationship among habitats, as predicted by model \( D \), corroborated the spatial distribution of *H. lepidulum* among forest habitats: resistance to establishment, as measured by the slope \( a \) of the dose-response curve, was lower in forest
creek and canopy gaps than in intact forest (Table 3c, Figure 2). More importantly however, differences in habitat resistance between forest and alpine habitats did not tally with the current low density of *H. lepidulum* in alpine habitats, with the lowest resistance to *H. lepidulum* establishment found in tussock and alpine creek habitats (Table 3c, Figure 2).

Differences in the dose-response curve parameters between forest and alpine habitats were evident from initial seedling emergence; but initial establishment rates were higher in forest than in the alpine habitats in both seed cohorts (Table 3a), as were saturation densities for the 2004 cohort. Over time, establishment rates and saturation densities declined in forest and scrub habitats but remained stable or increased in tussock and alpine creek habitats, so that two years after seed was sown, the highest rates of seedling establishment were in the tussock and alpine creek habitats (Table 3b, c, Figure 2).

The disturbed forest habitat category, i.e.; forest creeks and gaps, had the next highest rate of establishment, followed by scrub and intact forest (Table 3c, Figure 2). Saturation densities among habitats were not as variable as establishment rates; they were highest in alpine creeks, very similar in the three forest and the tussock habitat, and very low in the scrub (Table 3c, Figure 2).

These changes in the dose-response relationship over time indicate that rates of initial emergence and subsequent seedling mortality differ in the degree to which they determine final seedling abundance among habitats. In forest habitats, final seedling abundance is determined by the number of seedlings that survive out of a large initial cohort, while in tussock and alpine creek habitats, final seedling abundance results from ongoing seedling recruitment, and lower rates of seedling mortality from a smaller initial cohort. In scrub habitats, final abundance reflects low initial emergence, and subsequent seedling mortality. New seedlings were observed throughout the summer in every habitat (results not shown), but the number of new seedlings emerging was highest in the tussock and alpine creek, with new seedlings recorded in the second spring after seed was sown in more than 60% of plots in these habitats, versus 42% in the scrub, 26% in the forest and 14% in forest creeks and gaps.
The relative magnitude of dose-response curve parameters over time shows that safe site regulation of final seedling abundance was stronger in tussock and alpine creek habitats, with constant or increasing establishment rates over time, but decreasing saturation densities (Table 3). In the other four habitats, limiting factors acted to decrease establishment over the full range of seed densities, not just at the saturation level. In scrub, both overall limitation of establishment (establishment rate) and strong safe site limitation regulated establishment, while in the forest, overall limitation was strong, but safe site limitation was relatively weak (Table 3).

Establishment rates and saturation densities were higher in the 2004 cohort for all habitats and for both establishment phases (Table 3a, b), suggesting more favourable climatic conditions for the second cohort, and possibly explaining the difference in early establishment patterns between the two cohorts, i.e., the support for hypothesis FA for initial establishment in the 2003 cohort (Table 2).

**Environmental correlates**

**Correlations to dose-response parameters**

For all habitats combined, blocks with a higher rate of establishment (slope parameter $a$) had high vascular cover, high species richness, high light and low litter cover (Table 4). Blocks with high saturation density (asymptote $b$) had high species richness, light, soil moisture content and soil fertility (pH), and low litter cover (Table 4).

Within forests, only abiotic resource availability was correlated with dose-response curve parameters (Table 4). Blocks with high establishment rates had high light and high soil fertility (high pH, P, base saturation, low C:N ratio) (Table 4). Blocks with high saturation densities also had high soil fertility (high P, base saturation), but were not affected by light (Table 4).

In alpine habitats, both abiotic resource availability and community characteristics were correlated with dose-response curve parameters (Table 4). Blocks with high establishment rates had high species richness, high moss cover, and high soil moisture content, and low rock cover and soil fertility (low base saturation). Blocks with high saturation densities had
high species richness, high soil moisture content and light, low litter and rock cover, and low soil fertility (low N, P, high C:N ratio) (Table 4).

Habitat differences

The correlations between environmental variables and parameters of the dose-response curve help explain the observed differences in resistance to establishment among habitats. Habitats with relatively high species richness, vascular cover and light (tussock, alpine creek, forest creek and canopy gap) (Table 5), also had high rates of *H. lepidulum* establishment (high slope $a$). Habitats with a tendency for higher litter cover (forest and scrub) had low rates of establishment. However, the negative effect of litter cover may operate within habitats, as the differences among habitats in litter cover were not significant (Table 5a).

The positive correlation between soil fertility and light and dose-response parameters in the forest habitats reflects low soil fertility and low light in intact forest habitat, in which dose-response parameters were low, relative to forest creeks and canopy gaps (Table 5b). Although species richness and vascular cover were higher, and litter cover lower in canopy gaps and forest creeks relative to intact forest (Table 5a), there was no evidence that these variables were important in explaining among habitat differences in the dose-response curve (Table 4).

Among the alpine habitats, the positive relationship between vascular cover and establishment rate observed for all other habitats disappeared, and this was because while all three alpine habitats had high vascular cover (Table 5a), establishment rates in scrub were low. The negative relationship between rock cover and establishment arises because scrub had higher rock cover than tussock or alpine creeks (Table 5a). Again, the negative effect of litter on establishment rates in the alpine may indicate a general negative effect rather than a habitat effect, as there were no differences in litter cover among the alpine habitats. The negative correlation between soil fertility and establishment in the alpine also reflects differences between scrub versus tussock and alpine creek habitats: scrub had higher P, N, and base saturation (Table 5b). Thus, the negative correlation here probably does not reflect a causal relationship between high soil fertility and low establishment of *H. lepidulum* among alpine habitats.
Discussion

I quantified the dose-response relationship between propagule supply rate and seedling establishment of the invasive herb *H. lepidulum* in five habitats in Canterbury, South Island, New Zealand uplands. This allowed me to determine how resistance to *H. lepidulum* establishment varied among habitats in this landscape, and how mechanisms of resistance varied among habitats. Differences in habitat resistance showed that current low densities of *H. lepidulum* in alpine habitats are not due to high resistance to establishment; on the contrary, tussock grassland and alpine creek habitats had the lowest resistance to *H. lepidulum* establishment, with high rates of seedling establishment in these habitats for a given seed supply and high seedling saturation densities. Among forest habitats, differences in resistance did tally with current spatial patterns of distribution with forest creeks and canopy gaps less resistant to establishment than intact forest in terms of seedling establishment rate for a given seed supply. Scrub and intact forest habitats were the most resistant to *H. lepidulum* establishment: scrub habitat had both a low establishment rate and a low saturation density, while forest habitat had a low establishment rate.

Variation in seedling emergence and seedling mortality between forest and alpine habitats determined final seedling abundance. Forest habitats had higher initial emergence rates followed by high rates of seedling mortality. Initial emergence in the alpine was relatively low, but was followed by ongoing recruitment. This difference between forest and alpine habitats appeared to be related to differences in the availability of sheltering microsites that facilitated seedling survival.

Relative role of seed and safe site limitation of establishment

The relative magnitude of the dose response curve parameters controlling the rate of establishment (slope) and saturation density (asymptote) varied among habitats, demonstrating among habitat differences in the relative roles of seed and safe site limitation of establishment. In habitats where abiotic resource availability was low (forest), establishment was primarily seed limited. Where resource availability was higher, and where there was a high cover of resident vegetation and high species richness (tussock and alpine creek), establishment was predominantly safe site limited. These results support the hypothesis that safe site regulation of establishment is greater in habitats with higher
resident species cover and that seed limitation is more important in habitats where abiotic resources are limiting (Foster 2001, Fargione et al. 2003, Foster et al. 2004, Henry et al. 2004, Eskelinen and Virtanen 2005). Despite this difference in mechanisms regulating establishment, the saturation densities measured here indicate that in the end, both types of habitats may be susceptible to the same level of invasion given a high enough propagule supply.

Mechanisms of limitation

Resistance to *H. lepidulum* establishment was lowest when species richness and vascular plant cover was high. Here, this appeared to reflect a requirement for sheltering microsites in which seedlings could survive desiccation over the summer. This result ties in with what is known about the ecology of *H. lepidulum*. Nationally, *H. lepidulum* does not occur in drier lowland eastern areas (Chapter 2), on a landscape scale it occurs more often on moist, protected aspects (Rose et al. 1995, Wiser et al. 1998), and on a local scale it occupies sheltered microsites in alpine habitats (Chapter 3, Rose and Frampton 1999), suggesting that protection from desiccation may be an important determinant of *H. lepidulum* establishment.

*Hieracium lepidulum* does not appear to be repelled by competition with resident vegetation. Evidence for the importance of species richness, or of competition with resident species for resisting establishment of invasive plants is mixed (Levine and D'Antonio 1999, Levine et al. 2004). Many studies have shown that establishment is reduced when cover or biomass of resident vegetation is high (e.g., Gross and Werner 1982, Burke and Grime 1996, Foster and Gross 1998, Kotorová and Lepš 1999, Foster et al. 2004, Eskelinen and Virtanen 2005). Mechanistic explanations include reduced light availability (Foster and Gross 1998, Foster et al. 2004), increased competition for soil nutrients and moisture (Smith et al. 2004), and decreased availability of bare ground microsites for establishment (Crawley 1986, Rejmanek 1989, Burke and Grime 1996, Turnbull et al. 2000). However, as was the case here, establishment may instead be facilitated by resident cover, an effect that is thought to be especially important in stressful environments (such as alpine areas) where moisture or temperature may inhibit seedling survival (e.g., Hunter and Aarssen 1988, Greenlee and Calloway 1996, Smith et al. 2004).
Species richness was traditionally thought to reduce establishment success because resource usage in species rich habitats is higher (sensu Elton 1958). Some studies have demonstrated a negative relationship between establishment and species richness (e.g., Tilman 1997, Levine 2000, Naeem 2000), however, it is more common to find no effect, or a positive relationship (Robinson et al. 1995, Planty-Tabacchi 1996, Wiser et al. 1998, Smith et al. 2004, Eskelinen and Virtanen 2005). A positive relationship between invasive species establishment and species richness may reflect underlying environmental factors such as high resource abundance (e.g., Wiser et al. 1998, Levine and D'Antonio 1999, Planty-Tabacchi 2001, Eskelinen and Virtanen 2005), or, species richness may directly influence establishment by providing a more diverse array of microsites (Tilman et al. 1996, Wiser et al. 1998, Smith et al. 2004).

Here, species richness appeared to enhance establishment by providing a refuge from which seeds could germinate over a longer time period, or a short-term ‘seed bank’ of *H. lepidulum*. Species richness also appeared to enhance establishment by providing a diverse assemblage of microsites in which seedlings could survive desiccation over the summer (Fowler 1986, Hamrick and Lee 1987, Fowler 1988, Smith et al. 2004). However, without exploring in more detail the relationship between species richness and establishment within tussock and alpine creek habitats, I cannot discount underlying habitat suitability as an explanation for these results. The fundamentally different vegetation structure in tussock grasslands and alpine creek habitats to the other four habitats in this study, could also have led to the differences in establishment success.

In forest habitats, in the more homogenous ground cover of litter, moss and few vascular species, initial emergence occurred in a one large flush in early spring, thus these habitats did not provide the ‘seed bank’ offered in the alpine habitats, and seedlings were more exposed to desiccation. In the scrub, high vascular cover did not offer the same kind of facilitation provided by the tussock and alpine creek habitats. The scrub habitat differed from the tussock and alpine creek habitats in terms of species richness, but probably more importantly in terms of vegetation structure. Scrub habitats had a low canopy (5–75 cm) dominated by a single species (*Podocarpus nivalis*), underneath which the groundcover was occupied by rock, woody stems and litter. The very low seedling saturation density in the scrub probably results from the dominance of microsites by rock and woody stems.
Microclimate effects and changes in dose-response curve over time

In addition to differences in community composition and ground cover that may influence temporal patterns of seed germination, differences in microclimate between the forest and alpine habitats may also explain the initial higher rates of emergence in the forest relative to the alpine. In early spring, when seedling emergence begins, the forest microclimate would be more favourable for seedling emergence, as forest habitats would escape the low temperatures and frosts still frequent in alpine habitats. The differences in emergence patterns between the 2003 and 2004 cohorts coupled with differences in weather patterns between the two years provide evidence for such a microclimate effect. Essentially, differences in habitat resistance were apparent at an earlier stage in the 2004 cohort, while in the 2003 cohort, the strongest initial difference was between forest and alpine habitats. In 2004, early spring (November) was warmer and had fewer frost days. This was followed by a colder, wetter December, and then a warmer summer (Craigeburn Climate Station Data, Landcare Research Inc., unpublished data; available on request). The initial warm period in early spring would have lessened the difference in environmental conditions between the forest and the alpine, hence fast-tracking habitat resistance patterns.

Abiotic Resources

Resource availability is widely recognized as an important determinant of invasibility (Huenneke et al. 1990, Davis et al. 2000, Denslow 2003), with areas of resource rich habitats relatively more invaded (Gregory et al. 1991, Wiser et al. 1998, Stohlgren et al. 1999, Wilsey and Polley 2003), and resource poor habitats relatively difficult to invade (Huenneke et al. 1990, Levine et al. 2004). Resistance to *H. lepidulum* invasion is no exception, with differences in abiotic resources (light, soil fertility) correlated with establishment success among forest habitats in this study. This also supports what is already known about *H. lepidulum* ecology: in forests, *H. lepidulum* is more likely to occur in high soil fertility sites (Wiser et al. 1998).

New Zealand mountain beech forest has notoriously low soil fertility (McLaren and Cameron 1996, Platt et al. 2004); however, there are pockets of higher soil fertility within the forest such as tip-up mounds or newer creek terraces (Platt et al. 2004). These pockets could, in addition to those provided by canopy gaps, provide important entry points for *H. lepidulum* into the forest. Since these pockets of higher soil fertility also provide havens for
native species within these otherwise species impoverished forests (Wiser et al. 1998), *H. lepidulum* invasion likely poses a threat to forest biodiversity.

**Implications for spatial spread**

Differences among habitats in inherent resistance to establishment only partially explain the current spatial distribution of *H. lepidulum* in the study area. Among forest habitats, the spatial distribution of *H. lepidulum* corresponds with differences in habitat resistance: the abundance of *H. lepidulum* in intact mountain beech forest is low relative to forest creeks and canopy gaps because mountain beech forest has relatively high resistance to *H. lepidulum* establishment. Thus, the high density populations at the forest edge (Chapter 3), may result from a spatial mass effect driven by high density forest creek populations (*sensu* Shmida and Ellner 1984, Levine and Rees 2002), rather than a dynamic front of *H. lepidulum* spreading through the forest.

Current densities of *H. lepidulum* in alpine habitats are not low because of high resistance to *H. lepidulum* establishment; rather, resistance to establishment, at least in tussock grassland and alpine creeks, is low. This implies that low seed supply in the alpine may underlie the current patterns of distribution, and that future spread into the alpine is likely as *H. lepidulum* densities below tree line build, and as populations in the alpine become established.

A caveat to my results is that they extend to establishment after two years, at which point plants were still seedlings. The establishment response could change as establishment proceeds (Turnbull et al. 2000, Henry et al. 2004, Levine et al. 2004). However, given that trends in seedling mortality held for two years, and given the consistency of the results among establishment phases and seed cohorts, the general pattern of resistance to establishment should hold even if the magnitude of the dose-response parameters change.

Another consideration is potential density-dependent effects on seedling growth (*e.g.*, Goldberg et al. 2001, Lortie and Turkington 2002, Shilo-Volin et al. 2005). I had planned to measure biomass of *H. lepidulum* plants established in this experiment, but seedling growth rates were slower than expected. Hence, I decided to postpone harvest until plants were large enough to detect more meaningful differences. A final consideration is that I focused on the establishment phase of *H. lepidulum* invasion. Many studies of plant
population dynamics have shown that early establishment phases are critical for determining future patterns of distribution (e.g., Gross and Werner 1982); however, another important component of invasion is population growth and spread following establishment (Hobbs and Humphries 1995, Mack et al. 2000). I assess the potential contribution of differences in plant performance among habitats to explaining the uneven distribution of *H. lepidulum* across the landscape in Chapter 5.

**Summary**

My study is the first to use a comparative dose-response approach to quantify relative habitat resistance to establishment of an invasive plant species. The dose-response relationship between propagule supply rate and establishment success of the exotic plant invader *H. lepidulum* differed with habitat type, indicating that habitats differ in resistance to establishment of this invader. It differed both in terms of rate of seedling establishment at a given seed supply (slope), and at the saturation density at which further seed addition ceased to result in further seedling establishment (asymptote), and in terms of the relative importance of these parameters in regulating establishment. Changes in the dose-response curve parameters over time, and correlations of dose-response curve parameters with environmental variables allowed identification of the probable mechanisms underlying differences in habitat resistance to *H. lepidulum* establishment. Overall, establishment was facilitated in tussock grassland and alpine creek habitats, habitats that provided sheltering microsites that ameliorated conditions contributing to seedling mortality over summer. Abiotic resource availability was an important determinant of *H. lepidulum* establishment among forest habitats. The current spatial distribution of *H. lepidulum* among habitats is only partly a result of differences in habitat resistance; this has important implications for future patterns of spread of *H. lepidulum* in the mid-Canterbury upland landscape, with spread predicted to increase in alpine areas. These results illustrate the utility of the dose-response approach as a tool for quantifying resistance to invasive species establishment.

**References**


Institute, S. 1999. SAS 8.0. in, Carey, NC, USA.


Table 4.1.
A. Hypotheses tested to determine how habitats might differ in resistance to the establishment of *H. lepidulum* in the study area.
B. Structural equations for the specific models tested to determine whether and how the functional shape and/or parameters of the dose-response relationship between seed sowing density and number of seedlings establishing of *H. lepidulum* changes with habitat according to the above hypotheses. Linear models are of the general form $E = aS$, where $E$ is the number of seedlings establishing, $S$ is the number of seeds sown, and $a$ is the rate of establishment for a given seed density, or slope, and is estimated from the data. Saturating models are of the form $E = aS/(1 + aS/b)$, where $E$, $S$ and $a$ are as above, and $b$ is the saturation density where seed addition ceases to result in additional seedling establishment, or asymptote; both $a$ and $b$ are estimated from the data. Each habitat resistance model in (A) was fit to each functional shape (linear or saturating) of the dose-response curve (B). For the linear functional shape, only the slope $a$ could vary with habitat, thus each model was fit by including variables coding for the habitat resistance model (see A) as a determinant of the slope $a$. For the saturating functional shape, the slope $a$, the asymptote $b$, or both $a$ and $b$ could vary with habitat, thus each habitat resistance model was fit by including variables coding for the habitat resistance model to either $a$, $b$ or both together. All models were fit with and without a random block effect $u$, which was included as a determinant of either the slope $a$ or the asymptote $b$. When both $a$ and $b$ were varied, the random effect $u$ was included as a determinant of the slope $a$ only. All models were fit with a negative binomial error distribution to account for overdispersion, and include an overdispersion parameter $k$.

<table>
<thead>
<tr>
<th>Model</th>
<th>Habitat resistance hypothesis</th>
<th>Variables coding for habitat type*</th>
</tr>
</thead>
<tbody>
<tr>
<td>U</td>
<td>Uniform: no difference among habitats in resistance to establishment</td>
<td>fc, f, g, t, ac, s</td>
</tr>
<tr>
<td>H</td>
<td>Habitat: resistance differs uniquely in each habitat</td>
<td>F, A</td>
</tr>
<tr>
<td>FA</td>
<td>Forest vs. Alpine: resistance differs between forest and alpine habitats</td>
<td>F, t, ac, s</td>
</tr>
<tr>
<td>F</td>
<td>Forest equivalent: forest habitats do not differ in resistance, but alpine habitats differ uniquely</td>
<td>fc-g, f, t, ac, s</td>
</tr>
<tr>
<td>D</td>
<td>'Disturbed' forest habitats: forest creeks and gaps are less resistant than intact forest, alpine habitats differ uniquely</td>
<td>fc-g = combined forest creek and gap habitats, ac = alpine creek, s = scrub, F = all forest habitats (forest creek, forest, gap), A = all alpine habitats (tussock, alpine creek, scrub)</td>
</tr>
<tr>
<td>Functional Shape</td>
<td>Parameter varied</td>
<td>Model</td>
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<td>------------------</td>
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<td>-------</td>
</tr>
<tr>
<td>Linear</td>
<td>slope $a$</td>
<td>U</td>
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<td>H</td>
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<td>D</td>
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<td>D</td>
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<td>Asymptote</td>
<td>asymptote $b$</td>
<td>U</td>
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<td>D</td>
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<tr>
<td>Asymptote</td>
<td>$a$ and $b$</td>
<td>H</td>
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<td>FA</td>
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<td>F</td>
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<td>D</td>
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Table 4.2. ΔAICc values (with Akaike weights (\(w_i\)) in brackets if ΔAICc ≥ 10) for models describing how the dose-response relationship between *H. lepidulum* seed density and number of seedlings establishing changes with habitat. The dose-response relationship at initial seedling emergence, survival after one summer, and final establishment two years after seed was sown was examined for two seed sowing cohorts, 2003 and 2004. All models were greatly improved by the addition of a random block effect (ΔAICc ≥ 50), so only models that include the random effect are reported. The best-fitting model for each cohort and establishment phase is shown in bold*

<table>
<thead>
<tr>
<th>Cohort</th>
<th>Establishment Phase</th>
<th>Model</th>
<th>Linear</th>
<th>Saturating</th>
<th>Parameter varied</th>
</tr>
</thead>
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<tr>
<td>2003</td>
<td>Initial emergence</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>U</td>
<td>4.4 (0.06)</td>
<td>8.2</td>
<td>135.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>2.8 (0.14)</td>
<td>5.8</td>
<td>132</td>
<td>11.3</td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>2.4 (0.18)</td>
<td>32.8</td>
<td>133.9</td>
<td>19.7</td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>6 (0.03)</td>
<td>42.6</td>
<td>146.1</td>
<td>96.3</td>
<td></td>
</tr>
<tr>
<td>FA</td>
<td>0 (0.59)</td>
<td>2.8</td>
<td>136.3</td>
<td>11.3</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Summer1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>U</td>
<td>70.2</td>
<td>14.1</td>
<td>125.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>75.6</td>
<td>18.1</td>
<td>150.3</td>
<td>0.7 (0.42)</td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>74.2</td>
<td>58.7</td>
<td>110.8</td>
<td>24.9</td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>73.6</td>
<td>59.2</td>
<td>105.7</td>
<td>23.9</td>
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</tr>
<tr>
<td>FA</td>
<td>71</td>
<td>17.9</td>
<td>115.8</td>
<td>0 (0.58)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Final</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>U</td>
<td>112</td>
<td>23.6</td>
<td>208.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>100.2</td>
<td>11.7</td>
<td>152.9</td>
<td>5.5 (0.04)</td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>102.3</td>
<td>14.9</td>
<td>126.4</td>
<td>0.6 (0.41)</td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>108.6</td>
<td>10.5</td>
<td>121.4</td>
<td>0 (0.56)</td>
<td></td>
</tr>
<tr>
<td>FA</td>
<td>108.6</td>
<td>20.4</td>
<td>265</td>
<td>25.8</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Initial emergence</td>
<td>U</td>
<td>88.7</td>
<td>86.7</td>
<td>307.4</td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>47.1</td>
<td>72.8</td>
<td>177.4</td>
<td>4.5 (0.09)</td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>51.1</td>
<td>72.7</td>
<td>298.5</td>
<td>25.8</td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>45.1</td>
<td>66</td>
<td>298.8</td>
<td>0 (0.91)</td>
<td></td>
</tr>
<tr>
<td>FA</td>
<td>52</td>
<td>49</td>
<td>299.4</td>
<td>12.7</td>
<td></td>
</tr>
<tr>
<td>Summer1</td>
<td>U</td>
<td>147.7</td>
<td>95.4</td>
<td>252.5</td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>137</td>
<td>31.7</td>
<td>123.1</td>
<td>3.2 (0.1)</td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>141.8</td>
<td>95.6</td>
<td>133.6</td>
<td>48.2</td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>135.5</td>
<td>89.1</td>
<td>126.6</td>
<td>0.0 (0.83)</td>
<td></td>
</tr>
<tr>
<td>FA</td>
<td>144.8</td>
<td>39.5</td>
<td>222.2</td>
<td>16.5</td>
<td></td>
</tr>
</tbody>
</table>

*The best fitting model has ΔAICc = 0 (ΔAICc is the difference in AICc between the minimum AICc and the AICc of model i). Akaike weights provide an approximate probability that the best-fitting model is in fact the best of the candidate set.
Table 4.3. Parameter estimates and standard errors for the best fitting habitat resistance models for the dose-response curve describing the relationship between *H. lepidulum* seed density and number of seedlings establishing. A. initial emergence, B. survival after one summer, and C. Final establishment after two years for the 2003 and 2004 seed cohorts. (*a* is the slope parameter, representing the rate of establishment, *b* is the asymptote parameter, representing the saturation level, *k* is the dispersion parameter for the negative binomial error distribution, *u* is the random effect of individual blocks on slope parameter *a*, and *fC-g* is the combined forest creek and canopy gap habitat category).

A. Initial emergence

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>a</em> Alpine</td>
<td>0.058</td>
<td>0.0075</td>
</tr>
<tr>
<td><em>a</em> Forest</td>
<td>0.087</td>
<td>0.011</td>
</tr>
<tr>
<td><em>k</em></td>
<td>0.45</td>
<td>0.034</td>
</tr>
<tr>
<td><em>u</em></td>
<td>0.00088</td>
<td>0.00026</td>
</tr>
</tbody>
</table>

2004 cohort

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>- <em>a</em> Forest&lt;sub&gt;f-g&lt;/sub&gt;</td>
<td>0.22</td>
<td>0.015</td>
</tr>
<tr>
<td>- <em>a</em> Forest</td>
<td>0.15</td>
<td>0.023</td>
</tr>
<tr>
<td>- <em>a</em> Scrub</td>
<td>0.062</td>
<td>0.022</td>
</tr>
<tr>
<td>- <em>a</em> Alpine Creek</td>
<td>0.074</td>
<td>0.022</td>
</tr>
<tr>
<td>- <em>a</em> Tussock</td>
<td>0.11</td>
<td>0.023</td>
</tr>
<tr>
<td>- <em>b</em> Forest&lt;sub&gt;f-g&lt;/sub&gt;</td>
<td>18715</td>
<td>169</td>
</tr>
<tr>
<td>- <em>b</em> Forest</td>
<td>28656</td>
<td>0.0058</td>
</tr>
<tr>
<td>- <em>b</em> Scrub</td>
<td>427</td>
<td>181</td>
</tr>
<tr>
<td>- <em>b</em> Alpine Creek</td>
<td>1335</td>
<td>171</td>
</tr>
<tr>
<td>- <em>b</em> Tussock</td>
<td>1563</td>
<td>165</td>
</tr>
<tr>
<td>- <em>k</em></td>
<td>0.40</td>
<td>0.029</td>
</tr>
<tr>
<td>- <em>u</em></td>
<td>0.0012</td>
<td>0.00045</td>
</tr>
</tbody>
</table>

b) Summer

2003 cohort

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>a</em> Alpine</td>
<td>0.037</td>
<td>0.01</td>
</tr>
<tr>
<td><em>a</em> Forest</td>
<td>0.041</td>
<td>0.01</td>
</tr>
<tr>
<td><em>b</em> Alpine</td>
<td>260</td>
<td>41</td>
</tr>
<tr>
<td><em>b</em> Forest</td>
<td>729</td>
<td>2</td>
</tr>
<tr>
<td><em>k</em></td>
<td>0.63</td>
<td>0.05</td>
</tr>
<tr>
<td><em>u</em></td>
<td>0.00049</td>
<td>0.00016</td>
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</table>
## 2004 cohort

<table>
<thead>
<tr>
<th>Parameter</th>
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<th>se</th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forest f_{0-g}</td>
<td>0.13</td>
<td>0.016</td>
</tr>
<tr>
<td>Forest</td>
<td>0.06</td>
<td>0.025</td>
</tr>
<tr>
<td>Scrub</td>
<td>0.04</td>
<td>0.025</td>
</tr>
<tr>
<td>Alpine Creek</td>
<td>0.07</td>
<td>0.026</td>
</tr>
<tr>
<td>Tussock</td>
<td>0.12</td>
<td>0.028</td>
</tr>
<tr>
<td>b</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forest f_{0-g}</td>
<td>1018</td>
<td>191</td>
</tr>
<tr>
<td>Forest</td>
<td>969</td>
<td>408</td>
</tr>
<tr>
<td>Scrub</td>
<td>133</td>
<td>193</td>
</tr>
<tr>
<td>Alpine Creek</td>
<td>318</td>
<td>204</td>
</tr>
<tr>
<td>Tussock</td>
<td>481</td>
<td>216</td>
</tr>
<tr>
<td>k</td>
<td>0.55</td>
<td>0.041</td>
</tr>
<tr>
<td>u</td>
<td>0.00201</td>
<td>0.00066</td>
</tr>
</tbody>
</table>

## c) Final establishment

## 2003 cohort

<table>
<thead>
<tr>
<th>Parameter</th>
<th>estimate</th>
<th>se</th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forest f_{0-g}</td>
<td>0.035</td>
<td>0.007</td>
</tr>
<tr>
<td>Forest</td>
<td>0.011</td>
<td>0.011</td>
</tr>
<tr>
<td>Scrub</td>
<td>0.030</td>
<td>0.012</td>
</tr>
<tr>
<td>Alpine Creek</td>
<td>0.059</td>
<td>0.013</td>
</tr>
<tr>
<td>Tussock</td>
<td>0.072</td>
<td>0.014</td>
</tr>
<tr>
<td>b</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forest f_{0-g}</td>
<td>260</td>
<td>51</td>
</tr>
<tr>
<td>Forest</td>
<td>277</td>
<td>54</td>
</tr>
<tr>
<td>Scrub</td>
<td>68</td>
<td>53</td>
</tr>
<tr>
<td>Alpine Creek</td>
<td>392</td>
<td>121</td>
</tr>
<tr>
<td>Tussock</td>
<td>262</td>
<td>80</td>
</tr>
<tr>
<td>k</td>
<td>0.80</td>
<td>0.064</td>
</tr>
<tr>
<td>u</td>
<td>0.00041</td>
<td>0.00015</td>
</tr>
</tbody>
</table>
Table 4.4. Spearman rank correlations between the block-level slope \((a)\) and asymptote \((b)\) parameters of the dose-response curve of *H. lepidulum* establishment as a function of seed density in different habitats in the study area, and block-level environmental variables. The slope parameter estimates used for the correlation are the Best Unbiased Linear Predictors (BLUPs) from the best-fitting dose-response model describing final establishment two years after seed was sown; the saturation density is the mean rate of establishment in the two high density seed-sowing treatments. Environmental variables are mean values per block. (* = significant at \(P < 0.05\)).

<table>
<thead>
<tr>
<th></th>
<th>All habitats</th>
<th>Forest Habitats</th>
<th>Alpine Habitats</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Slope (a)</td>
<td>Asymptote (b)</td>
<td>Slope (a)</td>
</tr>
<tr>
<td><strong>Species Richness</strong></td>
<td>0.656*</td>
<td>0.611*</td>
<td>0.327</td>
</tr>
<tr>
<td><strong>Vascular Cover</strong></td>
<td>0.459*</td>
<td>0.293</td>
<td>0.235</td>
</tr>
<tr>
<td><strong>Litter Cover</strong></td>
<td>-0.339*</td>
<td>-0.381*</td>
<td>-0.207</td>
</tr>
<tr>
<td><strong>Rock Cover</strong></td>
<td>-0.044</td>
<td>-0.202</td>
<td>0.491</td>
</tr>
<tr>
<td><strong>Moss Cover</strong></td>
<td>-0.19</td>
<td>-0.0892</td>
<td>-0.162</td>
</tr>
<tr>
<td><strong>Light</strong></td>
<td>0.60*</td>
<td>0.529*</td>
<td>0.481*</td>
</tr>
<tr>
<td><strong>Soil Moisture Content</strong></td>
<td>0.243</td>
<td>0.335*</td>
<td>-0.385</td>
</tr>
<tr>
<td><strong>pH</strong></td>
<td>0.448*</td>
<td>0.323*</td>
<td>0.727*</td>
</tr>
<tr>
<td><strong>C:N ratio</strong></td>
<td>-0.298</td>
<td>-0.104</td>
<td>-0.156*</td>
</tr>
<tr>
<td><strong>Nitrogen</strong></td>
<td>0.202</td>
<td>0.0191</td>
<td>-0.24</td>
</tr>
<tr>
<td><strong>Phosphorous</strong></td>
<td>0.156</td>
<td>0.155</td>
<td>0.588*</td>
</tr>
<tr>
<td><strong>Base Saturation</strong></td>
<td>0.238</td>
<td>0.0550</td>
<td>0.811*</td>
</tr>
</tbody>
</table>
Table 4.5. Environmental characteristics for the six habitats in which resistance to invasion by *H. lepidulum* was determined. Values are means with standard errors in brackets, and exclude outlier blocks in which the establishment response was markedly above or below the mean habitat response. Habitats sharing the same letter do not differ in that environmental trait (ANOVA, Tukeys HSD test, *P* < 0.05). A. Species richness and groundcover. B. Abiotic characteristics.

A. Groundcover (Braun-Blanquet Cover Scale)

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Species richness</th>
<th>Vascular</th>
<th>Moss</th>
<th>Litter</th>
<th>Bare</th>
<th>Rock</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest Creek</td>
<td>a3.83 (0.33)</td>
<td>a3.30 (0.13)</td>
<td>a3.34 (0.18)</td>
<td>a4.66 (0.12)</td>
<td>0.022 (0.022)</td>
<td>a0.97 (0.97)</td>
</tr>
<tr>
<td>Forest</td>
<td>b1.12 (0.072)</td>
<td>b1.61 (0.12)</td>
<td>ad2.93 (0.14)</td>
<td>b5.70 (0.073)</td>
<td>0.17 (0.04)</td>
<td>b0.17 (0.17)</td>
</tr>
<tr>
<td>Gap</td>
<td>c2.57 (0.16)</td>
<td>c2.74 (0.14)</td>
<td>b4.08 (0.13)</td>
<td>a4.72 (0.12)</td>
<td>0</td>
<td>b0</td>
</tr>
<tr>
<td>Scrub</td>
<td>a3.79 (0.18)</td>
<td>d5.17 (0.09)</td>
<td>cd2.72 (0.13)</td>
<td>a4.86 (0.1)</td>
<td>0</td>
<td>c1.57</td>
</tr>
<tr>
<td>Alpine Creek</td>
<td>d9.81 (0.36)</td>
<td>d5.38 (0.093)</td>
<td>c2.23 (0.12)</td>
<td>c3.97 (0.11)</td>
<td>0</td>
<td>b0.38</td>
</tr>
<tr>
<td>Tussock</td>
<td>e7.07 (0.32)</td>
<td>e4.51 (0.1)</td>
<td>cd2.70 (0.13)</td>
<td>a4.82 (0.11)</td>
<td>0.033 (0.019)</td>
<td>b0.16</td>
</tr>
</tbody>
</table>

B. Light (% PPFD), Soil Moisture Content (%), pH, C:N ratio, Nitrogen, Phosphorus, Total Base Saturation (%)

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Light (% PPFD)</th>
<th>Soil Moisture Content (%)</th>
<th>pH</th>
<th>C:N ratio</th>
<th>Nitrogen</th>
<th>Phosphorus</th>
<th>Total Base Saturation (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest Creek</td>
<td>a10.57 (0.85)</td>
<td>a30.25 (7.87)</td>
<td>a4.90 (0.26)</td>
<td>abc19.63 (0.52)</td>
<td>a0.20 (0.062)</td>
<td>a9.33 (1.36)</td>
<td>ab24.70 (6.91)</td>
</tr>
<tr>
<td>Forest</td>
<td>b3.63 (0.22)</td>
<td>bcd59.58 (3.90)</td>
<td>bc4.10 (0.045)</td>
<td>a21.72 (0.93)</td>
<td>a0.26 (0.028)</td>
<td>a6.0 (1.86)</td>
<td>a7.03 (1.09)</td>
</tr>
<tr>
<td>Gap</td>
<td>ab8.33 (0.52)</td>
<td>bcd76.94 (3.73)</td>
<td>ac4.43 (0.088)</td>
<td>abc18.73 (0.28)</td>
<td>ac0.35 (0.036)</td>
<td>a8.83 (2.33)</td>
<td>ab14.25 (2.19)</td>
</tr>
<tr>
<td>Scrub</td>
<td>ca24.88 (1.93)</td>
<td>ab54.89 (7.69)</td>
<td>a4.77 (0.13)</td>
<td>bc15.97 (0.083)</td>
<td>b0.80 (0.088)</td>
<td>a8.50 (0.67)</td>
<td>b36.35 (6.85)</td>
</tr>
<tr>
<td>Alpine Creek</td>
<td>d60.99 (1.85)</td>
<td>cd83.93 (7.55)</td>
<td>a4.75 (0.096)</td>
<td>abc17.68 (0.048)</td>
<td>b0.66 (0.083)</td>
<td>a6.17 (0.95)</td>
<td>ab24.20 (3.07)</td>
</tr>
<tr>
<td>Tussock</td>
<td>e49.47 (1.54)</td>
<td>d84.09 (4.44)</td>
<td>ab4.55 (0.076)</td>
<td>c16.65 (0.051)</td>
<td>bc0.56 (0.039)</td>
<td>a6.5 (0.56)</td>
<td>a13.98 (2.74)</td>
</tr>
</tbody>
</table>
Figure 1. A. The dose-response relationship between propagule supply rate and number of individuals establishing. Number of individuals establishing \( E \) for a given number of propagules \( S \) is a function of establishment rate (slope, \( a \)), and saturation density where propagule addition ceases to result in additional establishment (asymptote, \( b \)). If habitats differ in resistance to the establishment of invasive species, the dose-response relationship should differ among habitats in terms of the functional shape (linear, I. or saturating, II.), and/or in terms of curve parameters (slope \( a \), or asymptote \( b \)). The functional shape has implications for the mechanisms limiting establishment. A linear shape implies that establishment is a function of propagule supply (i.e., rate of establishment is regulated by seed limitation). A saturating shape implies that establishment is regulated by both seed limitation (at low supply rates) and safe site availability (at high supply rates). The magnitude of the parameters of the dose-response curve imply different degrees of habitat resistance to establishment. A shallow slope \( a \) indicates that overall resistance to establishment is high. A low asymptote \( b \) indicates that safe site limitation strongly limits establishment above the threshold propagule supply rate.
Figure 2. Block level variation in the dose-response relationship between number of seed sown and the number of *H. lepidulum* seedlings establishing after two years in six habitats in New Zealand’s Southern Alps. The solid line is the mean habitat response (actual data), the dashed line is the predicted response from the best-fitting models describing the dose-response relationship (hypothesis D), and the dashed lines show the block level variation around the habitat mean. \( a \) is the predicted establishment rate and \( b \) is the predicted saturation density.
Chapter 5.

Variable plant performance among habitats partially explains the spatial distribution of an invasive weed

Introduction

As invading species spread in a new range, they encounter heterogeneous landscapes composed of mosaics of habitat types and environmental gradients. The spatial distribution of invasive species within such landscapes is often patchy, with some types of habitats and environmental conditions more invaded than others. This patchy distribution may reflect differences in habitat resistance to invasion, and/or differences in rates of propagule dispersal (Pierson and Mack 1990a, Quintana-Ascencio et al. 1998, Harrison et al. 2001, Cole and Wiernasz 2002). Following dispersal and establishment, variation in plant performance within established populations is an additional component that might contribute to a variable pattern of distribution. In habitats where plant performance is higher, populations will grow more quickly, leading to faster rates of spread in those habitats (Pulliam 1988, Pulliam and Danielson 1991, Dias 1996, Meekins and McCarthy 2002).

For example, habitats in which reproductive output is high, all else being equal, will fill more quickly. However, if reproductive output is high but establishment is low, population growth will be lower. Similarly, habitats where plants reach reproductive maturity the quickest will, all else being equal, fill more quickly. Habitats with high survival, fast growth, and early reproduction, may act as propagule sources facilitating invasion into nearby areas of other habitats where performance is lower or slower.

Demographic studies are a useful tool for determining how habitats differ in terms of plant performance measures and are frequently employed to guide management programs both for endangered species (e.g., Pavlik and Manning 1993, Brys et al. 2005), and for invasive species spread (Pierson and Mack 1990a, b, Crawley et al. 1993, Parker 2000, Meekins and McCarthy 2002, Buckley et al. 2003a, b). In this study, I determined whether plant performance, in terms of plant size, reproductive output and mortality, of the exotic
invasive herb *Hieracium lepidulum* (Asteraceae) varied among habitats in the mountainous landscape of the mid-Canterbury region of New Zealand's Southern Alps, in order to determine whether differences in plant performance was a component contributing to the patchy distribution of *H. lepidulum* in this landscape.

Population growth is determined by reproductive output, establishment and mortality rates (e.g., Crawley 1990). I measured seedling establishment rates in a separate seed-sowing experiment (Chapter 4); here I measured reproductive output and mortality of plants in established populations. I measured plant size because size is a measure of performance that is often correlated with reproductive output (e.g. Wesselingh et al. 1997, Buckley et al 2004a).

My previous survey work showed that *H. lepidulum* is not distributed equally among habitats in the study landscape, with a high abundance in forest creeks and canopy gaps relative to forest interior, and a decaying pattern of abundance with distance into forest interior (Chapter 3). Habitats above tree line (tussock grassland, subalpine scrub and alpine creek) have low abundance of *H. lepidulum* relative to habitats below tree line (Chapter 3). If differences in plant performance among habitats contribute to these distribution patterns, then measures of performance should be higher in plants in forest creek populations and in canopy gaps than in the forest interior. Similarly, plant performance measures should be lower in alpine habitats than in forest habitats.

My primary aim was to determine whether there were differences in plant performance among habitats that might help explain the current patterns of *H. lepidulum* distribution in the study landscape. To address this aim, I monitored plant performance of *H. lepidulum* in terms of plant size, reproductive output and mortality in seven different habitats over a two year period. Plant size, reproductive output and mortality could all be influenced either positively or negatively by local density (e.g., Belovsky and Joern 1995, Meekins and McCarthy 2000, Goldberg et al. 2001, Meekins and McCarthy 2002, Cappucino 2004), thus I accounted for local density by including distance to nearest conspecific neighbour in my analytical models.
Methods

Study Area

This study took place in catchments in the Broken River Skifield and Craigieburn Skifield basins in Craigieburn Forest Park, in the mid-Canterbury region of the Southern Alps, New Zealand (43°10’S, 172°45’E). This park is managed for recreation and conservation. The landscape is mountainous with elevations spanning 800 m to 2000 m. The mean annual temperature is 8.2°C and mean annual precipitation is 1532.7 mm (1964–2005 MetStation records, unpub. data, Landcare Research Inc.). Soils are recent or high-country yellow brown earths (Anonymous 1968). Mountain beech forest (*Nothofagus solandri* var. *cliffortiodes*) dominates from ~ 650 m to 1400 m elevation, and gives way to subalpine scrub, tussock grasslands (*Chionochloa* spp.) and alpine herbfields at higher elevations.

Experimental design

To compare plant performance among habitats, plant size, reproductive output and mortality were monitored in naturally occurring populations of *H. lepidulum* in seven habitat types: forest creek, forest edge, forest interior, canopy gap, alpine creek, tussock and scrub. These habitats were selected based on the dominant habitats invaded by *H. lepidulum* in the study area identified in my previous survey work (Chapter 3). To capture spatial variation within habitats, five populations in each habitat type were monitored. Within each population I aimed to monitor 40 individual plants; however, in four populations this was not possible because 40 individuals were not present: in one alpine creek population only 27 individuals were monitored, and in the tussock, 31, 26, and 37 individuals were respectively monitored in three of the five populations. This gave a total of 1361 individuals.

Population locations

All populations were located within five creeks randomly selected from the seven creeks occurring in the study area. Forest creek populations were located as the nearest population to a random distance up the relevant creek, and forest edge populations were located as the nearest population on the forest edge to a random distance up the creek. Because the frequency of *H. lepidulum* in the remaining five habitats is low (see Chapter 3), locations in forest interior, canopy gap, alpine creek, tussock and scrub habitat where *H. lepidulum* was known to be present were randomly chosen using plot locations from my previous
survey (Chapter 3). For these, I chose five plots for each habitat where *H. lepidulum* was present, and then located the population as the nearest population to the NZ260 Series grid coordinates of that plot. In each population, the 40 nearest plants (within a maximum 20 m radius) to a randomly located central point were permanently marked with an aluminium tag pegged to the ground at the base of each plant.

**Data collection**

The study began in January 2004 (austral summer). At this time plants were tagged, and the distance to nearest conspecific neighbour was recorded for each individual. Populations were monitored monthly from January to April 2004, and again the following spring (November 2004) and autumn (April 2005). At each monitoring date, I recorded plant size as the length of longest leaf. Leaf length has recently been used as a relative plant size trait measurement (e.g., Buckley et al. 2003a); it is quick and easy to measure, and, if it is correlated with biomass, provides a rapid, non-destructive way of obtaining plant size data for a large number of individuals. I also recorded measures of reproductive output (number of flowering stems, number of buds, inflorescences and seed heads). I recorded mortality, and replaced dead plants with the nearest untagged adult plant. For each measurement over the 2004 summer, a sample of seeding heads was collected to estimate the number of seeds produced per head; since monitoring occurred monthly, I was not able to collect seed heads from each flowering plant. At the last monitoring date (April 2005), 20 randomly chosen individuals from each population were harvested. Fresh plants were washed, separated into root, shoot and rhizome, dried for 48 hours at 65°C, and weighed.

**Analysis**

**Plant performance measures**

The following measures were compared among habitats to determine relative plant performance.

- **Leaf size**: the length (cm) of the longest leaf measured at the first monitoring date. Leaf length was used as a proxy for plant size.
- **Biomass**: total dry biomass (g) of harvested plants.
- **Probability of seed production**: whether an individual produced a seed head or not over the study period was coded as a binary variable (1 = yes, 0 = no). Whether an individual reproduces or not has obvious implications for population growth rates, could be determined by plant size, and could vary with habitat (Wesselingh et al. 1997, Buckley et al. 2003a).
- **Number of flowering stems, inflorescences and seed heads**: for each of these, I
used the maximum value counted at any one measurement. I used the maximum value for these measures because they all showed definite seasonal peaks which did not differ among habitats and differences in these maximal values captured habitat differences more effectively than the seasonal sum. Number of flowering stems was included because it is a likely determinant of the number of inflorescences and thus seeds that are produced. I examined inflorescences and seed heads separately because the presence of an inflorescence does not guarantee that a seed head will be produced. **Number of seeds per seed head:** the number of seeds produced per head for each sampled seed head. **Mortality:** Mortality rates were very low (<3.5% in all populations) over the study period, so no formal analysis was possible.

**Habitat differences**

I used maximum-likelihood based strength of evidence criteria to test seven hypotheses about how habitats might differ in terms of each of the above plant performance measures. These hypotheses were based on the observed spatial distribution of *H. lepidulum* in the study landscape (Chapter 3). This analytical method provides an alternative to traditional hypothesis testing (Burnham and Anderson 2002b). The advantage is that *a priori* hypotheses based on the biology of the study system are evaluated by the strength of evidence provided by the data, rather than using an arbitrary significance level to search for differences in the data (Burnham and Anderson 2002b).

**Habitat models**

1. **Uniform.** There is no difference in plant performance among habitats. I tested this by fitting a model with an intercept term only.
2. **Habitat.** Plant performance differs uniquely among each habitat. I tested this by fitting a model that included a categorical habitat variable with a separate category for each habitat. The next three hypotheses test for differences among forest habitats, and assume each alpine habitat differs from the others (i.e., I leave each alpine category as unique).
3. **Forest-edge.** Forest edge plants have higher levels of performance than forest interior plants, which might partially explain the high density of *H. lepidulum* in forest edges relative to forest interior. I tested this by coding forest and edge habitat as a single category and comparing this model to models where forest and edge were left as separate categories.
4. **Forest creek-gap.** Forest creek and canopy gap habitat, or disturbed forest habitats, have high levels of plant performance relative to forest interior. If this is the case, I expect no
difference in plant traits between forest creek and canopy gap habitats, but a difference between these ‘disturbed’ forest habitats and intact forest habitats. I tested this by coding forest creek and canopy gap habitat as a single category, and comparing this model to models where forest creek and canopy gap were left as separate categories.

5. Closed-disturbed forest. This hypothesis combines the previous two, with forest interior and edge comprising one closed forest habitat, and forest creeks and canopy gaps comprising one disturbed forest habitat.

6. Forest equivalent. Forest habitats do not differ in plant performance measures. I tested this by including a variable coding for ‘forest’ that comprised all four forest habitats.

7. Forest-alpine. Performance in alpine habitats is lower than in forest habitats. I tested this by including a variable coding for a ‘forest’ and an ‘alpine’ habitat type that encompassed the four forest and three alpine habitats as above.

Model fitting
I used mixed effects models (e.g., Pinheiro and Bates 2000) to test which of the seven hypotheses best explains variation in each plant performance measure. Individuals within populations are unlikely to be independent; to account for this pseudoreplication (Hurlbert 1984), I included population as a random effect in the models. For the number of seeds produced per head, multiple seed heads were sometimes collected from a single individual, meaning observations were clustered by individual. Therefore, I included individual nested within population as a random effect when testing for differences in number of seeds produced per head.

For continuous response variables (leaf size, biomass), or count variables whose distribution could be normalised with transformation (number of seeds per seed head), I used linear mixed effects models, using lme from the ‘nlme’ library in R 2.1.1 (R Core Development Team 2005, Pinheiro and Bates 2000). For binary (probability of seeding) and count variables whose distributions could not be normalised (number of flowering stems, inflorescences, seed heads), I used generalised linear mixed effects models using glmmML from the ‘glmmML’ library in R 2.1.1 (R Core Development Team 2005). For binary variables, I used a binomial error distribution, and for count variables, I used a Poisson error distribution. Both lme and glmmML provide maximum-likelihood estimates of model parameters, confidence intervals and AIC values.
I first tested the seven habitat models on each plant performance measure to determine how performance varied among habitats. I fitted models with and without the random population effect (and individual for number of seeds per seed head) included to assess the importance of population level (or individual level) variation. For vegetative performance measures (leaf size, biomass), I then tested whether density (measured as distance to nearest conspecific neighbour) added explanatory power to the best-fitting habitat model by including distance to nearest neighbour as a fixed effect. For reproductive performance measures (number of stems, inflorescences, seed heads, seeds per seed head and probability of seeding), I tested whether density or plant size added additional explanatory power to the best-fitting habitat model by including these as fixed effects. Biomass and leaf length were positively correlated (Pearson’s correlation coefficient, $r = 0.45$, $P < 0.05$), and reproductive models that included biomass or leaf length as a predictor variable produced similar results. Thus, because I had leaf length data for all individuals and biomass data for only a subset, I present the results for reproductive performance models with leaf length as an explanatory variable.

**Model Selection**

To evaluate which habitat model, and which additional explanatory variables explained variation in plant performance measures, I used strength of evidence model selection criteria to select the model best supported by the data (Burnham and Anderson 2002b, Johnson and Kristian 2004). I used Akaike’s Information Criterion (AIC) values as the strength of evidence criteria for each hypothesis. Models with the smallest AIC have the most support (Burnham and Anderson 2002a). I ranked models according to difference in AIC ($\Delta$AIC) and Akaike weight ($w_i$):

\[
{w_i} = \frac{-\exp(\Delta \text{AIC}_i)}{\sum \exp(\Delta \text{AIC})}
\]

Akaike weights provide an estimate of probability that a given model is the best fitting model of the candidate set (Burnham and Anderson 2002b, Hobbs et al. 2003). When $w_i > 0.90$, the model can be considered strongly supported by the data, when $w_i < 0.90$, the inferences resulting from each alternative model should be considered (Burnham and Anderson 2002a). When using parameter estimates from models to make inferences about the study system, and parameter estimates from alternative models are markedly different,
model averaging or model uncertainty estimates should be considered (Burnham and
Anderson 2002a). If inferences based on the set of reasonably fitting models are similar,
then sound inferences on the general result predicted by the model can be made using the
best-fitting model of the set; however the implication is that the hypothesis defined by that
particular model is not strong (Burnham and Anderson 2002a). Here, when several
candidate models were supported by the data (i.e., \( \omega_i < 0.90 \) for the best fitting model) I
examined parameter estimates of each model to determine whether model inferences
changed appreciably. I then chose the most parsimonious model.

Results

The uniform hypothesis (that all habitats are the same) was weakly supported by the data
for all plant performance measures (Table 1; see also summary of performance measures,
Table 2a), indicating that plant performance differed among habitats for all measures.
While none of the habitat models were strongly supported in terms of \( \omega_i \), (Table 1), there
was consistent support for the Forest-alpine model, and for the Forest-edge and Closed-
disturbed forest models (Table 1). Distance to nearest neighbour had a consistently positive
effect on both plant size and reproductive output, and larger plants were consistently more
fecund (Table 3).

Mortality

Mortality rates were very low in all habitats over the study period, with no evidence for a
difference in mortality rate among habitats (Table 2a).

Plant size

Leaf length (length of longest leaf) was best described by the Forest-alpine model (Table
1), with mean leaf length greater in alpine habitats than in forest habitats (Table 3a).
Although the Forest equivalent model had nearly identical support, parameter estimates
(not shown) indicated that differences in leaf length among the alpine habitats did not
warrant separation of these habitats, thus the Forest-alpine model most parsimoniously
explained the data. Biomass was best described by the Closed-disturbed forest model
(Table 1), with biomass in the closed (combined forest and edge) habitat lower than in the
open (combined forest creek and canopy gap) habitat. Biomass did not differ between open
forest, scrub and alpine creek habitat, and was highest in tussock (Table 3a).
Reproductive output

Number of flowering stems was best predicted by the Forest-edge model (Table 1); stem number was highest in tussock and alpine creek habitat, lowest in the combined forest and edge habitat, and intermediate in scrub, forest creek and canopy gap habitat (Table 3b).

Number of inflorescences, number of seed heads and number of seeds produced per seed head were all best predicted by the Forest-alpine model (Table 1), with measures higher in alpine habitats than in forest habitats in each case (Table 3b). Like other performance measures, plants close to neighbours produced more inflorescences, but number of seed heads and seeds per head was not affected by nearest neighbour distance (Table 3b).

The higher plant performance measures in the tussock habitat translated into the highest rate of per population seed production, estimated as the proportion of individuals flowering in a population of 40 individuals x the mean number of seed heads per individual x the mean number of seed per seed head (Table 2b). Alpine creek per population seed production was much lower than tussock habitat, while per population seed production was similar in forest creek and scrub habitat (Table 2b). Edge habitat had higher levels of per population seed production than gap habitat, and closed forest had the lowest level (Table 2b).

Discussion

The size and reproductive output of *H. lepidulum* plants differed among habitats monitored in this study. The most consistent difference in performance occurred between plants located in forest and alpine habitats, with plants in alpine habitats larger and more fecund than plants in forest habitats. This, in combination with the results of the seed-sowing experiment in Chapter 4, suggest that there are few barriers to both establishment and subsequent performance of *H. lepidulum* in alpine habitats. Thus, lack of sufficient seed dispersal to alpine habitats most likely explains the current relatively low abundance of *H. lepidulum* in the alpine. When forest habitats differed in plant performance measures, the results from this study show that where *H. lepidulum* was most abundant it also performed better: plant performance was lower in closed canopy forest relative to edge, forest creek and canopy gap habitat.
Implications of performance measures

In closed forest habitat, only 2% of plants monitored over the study period set seed, and in terms of total seed output, closed forest populations produced very few seed relative to all other habitats. This, and the results of the seed-sowing experiment of Chapter 4, indicates that population growth of *H. lepidulum* within closed forest systems is limited not only by low rates of establishment (Chapter 4), but is also strongly limited by seed production in established plants. This implies that the high abundance of *H. lepidulum* in forest edge habitat is due to seed input from forest creek populations, and that while these densities will remain high due to this spatial mass effect, the rate of decline in density with distance into the forest should remain steep (with the exception of canopy gaps).

Both plant performance, measured here, and seedling establishment (Chapter 4) were higher in disturbed forest habitat (forest creek and canopy gap). *Hieracium lepidulum* is similar to a suite of invasive species that are more successful in disturbed habitat in their new ranges (e.g., Crawley 1986, Fox and Fox 1986, Hobbs 1989, Hobbs and Huenneke 1992). *Alliaria petiolata*, an invasive herb in North American forest habitats, also occurs more frequently in disturbed sites, and this distribution probably arises in part because of low reproductive output in the low light conditions of closed canopy forest habitats (Meekins and McCarthy 2000). *Bromus tectorum*, a grass renowned for its dramatic invasion of the American west, also reaches smaller sizes and produces fewer seeds in forested versus open habitats (Pierson and Mack 1990a).

Total seed production was higher in forest creek habitat than in canopy gap habitat. While number of flower stems, number of inflorescences and number of seeds produced per seed head were slightly higher in canopy gap plants, canopy gap plants produced fewer seed heads than forest creek plants. Although I did not include it in this chapter, I recorded browse during population monitoring, and observed very high levels of browse on canopy gap plants; often plants were grazed back to petioles. I speculate that stronger browsing pressure on canopy gap plants relative to forest creek plants is responsible for lower total seed production in this habitat.

Alpine habitats consistently had better performing plants than forest habitats in this study: alpine plants were larger, had a greater likelihood of reproducing, and produced more seed.
per plant. In alpine creek habitat however, per population seed production was lower than in scrub or tussock habitat, resulting from a lower proportion of individuals seeding and from a lower mean number of seed heads per seeding individual in alpine creek habitat. Vegetation in alpine creek habitat tends to be composed of low, mat-forming species that do not provide the sheltering microclimates of tall tussock or shrub canopy. Possibly harsher conditions in this more exposed habitat leads to reduced reproduction. I did not observe higher levels of browse on alpine creek individuals, but it is possible that as with canopy gap habitat, higher levels of browse in alpine creek habitat, where plants are more exposed, may have reduced the number of seed heads produced.

The generally higher performance of individuals in alpine habitats parallels the results from the seed addition study (Chapter 4), in which seedling recruitment in alpine habitats was also greater than in forest habitats. Thus, competition with resident vegetation in the alpine does not prevent recruitment nor inhibit subsequent plant performance in *H. lepidulum* (although plant performance could be even higher in the absence of alpine vegetation, which I did not test). Often, recruitment is facilitated in such a manner, while later plant growth and/or fecundity are then restricted by competition with resident vegetation (Peart 1989, Meyer and Schmid 1999, Lord and Lee 2001, Foster et al. 2004, Smith et al. 2004, Eskelinen and Virtanen 2005). These results imply that alpine habitats are highly suitable for *H. lepidulum* population growth, and reinforces that low seed supply reaching the alpine may explain the current relatively low abundance of *H. lepidulum* in these habitats. As abundance of *H. lepidulum* builds below tree line, and propagule pressure in the alpine becomes greater, the spread of *H. lepidulum* in these species rich habitats is a real concern.

**Density**

Density had a positive affect on *H. lepidulum* performance measures, with plants that were located closer together being larger and more fecund. Density has been shown to have both positive and negative effects on both plant size and fecundity (Palmblad 1968, Shaw 1987, Meekins and McCarthy 2000, Lortie and Turkington 2002, Meekins and McCarthy 2002). The positive relationship between density and plant performance observed in this study could reflect favourable microsites shared by neighbours closer together, while plants in isolation could occur in less favourable microsites (e.g., Meekins and McCarthy 2002). It could also reflect increased competitive impacts of *H. lepidulum* at higher densities (e.g.,
A favourable microsite explanation is more likely here, as the result was consistent across all habitats which differ widely in resident species cover (see Chapter 4). For example, vascular plant cover in intact forest habitat is so low that competitive suppression is unlikely. However, the consistently positive relationship between *H. lepidulum* performance and proximity to neighbours warrants further study, as it has implications for how *H. lepidulum* impacts invaded communities.

**Additional factors**

Variation in the time to reproductive maturity, subsequent individual growth rates, life spans and mortality rates among habitats could also influence population growth rates and contribute to an uneven spatial distribution (Gross 1980, Wesselingh et al. 1997, Hamilton et al. 1999). For example, a slow time to reproductive maturity in alpine plants could offset the high reproductive output observed and could contribute to the current low abundances of *H. lepidulum* in alpine habitats. I intended to measure time to reproductive maturity and individual growth rates in the seed-sowing experiment, but seedling growth rates were too slow for this data to be included in this dissertation.

Mortality rates did vary among habitats, but as mortality rates were low over the course of the study period, models testing how mortality was explained by habitat differences did not converge. A longer monitoring period is necessary to obtain more accurate measures of mortality.

**Summary**

The performance of plants of the invasive herb *H. lepidulum* differed among habitats in my study area in terms of plant size and reproductive output. These differences in performance coincide partly with current spatial distribution patterns of *H. lepidulum* in this landscape, in that plants in closed forest populations had low performance relative to plants in forest creeks and canopy gap habitat, both of which are currently more invaded than closed forest. Poor performance leading to recruitment limitation may thus limit population growth in closed forest habitats, and spread within this habitat is likely to be slow. However, performance in alpine habitats, tussock grassland, alpine creek and subalpine scrub, was high, providing further support for the hypothesis that low propagule supply rates currently limit *H. lepidulum* abundance in the alpine.
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Table 5.1. Akaike weights ($w_i$) for models testing how individual performance of *H. lepidulum* varied among seven habitats. All models (linear mixed effects models for continuous response variables† and generalised linear mixed effects models for binary (binomial distribution) or count (Poisson distribution) response variables‡) were fit with and without population added as a random effect. Since all models were improved by the addition of this random effect ($\Delta$AIC ≥ 10), only models that include the random effect are reported. Best-fitting models (highest $w_i$), are in bold.

<table>
<thead>
<tr>
<th>Habitat model</th>
<th>leaf length (cm)†</th>
<th>total biomass (g)†</th>
<th># stems‡</th>
<th># inflorescences‡</th>
<th># seed heads‡</th>
<th># seeds/head‡</th>
<th>proportion seeding‡</th>
</tr>
</thead>
<tbody>
<tr>
<td>Uniform</td>
<td>0.04</td>
<td>0</td>
<td>0</td>
<td>0.14</td>
<td>0.06</td>
<td>0.06</td>
<td>0.057</td>
</tr>
<tr>
<td>Habitat</td>
<td>0.03</td>
<td>0.13</td>
<td>0.15</td>
<td>0.05</td>
<td>0.17</td>
<td>0.03</td>
<td>0.057</td>
</tr>
<tr>
<td>Forest-edge</td>
<td>0.08</td>
<td>0.33</td>
<td>0.41</td>
<td>0.03</td>
<td>0.16</td>
<td>0.09</td>
<td>0.057</td>
</tr>
<tr>
<td>Forest creek-gap</td>
<td>0.07</td>
<td>0.13</td>
<td>0.25</td>
<td>0.14</td>
<td>0.11</td>
<td>0.07</td>
<td>0.12</td>
</tr>
<tr>
<td>Closed-disturbed</td>
<td>0.18</td>
<td>0.33</td>
<td>0.15</td>
<td>0.09</td>
<td>0.11</td>
<td>0.19</td>
<td>0.15</td>
</tr>
<tr>
<td>Forest equivalent</td>
<td>0.3</td>
<td>0.05</td>
<td>0.03</td>
<td>0.14</td>
<td>0.12</td>
<td>0.15</td>
<td>0.18</td>
</tr>
<tr>
<td>Forest-alpine</td>
<td><strong>0.31</strong></td>
<td><strong>0.03</strong></td>
<td><strong>0.01</strong></td>
<td><strong>0.39</strong></td>
<td><strong>0.26</strong></td>
<td><strong>0.41</strong></td>
<td><strong>0.38</strong></td>
</tr>
</tbody>
</table>
Table 5.2. Summary of plant performance data for *H. lepidulum* individuals measured in seven different habitats. Mean values (± se) per individual are given for maximum leaf length, biomass, # stems, # inflorescences, # seed heads, and # seeds/seed head. Percentage mortality and percentage seeding is the proportion of individuals dying and the proportion of individuals producing seed out of the total number of individuals monitored per habitat. B. An estimation of per population seed production. Population seed production is estimated from the mean number of seed produced in a population of 40 individuals in one year: (% seeding) x (40 individuals) x (mean number seed heads/seeding individual) x (mean number of seeds/seed head).

A.

<table>
<thead>
<tr>
<th>habitat</th>
<th>leaf length (cm)</th>
<th>biomass (g)</th>
<th>% mortality</th>
<th>% seeding</th>
<th># stems</th>
<th># inflorescences</th>
<th># seed heads</th>
<th># seeds/seed head</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tussock (n = 174)</td>
<td>9.2 (0.26)</td>
<td>0.77 (0.099)</td>
<td>3.4</td>
<td>18</td>
<td>1.29 (0.13)</td>
<td>0.58 (0.038)</td>
<td>0.45 (0.10)</td>
<td>45.81 (0.93)</td>
</tr>
<tr>
<td>Alpine creek (n = 187)</td>
<td>7.46 (0.27)</td>
<td>0.63 (0.06)</td>
<td>2.7</td>
<td>8</td>
<td>0.74 (0.05)</td>
<td>0.58 (0.036)</td>
<td>0.14 (0.041)</td>
<td>49.28 (0.78)</td>
</tr>
<tr>
<td>Scrub (n = 200)</td>
<td>8.07 (0.28)</td>
<td>0.45 (0.073)</td>
<td>0.5</td>
<td>12</td>
<td>0.55 (0.055)</td>
<td>0.25 (0.031)</td>
<td>0.25 (0.059)</td>
<td>43.19 (0.81)</td>
</tr>
<tr>
<td>Forest creek (n = 200)</td>
<td>7.44 (0.23)</td>
<td>0.29 (0.032)</td>
<td>2</td>
<td>11</td>
<td>0.51 (0.072)</td>
<td>0.25 (0.031)</td>
<td>0.27 (0.074)</td>
<td>38.88 (0.88)</td>
</tr>
<tr>
<td>Gap (n = 200)</td>
<td>6.83 (0.23)</td>
<td>0.38 (0.06)</td>
<td>2.5</td>
<td>4</td>
<td>0.84 (0.088)</td>
<td>0.32 (0.033)</td>
<td>0.06 (0.022)</td>
<td>44.37 (1.11)</td>
</tr>
<tr>
<td>Edge (n = 200)</td>
<td>6.6 (0.20)</td>
<td>0.15 (0.011)</td>
<td>1</td>
<td>6</td>
<td>0.25 (0.033)</td>
<td>0.14 (0.025)</td>
<td>0.08 (0.026)</td>
<td>45.92 (0.94)</td>
</tr>
<tr>
<td>Forest (n = 200)</td>
<td>6.43 (0.19)</td>
<td>0.18 (0.019)</td>
<td>2</td>
<td>2</td>
<td>0.24 (0.033)</td>
<td>0.11 (0.022)</td>
<td>0.03 (0.013)</td>
<td>36.13 (1.86)</td>
</tr>
</tbody>
</table>

B.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>n</th>
<th>proportion seeding</th>
<th>mean seed heads</th>
<th>mean seeds per seed head</th>
<th>population seed production</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tussock</td>
<td>40</td>
<td>0.18</td>
<td>3.14</td>
<td>45.81</td>
<td>1036</td>
</tr>
<tr>
<td>Alpine creek</td>
<td>40</td>
<td>0.08</td>
<td>1.93</td>
<td>49.28</td>
<td>304</td>
</tr>
<tr>
<td>Scrub</td>
<td>40</td>
<td>0.12</td>
<td>3.58</td>
<td>43.19</td>
<td>134</td>
</tr>
<tr>
<td>Forest creek</td>
<td>40</td>
<td>0.11</td>
<td>3.93</td>
<td>38.88</td>
<td>672</td>
</tr>
<tr>
<td>Gap</td>
<td>40</td>
<td>0.04</td>
<td>1.9</td>
<td>44.37</td>
<td>135</td>
</tr>
<tr>
<td>Edge</td>
<td>40</td>
<td>0.06</td>
<td>1.88</td>
<td>45.92</td>
<td>207</td>
</tr>
<tr>
<td>Forest</td>
<td>40</td>
<td>0.02</td>
<td>1.13</td>
<td>36.13</td>
<td>33</td>
</tr>
</tbody>
</table>
Table 5.3. Parameter estimates (± se) for best-fitting mixed effects model for A. plant size and B. reproductive performance measures. All potential explanatory variables, including the different habitat categories defined by the habitat models (see text) are listed. (.) = variable is not present in the best-fitting model. (na) = variable was not in the set of candidate models, s.d. = standard deviation. More positive parameter estimates indicate higher performance measure values.

### A.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Performance measure (± se)</th>
<th>leaf length (cm)</th>
<th>biomass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Habitat category</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forest</td>
<td>6.78 (0.34)</td>
<td>.</td>
<td></td>
</tr>
<tr>
<td>Alpine</td>
<td>8.13 (0.52)</td>
<td>.</td>
<td></td>
</tr>
<tr>
<td>Forest-edge</td>
<td>.</td>
<td>-2.23 (0.19)</td>
<td></td>
</tr>
<tr>
<td>Forest creek-gap</td>
<td>.</td>
<td>-1.8 (0.14)</td>
<td></td>
</tr>
<tr>
<td>Forest creek</td>
<td>.</td>
<td>.</td>
<td></td>
</tr>
<tr>
<td>Gap</td>
<td>.</td>
<td>.</td>
<td></td>
</tr>
<tr>
<td>Forest Edge</td>
<td>.</td>
<td>.</td>
<td></td>
</tr>
<tr>
<td>Tussock</td>
<td>.</td>
<td>-1.07 (0.27)</td>
<td></td>
</tr>
<tr>
<td>Alpine creek</td>
<td>.</td>
<td>-1.78 (0.27)</td>
<td></td>
</tr>
<tr>
<td>Scrub</td>
<td>.</td>
<td>-1.78 (0.23)</td>
<td></td>
</tr>
<tr>
<td>Nearest neighbour</td>
<td>.</td>
<td>.</td>
<td>0.0019 (0.0012)</td>
</tr>
<tr>
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</tr>
<tr>
<td>Population s.d.</td>
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<td>0.3</td>
<td></td>
</tr>
<tr>
<td>Residual s.d.</td>
<td>3.01</td>
<td>0.97</td>
<td></td>
</tr>
<tr>
<td>Variable</td>
<td># stems</td>
<td>stem height</td>
<td>inflorescences</td>
</tr>
<tr>
<td>---------------------------</td>
<td>---------</td>
<td>-------------</td>
<td>----------------</td>
</tr>
<tr>
<td><strong>Habitat category</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forest</td>
<td>-2.59 (0.22)</td>
<td>-3.22 (0.28)</td>
<td>40.6 (1.41)</td>
</tr>
<tr>
<td>Alpine</td>
<td>0.002 (0.0006)</td>
<td>0.003 (0.001)</td>
<td></td>
</tr>
<tr>
<td>Forest-edge</td>
<td>-2.02 (0.21)</td>
<td>-2.35 (0.37)</td>
<td>45.64 (1.31)</td>
</tr>
<tr>
<td>Forest creek-gap</td>
<td>-1.85 (0.16)</td>
<td>1.57 (0.17)</td>
<td></td>
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<tr>
<td>Forest creek</td>
<td>-1.44 (0.20)</td>
<td>0.28 (0.16)</td>
<td></td>
</tr>
<tr>
<td>Gap</td>
<td>-1.59 (0.21)</td>
<td>0.71 (0.19)</td>
<td></td>
</tr>
<tr>
<td>Forest Edge</td>
<td>-2.19 (0.23)</td>
<td>0.64 (0.25)</td>
<td></td>
</tr>
<tr>
<td>Tussock</td>
<td>-1.44 (0.20)</td>
<td>0.28 (0.16)</td>
<td></td>
</tr>
<tr>
<td>Alpine creek</td>
<td>-1.59 (0.21)</td>
<td>0.71 (0.19)</td>
<td></td>
</tr>
<tr>
<td>Scrub</td>
<td>-2.19 (0.23)</td>
<td>0.64 (0.25)</td>
<td></td>
</tr>
<tr>
<td>Nearest neighbour</td>
<td>0.16 (0.001)</td>
<td>0.061 (0.016)</td>
<td>0.33 (0.02)</td>
</tr>
<tr>
<td>Leaf length</td>
<td>0.43</td>
<td>0.11</td>
<td>1.44</td>
</tr>
<tr>
<td>Population s.d.</td>
<td>na</td>
<td>na</td>
<td>na</td>
</tr>
<tr>
<td>Plant s.d.</td>
<td>na</td>
<td>na</td>
<td>na</td>
</tr>
<tr>
<td>Residual s.d.</td>
<td>0.053</td>
<td>0.56</td>
<td>3.01</td>
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</table>
Figure 1. Illustration of a single-rosetted *H. lepidulum* plant with measured parts labelled.
Chapter 6.

Quantifying the dispersal curves of the invasive herb *Hieracium lepidulum* among multiple habitats

Introduction

Variation among habitats in seed dispersal, both into and within habitats, may be an important mechanism underlying the uneven distribution of invasive species across the landscape (Williamson 1996, Lonsdale 1999, Rouget and Richardson 2003). Variation in seed dispersal rates may arise from differences among habitats in the characteristics or abundance of dispersal vectors, such as wind (Augspurger and Franson 1988, Nathan et al. 2002b, Bullock et al. 2003, Nuttle and Haefner 2005) or animals (e.g., Alcantara et al. 2000). Habitat variation in dispersal may also result from differences in how the vegetation provides a barrier to dispersal (McEvoy and Cox 1987, Bergelson et al. 1993, Cadenasso and Pickett 2001, Coulson et al. 2001, Bullock et al. 2003).

Spatial variation in dispersal rates will affect rates of population spread across the landscape (Clark et al. 2001, Bullock et al. 2002, Greene and Calogeropoulos 2002, Bullock et al. 2003): habitats in which more seeds are dispersed greater distances will be colonised at a faster rate. Thus, quantifying the relative contribution that dispersal makes to variation in the abundance of invasive species among habitats is necessary for interpreting patterns of invasive species distribution, and for accurately modelling future spread (Greene and Calogeropoulos 2002, Bullock et al. 2003, Skarpaas et al. 2005).

Dispersal is a notoriously difficult process to measure, with an intensive sampling effort required to quantify even one dispersal curve (the distribution of seed dispersed around a seed source) (Bullock and Clarke 2000, Bullock et al. 2003, Skarpaas et al. 2005). This has meant that the measurement of multiple dispersal curves in several habitats, providing the information necessary to compare dispersal patterns among habitats, is rare.
Here, my aim was to determine whether dispersal patterns of the invasive herb *Hieracium lepidulum* varied among habitats in the mid-Canterbury Southern Alps, New Zealand, in order to determine whether dispersal differences might account for differences in the abundance of *H. lepidulum* in this landscape.

My previous survey work showed that *H. lepidulum* was more abundant in forest creeks than in adjacent forest, more abundant in canopy gaps within the forest than closed forest, and evenly distributed among alpine habitats where mean abundance was low (Chapter 3). If differences in dispersal among habitats were to explain these patterns, then I predict that the number of seeds dispersing and the distance that seeds disperse away from a source should be highest in forest creeks and lowest in closed forest. Between alpine habitats, there should be little difference in seed dispersal. Differences in vegetation and landscape structure among habitats lend weight to these predictions. In the forests, creeks may act as a tunnel for wind (and thus wind-dispersed seeds), with dispersal into the forest inhibited by the physical barrier of the forest edge and by low wind speeds under the forest canopy (Willson and Crome 1989, Brothers and Spingarn 1992, Parendes and Jones 2000, Cadenasso and Pickett 2001). In the alpine, the open structure of the vegetation means that creeks do not function as a dispersal corridor to the extent that they do through forest, and once seeds reach the alpine they are relatively free to disperse throughout.

To determine whether these predictions were true, I measured twenty-five dispersal curves for *H. lepidulum* in five habitats. To allow the measurement of this relatively large number of dispersal curves, I did not increase trap area with distance from source, as necessary to maintain a constant sampling effort (e.g. Bullock and Clarke 2000, Greene and Calogeropoulos 2002, Bullock et al. 2003). Instead, I derived a model describing the dispersal curve as a function of distance from source and trap area that was based on my experimental design. This model allowed me to quantify the dispersal curve while taking into account the decline in trap area with increasing distance. I then used this model to test whether dispersal curves of *H. lepidulum* differed consistently among habitats or days on which curves were measured.

My framework for the study consisted of 1. Quantifying the dispersal curve of *H. lepidulum* by measuring the distribution of seed away from a point source in each of five habitats, in each of five locations while simultaneously recording wind speed and direction.
2. Deriving a model to describe the shape of the dispersal curve taking into account the decline in trap area with distance from source. 3. Testing whether the parameters of the dispersal curve describing the number of seeds falling at the source, and the rate of decline of seeds with distance away from the source, differed among habitats and/or days. 4. Exploring how wind characteristics explained dispersal curve parameters.

**Methods**

**Study Species**

*Hieracium lepidulum* (Asteraceae) is an exotic perennial herb that is invasive throughout mountainous areas of the South Island of New Zealand. It is rosette-forming, with flowering stems up to 80 cm tall. It reproduces solely by asexually produced seed (Chapman et al. 2004). Seed are achenes, c. 3 x 0.5 mm, with pappus 6 to 7 mm (Webb et al. 1988), and wind is the dominant mechanism of dispersal. Flowering and seeding occurs in the study region from October to May, with a peak in seed production in March (Chapter 5).

**Field Site**

This study took place in Craigieburn Forest Park, in the mid-Canterbury region of the Southern Alps, New Zealand (43°10'S, 172°45'E). This park is managed for recreation and conservation. The landscape is mountainous with elevations spanning 800 m to 2000 m. The mean annual temperature is 8.2°C and mean annual precipitation is 1532.7 mm (1964–2005 MetStation records, unpub. data, Landcare Research Inc.). Soils are recent or high-country yellow brown earths (Anonymous 1968). Mountain beech forest (*Nothofagus solandri* var. *cliffortiodes*) dominates from ~650 m to 1400 m elevation, and gives way to subalpine scrub, tussock grasslands (*Chionochloa* spp.) and alpine herbfields at higher elevations.

**Experimental design**

To determine whether the dispersal curve of *H. lepidulum* varied with habitat type, I quantified the dispersal curve of *H. lepidulum* in each of five habitats: forest creeks, forest interior, canopy gaps, alpine creeks and tussock grassland. These habitats encompass the dominant habitat types invaded by *H. lepidulum* in the study landscape, and were used in
parallel experimental and demographic work (Chapters 3, 4, 5). I did not include scrub habitat here because of the logistical difficulty in setting up the experiment in dense scrub.

**Habitats**

Forest creek. Two creeks were used in this study: Cave Stream and Broken River. Creeks were narrow (creek bed width 5 m–30 m), and were bordered either by forested terraces or forested slopes.

Forest interior. Forest interior refers to closed mountain beech forest. This forest is monospecific with little understorey and a canopy of 10 to 20 m tall.

Canopy gaps. Canopy gaps were treefall gaps within the mountain beech forest. Gaps had a minimum diameter of 18 metres. Gaps were open with scattered shrubs (*Coprosma* spp.) and mountain beech saplings and seedlings.

Alpine creek. Two branches of Craigieburn stream were used for the alpine creek habitat. Creeks were narrow with a mean width of 2 metres, and were bordered by herb field and tussock grassland.

Tussock grassland. Tussock grassland was dominated by snow tussock (*Chionochloa* spp.), with subdominant grasses and forbs in intertussock gaps.

Dispersal curves in the three forest habitats (forest creek, forest interior and canopy gap) were measured simultaneously on each of five days, and the two alpine habitats (alpine creek and tussock) were measured simultaneously on each of five days different from those used for the forest measurements. Ideally dispersal would have been measured in all five habitats concurrently, but I was constrained by datalogger availability. On each day, I measured dispersal at a different location within each habitat. This design meant that locations were not replicated, but five replicate locations were measured in each habitat, allowing me to test for differences in dispersal among habitats. Habitat locations were chosen subjectively because I had to locate each canopy gap, closed forest and forest creek site in close proximity to each other, and relatively close to the road, so that curves could be set up and taken down relatively quickly. I did not include any other constraints on location selection.

**Dispersal curve measurement**

Dispersal curves were constructed by measuring the distribution of seeds dispersed away from a point source. The point source consisted of 240 flower stems of *H. lepidulum* with 2
to 4 seed heads per stem, representing approximately 38,000 seeds (on average, 240 flower stems x 3 seed heads per stem x 53 seeds per head), inserted into a 10 cm x 30 cm block of horticultural sponge. Hieracium lepidulum flowers form seeds within 1 to 2 days of being picked, so flowering stems were collected from the field, sorted, and placed in the sponge. While this represented an artificial situation, in that dispersal was not measured from live plants, I still measured dispersal resulting from abscission of seeds from the capitula. This method was therefore more realistic than releasing collected seed which is commonly used to measure dispersal curves (e.g., Greene and Calogeropoulos 2002 and references therein), as the resulting dispersal curve incorporates the variation in resistance that wind needs to overcome to dislodge different seeds from the capitula. This method also allowed me to measure more dispersal curves, over a range of wind conditions, than would have been possible using live plants whose seeding phenology I could not control.

The point source was placed on a centre square of plastic (0.5 m x 0.5 m), and seeds were trapped in four directions away from the source along 10 m x 0.5 m transects, consisting of strips of plastic coated with Tangle-Trap Brush-On™ insect coating (Figure 1). Transect orientation was set by the creek bed orientation: two arms ran up and down the creek bed from the point source while the other two arms were perpendicular to the creek bed. Transect directions in the non-creek habitats matched the nearby creek transect directions.

At each location, the dispersal experiment was set up in the morning and seeds were left to disperse until evening, with a total dispersal time of approximately six hours. Wind speed, wind direction, and maximum 3 second gust speed were averaged at 10 minute intervals using a Campbell Scientific datalogger over this period at each location. All stems of H. lepidulum within 50 meters of a transect were removed prior to setting up the dispersal experiment. To minimize local establishment of additional H. lepidulum as a result of this study, seed was irradiated before being placed in the field by microwaving for 5 x 60 second intervals (this reduced seed viability from 85% to less than 6%, unpub. data). The number of seeds trapped in 5 cm segments along each transect was counted.

Analysis

Model derivation
I derived a model describing the dispersal curve of H. lepidulum that accounted for the decline in trapping area with distance from source (see Figure 1). Here the dispersal curve
was quantified in terms of the number of seeds dispersing into a trap segment at a given distance from the source, rather than density at a given distance. The total area that seeds could land in for a given trap segment of length \( l \) at a given distance \( d \) is the area of the arc described by circle of radius \( d + l \) minus circle of radius \( d \):

(Eq. 1) \[ \pi(d + l)^2 - \pi d^2 \]

or

(Eq. 2) \[ 2 \pi dl + \pi l^2 = \pi l(2d + l) \]

The width of the area sampled remains constant, and is four times (for the four transects) each trap segment of length \( l \) and with transect width \( w \). This area is approximated by:

(Eq. 3) \[ 4wl \]

Thus the relative area trapped at a given distance \( d \) is:

(Eq. 4) \[ \frac{4wl}{\pi l(2d + l)} = \frac{4w}{\pi(2d + l)} \]

If we assume a constant number of the available seeds, \( x \), falls in a given trap segment, then the actual number of seeds \( S \), landing in each trap segment is defined by:

(Eq. 5) \[ S = \frac{4wx}{\pi(2d + l)} \]

I then allow \( x \) to vary with distance, defined by a power function where \( a \) = a constant describing the number of seeds falling at the source, and \( b \) describes the rate of decline in the number of seeds falling with distance from source.

(Eq. 6) \[ x = ad^b \]
substituting into Eq. 6 we get

(Eq. 7) \[ S = \frac{4 w a d^b}{\pi (2d + l)} \] Trap area model

I used a power function because it is commonly used to describe dispersal curves, and it fit the data well. Although there are other functions that I could also have used, for example, the negative exponential, Clark et al.'s (1999) 2Dt model, or Bullock and Clarke’s (2002) MIX model, my aim in this study was to determine whether dispersal curve parameters differed among habitats, not to exhaustively test which of many potential curves fit the data best (e.g., Skarpaas et al. 2004). The derived model describes the number of seed falling in a given trap segment as a function of distance \( d \) and the dimensions of the sampled area.

**Describing the curve**

I compared the fit of the trap area model (Eq. 7) to a traditional power model (i.e., trap area not accounted for) to the data (Table 1).

My response variable, number of seed trapped, was a count, and the data were highly overdispersed. I therefore used a negative binomial error distribution which greatly improved the model fit relative to both a normal and a Poisson distribution (results not shown). Since the data from trap segments belonging to transects from the same location were likely to be correlated, I used mixed models that included a random location effect (e.g., Pinheiro and Bates 2000). Since I could include only one random effect in the model, I compared AIC values between model with the random effect added to either \( a \) or \( b \) to determine where the random effect could be added most effectively (Table 1).

**Habitat and day effects**

I tested for habitat differences in the slope and intercept of the dispersal curve using a model selection process. Since dispersal curves in the forest and alpine habitats were measured separately, I conducted the analyses for forest and alpine separately. For the forest and alpine, I tested four hypotheses explaining how differences in habitat and/or day could explain differences in the slope and intercept of the curve (Table 2):
1. There is no difference in the dispersal curve among habitats or day. If this is the case then the dispersal curve should be the same for all habitat x day replicates, and I tested this by fitting a model where seed dispersal is a function of distance only.

2. The dispersal curve parameters are determined by both habitat and day. I tested this hypothesis by adding both a habitat and day effect to the number of seed falling at the source \((a)\) and rate of decline of seeds falling with distance from source \((b)\) parameters of the model, and to each parameter separately.

3. Habitat differences explain differences in the dispersal curve. I tested this hypothesis by adding only a habitat effect to model parameters as above.

4. Day differences explain differences in the dispersal curve, while habitat differences are not important. I tested this hypothesis by adding only a day effect to model parameters as above.

Each model included a random location effect added to the slope parameter \(b\). All models were fit using PROC NLMIXED in SAS Version 8.0 (SAS Institute 1999) providing maximum-likelihood estimates of model parameters, confidence intervals and AIC values using the Newton-Raphson optimisation technique and the Gauss-Hermite quadrature integration to estimate random effects.

**Model Selection**

To evaluate which of the candidate dispersal curve models best described the data, I used strength of evidence model selection criteria (Burnham and Anderson 2002, Johnson and Kristian 2004). I used Akaike weights \((w_i)\) to rank models. Akaike weights are calculated from the difference in AIC values \((\Delta \text{AIC})\) between each candidate model \(i\) and the model with the smallest AIC:

\[
 w_i = \frac{-\exp(\Delta \text{AIC}_i)}{\sum \Delta \text{AIC}} 
\]

Akaike weights provide an estimate of probability that the chosen model supports the data well; if \(w_i > 0.90\), the model is considered well-supported (Burnham and Anderson 2002, Hobbs et al. 2003).
Wind and dispersal correlations

To explore how differences in wind characteristics among locations may explain differences in the dispersal curve, I tested how wind speed and direction were correlated with the number of seeds falling at the seed source \((a)\) and rate of decline \((b)\) parameters of the dispersal curve using Spearman rank correlations at the location level. For the slope parameter, I used the Best Unbiased Linear Predictors (BLUPS) from the best-fitting model identified by the model selection process above. Since I could not estimate the \(a\) parameter in this way, I instead used the number of seed dispersing in the first 20 cm for each location.

I also explored whether wind had a directional effect on seed dispersal by correlating the number of seed dispersing in each transect direction with the cumulative frequency (number of 10 minute intervals) and the mean speed of wind blowing in that direction.

Wind-habitat differences

I tested whether wind and gust speed differed among habitats with a general linear model with wind or gust speed as the response and habitat, day and a habitat:day interaction as the response. As above, I did separate analyses for the forest and alpine habitats. Models were fit using glm in R2.1.1 (R Core Development Team 2005), and wind and gust speed were log-transformed to improve normality.

I tested for directionality in wind using Chi-square tests of independence for the cumulative number of intervals that the wind blew and transect direction within each habitat.

Results

Dispersal curve fit

The trap area model (Eq. 7) described the dispersal curve of \(H.\ lepidulum\) well, and provided a better fit to the data than the traditional power model (Table 3, Figure 2). The model best supported by the data allowed the rate of decline \(b\) to vary randomly with location (Table 3).
Habitat and day effects

Individual dispersal curves differed from one another in terms of the number of seed falling at the source \((a)\), and in terms of the rate of decline of seeds falling with distance from the source \((b)\) (Figures 3, 4). There were consistent differences among days on which curves were measured in the number of seed dispersing at the source \((a)\) in both the forest and alpine habitats, with the day model that allowed \(a\) to vary best supported by the data in both areas, and little support for models that included habitat, or for the uniform model (Table 4). For the alpine, the lack of a consistent difference between tussock and alpine creek habitats in dispersal curve parameters was as expected. Among forest habitats however, I did expect a difference in dispersal curve parameters, and although habitat models were not well supported by the data relative to the day models (Table 4), parameter estimates from habitat models indicated a trend for greater dispersal in forest creek relative to canopy gap and closed forest habitat (Table 5). This is also shown by the parameter estimates in Figure 4, although the figure shows that dispersal was not always greater in forest creek habitat. Canopy gap and forest habitats did not differ consistently in dispersal curve parameters (Figure 4).

Wind and dispersal correlations

As expected, the number of seeds falling at the seed source \((a)\) was greater with stronger wind \((r = 0.48, p < 0.05)\) and gust speeds \((r = 0.36, p < 0.1)\). Also as expected, the rate of decline of seeds falling with distance from source \((b)\) was negatively correlated with wind \((r = -0.34)\) and gust speeds \((r = -0.30)\). In other words, the number of seeds dispersing to greater distances was lower when wind and gust speed tended to be lower, although these correlations were not statistically significant.

The direction of dispersal was also associated with wind characteristics, with more seed dispersing in a given transect direction when the prevailing wind was in that direction (cumulative frequency of wind blowing in a transect direction) \((r = 0.30, p < 0.01)\), and when a stronger, prevailing wind blew in the transect direction \((r = 0.41, p < 0.0001)\).

Wind-habitat differences

Wind and gust speed differed for each replicate among forest habitats and between the two alpine habitats, with a significant day x habitat interaction for both areas (Table 6a, 6b). In
the forest, mean wind and gust speed were unexpectedly high relative to forest creek and
gap habitat (Table 6a). In the alpine, mean wind and gust speed were higher in tussock than
in alpine creek habitat (Table 6b).

There were no significant directional differences in wind among habitats, although wind
tended to be more directional in forest creeks (Figure 5).

Discussion

I quantified twenty-five dispersal curves of the invasive herb *H. lepidulum* in five different
habitats under different weather conditions in mid-Canterbury uplands. These individual
curves differed from one another in terms of the number of seeds falling at the source, and
in terms of the decline in seeds falling with distance from source. There were consistent
differences among curves measured on different days, but no statistically significant
differences among habitats.

The lack of a difference in seed dispersal curves between forest creek and forest interior
(both canopy gap and closed forest) may be a consequence of a lack of statistical power.
The data showed a trend for a greater number of seeds dispersing in forest creek habitat
relative to closed forest and canopy gap habitat, thus weakly supporting the hypothesis that
differences in seed dispersal among forest habitats partially explains the high abundance of
*H. lepidulum* in forest creeks relative to forest interior. There were no consistent
differences among closed forest and canopy gap habitat, indicating that differences in
habitat resistance to invasion are more likely to explain differences in *H. lepidulum*
distribution between these two habitats.

The movement of wind-dispersed seeds is strongly influenced by vegetation structure and
site topography because these factors directly affect wind speed, direction and turbulence
(Greene and Calogeropoulos 2002, Nathan et al. 2002a, Bullock et al. 2003, Tackenberg
2003, Nuttle and Haefner 2005). For example, wind speeds beneath forest canopies are low
(Brothers and Spingarn 1992, Nuttle and Haefner 2005), forest creeks (or roads or tracks),
may act as a corridor through which wind can travel (Gregory et al. 1991, Parendes and
Jones 2000, Planty-Tabacchi 2001), while the forest edge can act as a barrier to seed
dispersal (Cadenasso and Pickett 2001). I therefore expected a greater number of seeds
dispersing and greater dispersal distances in forest creek relative to forest interior habitat. I also expected that dispersal might be greater in canopy gaps relative to closed forest because of differences in wind characteristics between these two habitats, although canopy gaps could also act as a funnel for wind and thus seeds travelling over the forest canopy (Augspurger and Franson 1988). I attempted to address the latter by quantifying natural seed rain into canopy gaps relative to closed forest in a parallel study, but data were too sparse to draw any conclusions (unpublished data).

Here, I showed that dispersal patterns of *H. lepidulum* were correlated with wind characteristics; however, I could not show that differences in wind characteristics among habitats led to differences in seed dispersal among habitats. Instead, this study shows that seed dispersal and wind patterns are highly variable and site specific. Over a topographically complex landscape such as my study site, five replicate locations do not appear to be sufficient to find general patterns in this variation. On the other hand, the results could accurately reflect the biological reality of wind conditions in a windy, mountainous landscape with relatively short, open forests. Perhaps habitat differences can not be expected to override the effects of dramatic differences in weather conditions.

**Summary**

I quantified twenty-five dispersal curves of *H. lepidulum* in five different habitats under different weather conditions; a greater number of dispersal curves over a wider range of conditions than has previously been measured. Dispersal curves differed among days on which curves were measured, and dispersal curve parameters were correlated with wind conditions with a greater magnitude of dispersal and longer dispersal distances in windier conditions. There were no significant differences in dispersal curves among the experimental habitats, although there was a tendency for a greater number of seeds to disperse longer distances in forest creeks relative to forest interior. There were no consistent differences in dispersal curves between canopy gap and closed forest habitat, or between tussock grassland and alpine creek habitat. These results provide limited support for the hypothesis that facilitation of seed dispersal in forest creeks, due to channelling of wind, contributes to the high abundance of *H. lepidulum* in forest creeks relative to forest interior, and that dispersal differences are unlikely to drive differences in *H. lepidulum* abundance among alpine habitats.
References


Institute, S. 1999. SAS 8.0. in, Carey, NC, USA.


Nathan, R., H. S. Horn, J. Chave, and S. A. Levin. 2002a. Mechanistic models for tree seed dispersal by wind in dense forest and open landscapes. Pages 69-82 in D. J. Levey,


Table 6.1. Structural equations for models tested to describe the shape of the dispersal curve of *H. lepidulum* in the study area. The trap area model (Eq. 7 in text) models the number of seed dispersing a given distance \( d \) while taking trap area into account. The power model \((\log(S) = a + b*\log(d))\), models the density of seed dispersing a given distance \( d \). In both models, \( S \) is the number of seeds landing at a given distance, \( a \) is a parameter controlling the intercept, or number of seeds falling at the source, and \( b \) is a parameter controlling the slope, or rate of decline in the number of seeds falling with increasing distance away from the source. Each model was fit with and without a random location effect \((u)\) added to each of \( a \) and \( b \). All models were fit with a negative binomial error distribution to account for overdispersion, and include an overdispersion parameter \( k \).

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter random effect ((u)) added to</th>
<th>Model Structure</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trap area</td>
<td>no random effect</td>
<td>( 200ad^b/n(2d + 5) )</td>
</tr>
<tr>
<td></td>
<td>( b )</td>
<td>( 200ad^{(b+u)}/n(2d + 5) )</td>
</tr>
<tr>
<td></td>
<td>( a )</td>
<td>( 200(a+u)d^b/n(2d + 5) )</td>
</tr>
<tr>
<td>Power</td>
<td>no random effect</td>
<td>( a + b^*\log(d) )</td>
</tr>
<tr>
<td></td>
<td>( b )</td>
<td>( a + (b+u)^*\log(d) )</td>
</tr>
<tr>
<td></td>
<td>( a )</td>
<td>( (a+u) + b^*\log(d) )</td>
</tr>
</tbody>
</table>

Table 6.2. Structural equations for models tested to determine how the dispersal of *H. lepidulum* differs among habitats and weather conditions (days) in the study area. All models use the trap area model (Eq. 7 in text), and are fit with a random location effect \((u)\) added to parameter \( b \). All models were fit with a negative binomial error distribution to account for overdispersion, and include an overdispersion parameter \( k \).

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter varied with habitat and/or day</th>
<th>Model Structure</th>
</tr>
</thead>
<tbody>
<tr>
<td>Uniform</td>
<td>( b )</td>
<td>( 200*(a)^*d^b/n(2d + 5) )</td>
</tr>
<tr>
<td></td>
<td>( a )</td>
<td>( 200*(a+u)^*d^b/n(2d + 5) )</td>
</tr>
<tr>
<td>Habitat</td>
<td>( b )</td>
<td>( 200*(a)^*d^{(b+\text{habitat})}/n(2d + 5) )</td>
</tr>
<tr>
<td></td>
<td>( a )</td>
<td>( 200*(a + \text{habitat})^*d^b/n(2d + 5) )</td>
</tr>
<tr>
<td>Day</td>
<td>( b )</td>
<td>( 200*(a + \text{day})^*d^b/n(2d + 5) )</td>
</tr>
<tr>
<td></td>
<td>( a )</td>
<td>( 200*(a + \text{day})^*d^b/n(2d + 5) )</td>
</tr>
<tr>
<td>Habitat + Day</td>
<td>( a )</td>
<td>( 200*(a)^*d^{(b+\text{habitat} + \text{day})}/n(2d + 5) )</td>
</tr>
<tr>
<td></td>
<td>( b )</td>
<td>( 200*(a + \text{habitat} + \text{day})^*d^b/n(2d + 5) )</td>
</tr>
<tr>
<td></td>
<td>( a ) and ( b )</td>
<td>( 200*(a + \text{habitat} + \text{day})^*d^{(b+\text{habitat} + \text{day})}/n(2d + 5) )</td>
</tr>
</tbody>
</table>
Table 6.3. Akaike weights ($w_i$) for candidate models describing the shape of the dispersal curve of *H. lepidulum* in the study area. The best-fitting model (bold) has the highest $w_i$.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter random effect ($\mu$) added to $w_i$</th>
<th>$w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trap area</td>
<td>no random effect</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td><strong>0.95</strong></td>
</tr>
<tr>
<td></td>
<td>a</td>
<td>0.05</td>
</tr>
<tr>
<td>Power</td>
<td>no random effect</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>a</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 6.4. Akaike weights ($w_i$) for models testing how dispersal of *H. lepidulum* differs with habitat and day in New Zealand’s Southern Alps for A. forest habitats (forest creek, forest interior, canopy gap) and B. alpine habitats (alpine creek, tussock grassland). The best-fitting model (bold) has the highest $w_i$.

A.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter varied with habitat and/or day</th>
<th>$w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Uniform</td>
<td>b</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>a</td>
<td>0</td>
</tr>
<tr>
<td>Habitat</td>
<td>b</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>a</td>
<td>0.03</td>
</tr>
<tr>
<td>Day</td>
<td>b</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>a</td>
<td><strong>0.88</strong></td>
</tr>
<tr>
<td>Habitat + Day</td>
<td>b</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>a</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>a and b</td>
<td>0</td>
</tr>
</tbody>
</table>

B.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter varied with habitat and/or day</th>
<th>$w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Uniform</td>
<td>b</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>a</td>
<td>0</td>
</tr>
<tr>
<td>Habitat</td>
<td>b</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>a</td>
<td>0.0045</td>
</tr>
<tr>
<td>Day</td>
<td>b</td>
<td><strong>0.99</strong></td>
</tr>
<tr>
<td></td>
<td>a</td>
<td>0.0039</td>
</tr>
<tr>
<td>Habitat + Day</td>
<td>b</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>b</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>a and b</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 6.5. Parameter estimates for *H. lepidulum* dispersal curves estimated by the trap area model in three forest habitats (forest creek, canopy gap, closed forest). Although this model was not the best-fitting of the candidate models (Table 4a), it illustrates that there was a trend for greater dispersal in forest creek habitat relative to gap and closed forest habitat. The best-fitting forest habitat model allowed parameter $a$ (the number of seed falling at the source) to vary with habitat, while $b$ (the rate of decline in seeds falling with distance from source) remained constant. ($u$ is the random effect of location on slope parameter $b$, $k$ is the dispersion parameter for the negative binomial error distribution).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>estimate</th>
<th>se</th>
</tr>
</thead>
<tbody>
<tr>
<td>a Forest creek</td>
<td>1078.97</td>
<td>272.48</td>
</tr>
<tr>
<td>Gap</td>
<td>402.67</td>
<td>288.31</td>
</tr>
<tr>
<td>Forest</td>
<td>763.3</td>
<td>332.03</td>
</tr>
<tr>
<td>b</td>
<td>1.18</td>
<td>0.092</td>
</tr>
<tr>
<td>k</td>
<td>0.5</td>
<td>0.049</td>
</tr>
<tr>
<td>u</td>
<td>0.10</td>
<td>0.0012</td>
</tr>
</tbody>
</table>
Table 6.6. Habitat mediation of wind and gust speed (m/s). Mean wind and gust speed were measured simultaneously in A. forest creek, forest and gap habitats on five days, and B. alpine creek and tussock habitats on five separate days. ( = data not available).

### A.

<table>
<thead>
<tr>
<th>Day</th>
<th>wind† or gust ‡ speed (m/s)</th>
<th>Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Forest creek</td>
</tr>
<tr>
<td>1</td>
<td>wind</td>
<td>0.33</td>
</tr>
<tr>
<td></td>
<td>gust</td>
<td>0.24</td>
</tr>
<tr>
<td>2</td>
<td>wind</td>
<td>2.54</td>
</tr>
<tr>
<td></td>
<td>gust</td>
<td>1.51</td>
</tr>
<tr>
<td>3</td>
<td>wind</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td>gust</td>
<td>0.33</td>
</tr>
<tr>
<td>4</td>
<td>wind</td>
<td>1.86</td>
</tr>
<tr>
<td></td>
<td>gust</td>
<td>1.06</td>
</tr>
<tr>
<td>5</td>
<td>wind</td>
<td>0.66</td>
</tr>
<tr>
<td></td>
<td>gust</td>
<td>0.03</td>
</tr>
</tbody>
</table>

†glm results: habitat \( F_{2,584} = 7.01, p < 0.01 \); day \( F_{4,584} = 68.54, p < 0.0001 \); day:habitat interaction \( F_{7,584} = 64.78, p < 0.0001 \)

‡ glm results: habitat \( F_{2,584} = 27.57, p < 0.0001 \); day \( F_{4,584} = 1.04, p = 0.38 \); day:habitat interaction \( F_{7,584} = 90.95, p < 0.0001 \)

### B.

<table>
<thead>
<tr>
<th>Day</th>
<th>wind† or gust ‡ speed (m/s)</th>
<th>Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Alpine creek</td>
</tr>
<tr>
<td>1</td>
<td>wind</td>
<td>0.68</td>
</tr>
<tr>
<td></td>
<td>gust</td>
<td>0.31</td>
</tr>
<tr>
<td>2</td>
<td>wind</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>gust</td>
<td>0.45</td>
</tr>
<tr>
<td>3</td>
<td>wind</td>
<td>.</td>
</tr>
<tr>
<td></td>
<td>gust</td>
<td>.</td>
</tr>
<tr>
<td>4</td>
<td>wind</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>gust</td>
<td>0.04</td>
</tr>
<tr>
<td>5</td>
<td>wind</td>
<td>0.65</td>
</tr>
<tr>
<td></td>
<td>gust</td>
<td>0.01</td>
</tr>
</tbody>
</table>

†glm results: habitat \( F_{1,671} = 1384.89, p < 0.0001 \); day \( F_{4,671} = 236.24, p < 0.0001 \); day:habitat interaction \( F_{3,671} = 120.24, p < 0.0001 \)

‡ glm results: habitat \( F_{1,671} = 642.05, p < 0.0001 \); day \( F_{4,671} = 121.33, p < 0.0001 \); day:habitat interaction \( F_{7,584} = 12.175, p < 0.0001 \)

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Figure 6.1. Experimental design for quantifying the dispersal curve of *H. lepidulum*, with dimensions used to derive the trap area model (Eq. 7 in text). A seed source (a block of seeding stems) was placed in the centre of four 10 m x 0.5 m transects aligned at right angles. Transects were strips of plastic coated with Tangle-Trap Brush-On™ insect glue. A photograph of the experimental set-up in closed forest habitat is also shown.
Figure 6.2. The dispersal curve of *H. lepidulum* predicted by the trap area model (solid line) and actual dispersal data (points). The actual data are the mean number of seed dispersing per 20 cm trap segments plotted versus distance from source.
Figure 6.3. Seed dispersal curves of *H. lepidulum* for three forest habitats on five days predicted day the best-fitting model (see Table 2 for candidate models). The best-fitting model allowed the number of seed dispersing at the source \((a)\) to vary with day, and the day estimates for \(a\) from this model are provided in the plot margin to the left. The parameter estimates for the rate of decline in the number of seed dispersing with increasing distance \((b)\) given for each curve are from the Best Unbiased Linear Predictors (BLUPS) estimated for \(b\) from this model, while the \(a\) estimates for each curve are the total number of seed dispersing up to 20 cm. The total number of seed trapped in 5 cm trap segments for the four transects combined is plotted versus distance from source.
Figure 6.4. Seed dispersal curves of *H. lepidulum* for two alpine habitats on five days predicted by the best-fitting model (see Table 2 for candidate models). The best-fitting model allowed the number of seed dispersing at the source (*a*) to vary with day, and the day estimates for *a* from this model are provided in the plot margin to the left. The parameter estimates for the rate of decline in the number of seed dispersing with increasing distance (*b*) given for each curve are from the Best Unbiased Linear Predictors (BLUPS) estimated for *b* from this model, while the *a* estimates for each curve are the total number of seed dispersing up to 20 cm. The total number of seed trapped in 5 cm trap segments for the four transects combined is plotted versus distance from source.
Direction

Figure 5. The relative frequency (number of 10 minute intervals) of wind blowing in the four transect directions for the three forest habitats on five days.
Chapter 7.

General Conclusions

Chapter 2. Spatiotemporal spread dynamics

*Hieracium lepidulum* occurs in nearly half of the NZMS 260 series grid squares on the South Island. Spatial distribution is centred in Canterbury, Otago and inland Marlborough, all sites where *H. lepidulum* was recorded relatively early. Spread rates and frequency of occurrence have been highest in Canterbury and Otago, although the recent arrival of *H. lepidulum* on the West Coast and in Southland may see an increase in the spread of *H. lepidulum* in these regions in the near future. *Hieracium lepidulum* has been most frequently recorded in tussock grasslands and scrub, although it has occurred in a range of habitats since it was first recorded in New Zealand, including indigenous forest, riparian and rock habitats, herb fields, ruderal habitats and exotic pastures and forestry plantations.

Chapter 3. Creeks as sources of spread in the landscape

Within the mid-Canterbury region of the Southern Alps, *H. lepidulum* invasion has so far been concentrated in forest creek habitat, where abundance of *H. lepidulum* is high relative to surrounding beech forest and alpine habitats. The abundance of *H. lepidulum* declined with increasing distance into the forest from creeks, the abundance of *H. lepidulum* in adjacent forest was correlated with abundance in forest creeks, and the strength of the correlation declined with increasing distance into the forest. This relationship held when environmental variables that also explained *H. lepidulum* abundance were controlled for. This suggests that high density populations of *H. lepidulum* in forest creeks are acting as sources for spread into adjacent forest.

Among alpine habitats, *H. lepidulum* was sparse and abundance was not concentrated in alpine creeks, but was patchily distributed throughout all habitats. However, when *H. lepidulum* was more abundant in alpine creeks, it was more likely to be present in adjacent alpine habitats, implying that propagule supply is also important in driving spread in the alpine.
There was also evidence that forest creeks act as a source of spread of *H. lepidulum* into the alpine, with *H. lepidulum* more likely to occur in Craigieburn alpine habitats with higher abundances of *H. lepidulum* below tree line.

The landscape level distribution patterns of *H. lepidulum* in mid-Canterbury suggest that forest creeks act as sources for spread both into surrounding forest and up into the alpine. The steep decline of *H. lepidulum* into forests and patchy distribution throughout the alpine suggested that dispersal might limit the spread of *H. lepidulum* from creek populations into forests, but was less likely to be important in the alpine. This made sense in terms of the differing vegetation structure of the two environments, with the forest edge providing a barrier to wind and thus dispersal, and no such barrier in the alpine. However, habitat differences in resistance to invasion also provided a plausible explanation for these spatial distribution patterns. Without knowledge of relative invasion resistance among habitats, I could not say whether spread into the forest and/or alpine was a dynamic moving front, or a static 'spatial mass' effect. And without knowing anything about population dynamics or dispersal patterns within established populations, I could not say how these also might contribute to the measured distribution patterns.

**Chapter 4. Quantifying resistance to establishment**

In Chapter 4, I quantified habitat resistance of forest creek, canopy gap, forest interior, alpine creek, tussock grassland and subalpine scrub habitat to *H. lepidulum* establishment using a comparative dose-response approach, wherein the establishment response of *H. lepidulum* to seed sowing density was measured in each habitat. I defined resistance as the rate of seedling establishment given a propagule supply, or the slope of the dose-response curve, and as the saturation density at which further seed addition ceased to result in additional seedling establishment, or the asymptote of the dose-response curve.

Habitat resistance to *H. lepidulum* establishment was lowest in tussock grassland and alpine creek habitats, with both high rates of establishment and high saturation densities in these habitats. This implies that resistance to establishment does not explain the low abundance of *H. lepidulum* in alpine areas. Among forest habitats, resistance to invasion was low in forest creek and canopy gap habitat relative to the interior, implying that differences in resistance to establishment among forest habitats could at least partly explain
the high abundance of *H. lepidulum* in forest creeks and canopy gaps relative to the forest
interior.

This experiment suggested that differences in timing of recruitment between the forest and
alpine explained final differences in establishment success, with high rates of initial
seedling emergence in the forest followed by high seedling mortality, and continuous rates
of seedling emergence in the alpine with low mortality. I suggest that the sheltering effects
of the diverse vegetation present in tussock grassland and alpine creek habitat provided
safe sites for establishment that were not provided in the forest.

In forest habitats, establishment rates and saturation levels were higher with higher soil
fertility and light levels. This could partially explain differences among habitats in *H.
lepidulum* abundance, with both soil fertility and light higher in forest creek and gap
habitat than forest interior.

In summary, this experiment indicated that resistance to establishment did not explain the
low abundance of *H. lepidulum* in alpine areas, suggesting that lack of seed reaching the
alpine was a more likely explanation. However, differences in resistance to establishment
could, at least in part, explain the low density of *H. lepidulum* in closed forest habitat
relative to forest creeks and canopy gaps. However, variation in plant performance in
established populations could potentially also contribute to the observed spatial distribution
patterns. For example, alpine plants could perhaps establish easily, but could then be
outcompeted by the vegetation that facilitated their establishment and have low
reproductive output. Or forest seedlings could have difficulty establishing, but once
established may reproduce prolifically. I could also not discount the additional effect that
variation in dispersal patterns within habitats could have on patterns of distribution. For
example, facilitation of seed dispersal within forest creeks could also contribute to the high
abundance of *H. lepidulum* in forest creek habitat beyond differences in resistance to
establishment.

**Chapter 5. Variation in plant performance among habitats**

Plant performance, in terms of size and reproductive output, did vary with habitat, and
varied in a manner consistent with the patterns identified in chapter 4: performance in
alpine habitats was high, and performance in forest creek and canopy gap habitat was high
relative to forest interior. This reinforced my conclusions from chapter 4, strengthening the argument that a lack of seed dispersal into alpine habitats to date has meant that these areas have remained relatively sparsely invaded. The high performance of plants in alpine populations, coupled with high rates of establishment are a cause for concern about spread of *H. lepidulum* in the alpine, as once *H. lepidulum* becomes established more widely in the alpine, the potential for rapid spread is high. *Hieracium lepidulum* has the potential to dominate alpine areas: in a few alpine locations in parts of central Otago, it is present at close to 100% cover (Alan Mark, pers. comm.), while in induced lowland grasslands in the Harper-Avoca *H. lepidulum* dominates on south-facing slopes; in later summer slopes are painted yellow with *H. lepidulum* flowers (pers. obs.). This should provide incentive for land managers to target control efforts on alpine populations while populations are still relatively small. As forest creek populations do appear to be acting as a source for *H. lepidulum* spread into the alpine, then high density forest creek populations also need to be targeted. Unfortunately, at this point this is easier said than done. If an effective biocontrol agent for *H. lepidulum* is found, then release sites could be focussed within forest creek habitats.

**Chapter 6. Quantifying dispersal curves**

Variation in the dispersal curve of *H. lepidulum* was better described by differences among days on which the curves were measured than by differences among habitats. Nevertheless, there was a trend for more seed to disperse longer distances in forest creek relative to forest interior and canopy gap habitat. Forest creek habitat had a greater tendency to channel the wind, but did not have higher mean wind or gust speeds than forest interior or canopy gap habitat. The number of seed dispersing and the rate of decline in the number of seed dispersing with distance were correlated with wind speed and direction: more seed dispersed further with a stronger prevailing wind. Thus, the channelling of the wind in forest creeks may lead to higher rates of seed dispersal, and this likely contributes to the high density of *H. lepidulum* in forest creeks.

**Conclusions: Population growth and spread of *H. lepidulum***

The data presented in this dissertation, in addition to seed longevity data and other demographic data collected but not presented here, will be used in future work to simulate the spatial spread of *H. lepidulum* over the landscape. This simulation does not appear in this dissertation. However, here I use the data to calculate the finite rate of increase (λ) per
habitat, and discuss the implications of this in terms of spread over the mid-Canterbury upland landscape.

I calculated $\lambda$ as:

$\lambda = \frac{N_t}{N_{t-1}} \quad \text{(Eq. 1)}$

$N_{t-1}$ here, is a population of 40 individuals of *H. lepidulum*. $N_t$ is the estimated size of this population after one year, resulting from recruitment (R) and mortality (M):

$N_t = N + R - M \quad \text{(Eq. 2)}$

$R =$ number of new recruits into the population. Recruitment was estimated as per population seed production (estimated as $N_{t-1} \times$ the proportion of individuals in a population seeding $\times$ the mean number of seed heads produced per seeding individual $\times$ the mean number of seeds/seed head (Chapter 5, Table 2b)) $\times$ the rate of seedling establishment (estimated from the dose-response curve (Chapter 4, Table 3c)).

$M =$ number of adult plants dying over the study period. Mortality was estimated as $N_{t-1} \times$ the proportion of individuals dying (Chapter 5, Table 2).

If $\lambda > 1$, then population growth is positive, and *H. lepidulum* is spreading, if $\lambda = 1$, then the population is stable, and if $\lambda < 1$, then population growth is negative and *H. lepidulum* is declining.

The finite rate of increase ($\lambda$) was greater than one in all three alpine habitats and in forest creek habitat, and close to one in canopy gap, forest edge and closed forest habitat (Table 1). Thus, without external seed inputs, *H. lepidulum* is capable of invading and spreading in all alpine habitats and in forest creek habitat, and capable of maintaining a stable population in canopy gap, and closed forest edge and interior habitat. This indicates that once established, populations in forest habitats can maintain themselves, but will not spread without additional seed input. Thus, seed inputs from high density forest creek populations appear necessary for *H. lepidulum* to continue spreading in the forest.
Different factors limit the rate of population increase among habitats. Population growth in alpine creek habitat is reduced by low seed production due to low proportion of individuals flowering and production of a relatively low number of seed heads per individual. In scrub habitat, low rates of seedling establishment, are offset by high seed production. Population growth in canopy gap habitat is also limited by seed production, and this is perhaps due to higher browse on inflorescences and seed heads in this habitat. Growth of populations in closed forest habitat is limited by both low seed production and low seedling establishment rates.

**Limitations**

Additional factors could influence population growth rates and thus contribute to an uneven spatial distribution among habitats. Time to reproductive maturity, individual plant growth rates and life span could influence population growth rates, and I do not yet have estimates for these parameters. Habitats in which time to reproductive maturity is faster will see faster population growth rates, and it is possible that a more rapid time to reproductive maturity could offset individual reproductive output. Similarly, based on the positive relationship between plant size and reproductive output demonstrated in Chapter 5, plants that grow more quickly as adults will produce more offspring. Plants growing in alpine habitats could be expected to grow more slowly than plants below tree line because of the harsher climate in the alpine, and this could potentially slow population growth in the alpine.

I measured seedling growth rates in the seed-sowing experiment (Chapter 4), but did not include those results in Chapter 4 as seedlings were still very small and data were preliminary. Two years after seed was sown, seedlings were largest in scrub habitat, smallest in forest creek habitat, and similar in the remaining four habitats. I recorded changes in leaf length over time in Chapter 5 as a measure of individual growth, but over the relatively short time frame that plants were monitored, did not observe a significant change. At this point, I therefore cannot draw any conclusions about habitat variation on time to maturity or subsequent individual growth rates, and can only say that these could alter the results reported here.
My estimate of recruitment (R) was based on seedling establishment given within-population seed production and estimated within-habitat seedling establishment rate. The seedling establishment rate incorporates both seed and seedling mortality, but it does not account for any differences in initial seed viability among habitats. I tried to test for among-habitat variation in seed viability with the seed collected from natural populations in Chapter 5, but was unsuccessful due to fungal contamination of Petri dishes.

I estimated recruitment based on seed production within populations, and did not consider seed addition from external (i.e., outside population sources). Variation in external seed inputs, which I did not measure, could change the rates of population increase.

Conclusions
Together, the results presented here indicate that variation in population vital rates and external seed inputs (implied based on the results) can explain the uneven distribution of *H. lepidulum* among habitats in the mid-Canterbury Southern Alps landscape. Variation in dispersal patterns among habitats appears less important in contributing to the spatial distribution of *H. lepidulum*. High density populations of *H. lepidulum* in mid-Canterbury forest creeks act as a source of spread for *H. lepidulum* into adjacent forests. The observed pattern of decline of *H. lepidulum* with distance into the forest reflects a spatial mass effect, with external seed inputs necessary for *H. lepidulum* to spread in forest interior habitats (including edge, canopy gap, and closed forest). Forest creeks also appear to act as a source for spread into alpine habitats, but in the alpine, there is a dynamic invasion front, current low abundance of *H. lepidulum* in the alpine is low because of an apparent paucity of seed reaching the alpine, and *H. lepidulum* is expected to increase in alpine habitats.
Table 7.1. The finite rate of increase ($\lambda$) of *H. lepidulum* in seven habitats, if $\lambda > 1$, population growth is positive and *H. lepidulum* is increasing, if $\lambda = 1$, population growth is stable, if $\lambda < 1$, population growth is negative and *H. lepidulum* is declining.

$$\lambda = \frac{N_t}{N_{(t-1)}}$$

$N_{(t-1)}$ is taken as a population of 40 individuals of *H. lepidulum.*

$N_t$ is the estimated size of this population after one year, resulting from recruitment (R) and mortality (M):

$$N_t = N + R - M$$

$R$ = number of new recruits into the population, estimated as per population seed production (estimated as $N_{(t-1)} \times$ the proportion of individuals in a population seeding $\times$ the mean number of seed heads produced per seeding individual $\times$ the mean number of seeds/seed head (Chapter 5, Table 2b)) $\times$ the rate of seedling establishment (estimated from the dose-response curve (Chapter 4, Table 3c)).

$M$ = number of adult plants dying over the study period (estimated as $N_{(t-1)} \times$ the proportion of individuals dying (Chapter 5, Table 2)).

<table>
<thead>
<tr>
<th>Habitat</th>
<th>$N_{(t-1)}$</th>
<th>proportion seeding</th>
<th>mean seed heads/seeding individual</th>
<th>mean seeds/seed head</th>
<th>population seed production</th>
<th>rate of establishment</th>
<th>new recruits (R)</th>
<th>proportion dying</th>
<th>number dying (M)</th>
<th>$N_t$</th>
<th>$\lambda$</th>
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<tbody>
<tr>
<td>Tussock</td>
<td>40</td>
<td>0.18</td>
<td>3.14</td>
<td>45.81</td>
<td>1035.52</td>
<td>0.072</td>
<td>74.56</td>
<td>0.034</td>
<td>1.36</td>
<td>113.2</td>
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<td>1.93</td>
<td>49.28</td>
<td>304.13</td>
<td>0.059</td>
<td>17.94</td>
<td>0.027</td>
<td>1.08</td>
<td>56.86</td>
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<tr>
<td>Scrub</td>
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<td>3.58</td>
<td>43.19</td>
<td>741.54</td>
<td>0.03</td>
<td>22.25</td>
<td>0.005</td>
<td>0.2</td>
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<tr>
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<td>38.88</td>
<td>672.49</td>
<td>0.035</td>
<td>23.54</td>
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<tr>
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<td>45.92</td>
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<td>0.011</td>
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<td>0.8</td>
<td>39.56</td>
<td>0.99</td>
</tr>
</tbody>
</table>
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