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Simulating the spread of *Hieracium lepidulum* in heterogeneous landscapes

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

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by Steven Wangen 2012

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Abstract for a thesis submitted in partial fulfilment of the requirements for the Degree of Doctor of Philosophy.

Simulating the spread of *Hieracium lepidulum* in heterogeneous landscapes

by Steven R. Wangen

The invasion of non-indigenous species represents a severe threat to the health of native communities world-wide. In order for us to be effective and efficient at mitigating the economic and ecological impacts of these invasions, it is critical that we improve our understanding of how specific traits of the invader interact with characteristics of their new environment. Understanding these dynamics can help to improve the efficacy and economy with which we are able to apply control efforts. At the same time, we can examine if there are predictable patterns of spread which are produced from those interactions, and generalise those patterns to other invasions. In order to address these aspects of invasion, I developed a simulation model utilising a highly detailed and expansive data set which reflects the demography and dispersal of one particular species, *Hieracium lepidulum*, as it invades a mountainous area on the South Island of New Zealand. The scope and fidelity of this dataset is such that it permits me to develop models of the demography and dispersal of the species reflecting habitat-specific variation within the invaded area. These models are then combined using a customised simulation software to create a spatially and temporally explicit simulation of *H. lepidulum* spread. These simulations are applied across a range of hypothetical landscapes which are constructed to represent varying degrees of abstraction of the actual landscape; the simulations are applied at different scales, and the landscapes represent mixtures of the component habitats at varying degrees of complexity and spatial configurations. The outcomes of these simulations are then used to address a number of general questions intended to identify if there are some simplifying principles that can be used when evaluating invasive spread, and to examine how these results compare to currently postulated theories regarding the spread of invasions, and how their progression is influenced by context of the landscape.

Keywords: dispersal, demography, invasive spread, *Hieracium lepidulum*, simulation, matrix population model, Bayesian hierarchical modelling

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Chapter 1

Introduction

1.1 Introduction

Non-indigenous invasive species constitute one of the largest threats to the health of ecosystems worldwide. Examples of the competitive dominance of these invaders over native species has been well documented, and threatens the overall health and stability of native communities (Wilcove et al. 1998; Gurevitch & Padilla 2004; Pimentel et al. 2005; Schwartz et al. 2006; Hejda et al. 2009; Vilà et al. 2011; Pyšek et al. 2012). While the definition of what constitutes an 'invasive' is debated, for the purposes of this work I will consider an invasive species to be any non-native pest organism which threatens the health, productivity, or diversity of a native community. The addition of these new species to the local pool can superficially have a positive effect on biodiversity, however the shift in dominance and the resulting increase in competition can threaten the existence of some local native species, pushing them closer to eventual extirpation or extinction (Ricciardi 2004) and promoting an increase in biological homogenisation (McKinney & Lockwood 1999; Collins & Storfer 2003; Olden & Rooney 2006). Additionally, the change in community structure brought about by invasion may incur indirect effects, such as the modification of ecosystem functioning. Examples include the lowering of water tables (Zavaleta 2000), alteration of fire regimes (Anable et al. 1992; Brooks et al. 2004), and impacting soil properties (Vitousek & Walker 1989; DiTomaso 2000; Liao et al. 2008).

The economic burden of mitigating these impacts is impressive; one study estimates that the economic cost of invasive species in the United States exceeds \$120 billion USD annually (Pimentel et al. 2005). The most recent estimates for Great Britain suggest that these costs exceed \$2.7 billion USD (Williams et al. 2010), and more than \$1.4 billion USD in New Zealand (Ministry of Forestry and Agriculture 2010). The economic burden wrought by invasions are not only due to the direct costs of controlling the invasions, but are further compounded by associated decreases in productivity of desired species (Pimentel et al. 2005). While the most cost-effective solution to mitigating the economic effects of non-indigenous invasive species is often preventative action (Leung et al. 2002), these measures can be difficult to justify politically and challenging to fund. Currently, individual species invariably slip through the established safeguards, and a fraction of those proceed to incur serious impacts on the economy, ecological systems, and even human health (Lodge et al. 2006).

While the long-term nature of these impacts and our role in altering invasion processes is currently debated (Collins et al. 2002; Brown & Sax 2004; Cassey et al. 2005; Stohlgren et al. 2008), the majority of management directives seek to actively pursue their removal and the minimisation of impacts whenever possible. As such, one of the primary benefits that research into invasions can provide is to increase the accuracy with which we can predict invasive species movement. This helps in two ways; first, we can increase the economy of control efforts. With the limited budgets inherent to natural resource management, increases in efficiency effectively permit the expansion of efforts to address a greater range of threats, instead of narrowing the focus to only a few. Additionally, the increased economy of control efforts may free up some resources for enacting preventative measures. The second benefit of increasing the predictive accuracy is the potential to reduce potentially harmful non-target impacts that may materialise as an unintended consequence of control efforts; i.e. unintentionally opening up growing space for herbicide-resistent invaders through the use of herbicides, or ineffectively applying mechanical control efforts that unintentionally promote dominance by the invasion (Smith et al. 2006). More judicious and effective application of management may be possible by improving our understanding of the processes involved. Together these benefits can go a long way towards furthering the health of native systems.

An example of a potentially detrimental invasion is the expansion of *Hieracium lepidulum* (Stenstroem) Omang (Asteraceae), a European native, into mountain stream catchments in the Southern Alps of New Zealand. *H. lepidulum* is an aggressive invader which has been associated with decline in native communities and pasture productivity in New Zealand (Rose et al. 1995; Radford et al. 2007, cf. Meffin et al. 2010). Other *Hieracium* species are also invasive in New Zealand; in particular, *Hieracium pilosella*, which tends to be more abundant in both protected areas (Jesson et al. 2000) and particularly in locations utilized for pasture (Duncan et al. 1997; Rose & Frampton 1999)where it can decrease the productivity of pasture lands (Bosch et al. 1996). *H. pilosella* relies on wind dispersal for long distance dispersal, but local spread is clonal via rhizomes (McIntosh et al. 1995). In contrast, *H. lepidulum* spread is wholly reliant on seed dispersal, resulting in spread and demographic dynamics which are uniquely different to those of *H. pilosella*.

While the relative isolation of New Zealand may make is less likely to be exposed to invaders, the high level of endemism present has been linked to increased invasibility (Borges et al. 2006; Daehler et al. 2006). Recent surveys identify *H. lepidulum* as becoming established to varying degrees in the different habitats that make up these catchments (Miller 2006). In an effort to obtain a clear picture on the dynamics and impacts of this invasion, a series of seed sowing trials were initiated, in which *H. lepidulum* was sown

at a range of densities across the spectrum of habitats found in these catchments and monitored over a period of years. The results of these trials have been used to examine the spatial patterning (Miller 2006) and the impacts (Meffin 2010) of the invasion.

This dissertation extends the previous work of Miller (2006), who initiated the seed sowing trials in order to investigate the invasion of H. lepidulum into stream catchments of the Craigieburn Range in Canterbury, New Zealand. The results of those sowing trials revealed that the germinability of H. lepidulum is highly dependent on the vegetative context, defined using six different habitat classifications. These germinability trials suggested that the forest habitat (which is situated between the higher elevation alpine habitats and the anthropomorphic landscape below) was relatively unsuitable for H. lepidulum, and its position in the landscape could potentially act as a barrier, restricting the invasion from reaching the higher elevation alpine habitats. These trials also indicated a high level of germination in the riparian forest creek corridors. This was particularly important because these forest creek corridors form a contiguous link through the forest habitat, connecting the higher elevation alpine areas to the anthropogenic landscape below. Because of their invasibility and spatial juxtapositioning, these corridors could potentially facilitate the invasion of H. lepidulum into the higher elevation alpine habitats by allowing it to bypass the barrier posed by the forest habitats.

The previous work initially set out to investigate the validity of this theorised spread dynamic by developing a demographic model describing the entire lifecycle of H. *lepidulum*. Unfortunately, the development of H. *lepidulum* in these sowing trials was much slower than initially anticipated; so much so that none of the recruits became reproductive during the timespan of the original analyses. Because of this delay, the original analysis was limited to focusing on the initial recruitment, and was therefore not able to address the longer-term sustainability of the invasion. However, following the initial investigation, the sowing plots continued to be revisited and reassessed annually over the next few years. This additional observational period expanded the original data source to reflect a more complete picture of the lifecycle of H. *lepidulum*.

In this thesis I will use this expanded source of demographic data coupled with additional datasources to develop a spatial spread model which incorporates detailed demographic and dispersal components. These models are implemented in a spatial context using a simulation platform which is built around a geographic information system. This approach allows me to simulate the growth and spread of the population, which in turn provides an opportunity to investigate a number of questions which are both specific to this invasion and address invasive processes in general. My primary lines of investigation regarding the invasion are as follows:

1. does the inclusion of spatial interactions alter demographic dynamics within the population?

- 2. How does spatial heterogeneity in landscape structure influence demographic performance?
- 3. How does spatial heterogeneity in landscape structure influence invasive spread?

The focus of this thesis lies in exploring the details of the invasive population dynamics, and the invasion progression across the landscape. Addressing these aspects of the invasion allow me to evaluate which locations and community assemblages are at highest risk of invasion, and how the spatial configuration of the landscape can influence invasion success. Understanding these dynamics can provide an improved comprehension of how control efforts can best be applied to achieve the desired outcome. As this is a complex suite of questions that covers a large spatial and temporal extent, it does not lend itself well to being tested with traditional field manipulation experiments. Instead, I employ a simulation-based approach, through which I can project the spread of invasion across artificially manipulated landscapes that represent the existing landscape at different levels of complexity. This simulation is developed by combining detailed dispersal modelling with comprehensive demographic models to create virtual populations of an invasive plant, and allows me to recreate landscapes and their relevant features virtually, and use these representations to simulate spread. This approach provides an economy that allows me to address a much larger range of situations using real-world data than would otherwise be possible.

1.2 Biological Context

The bulk of the data utilised in this thesis is obtained from a data collection effort focused on describing the invasion of *H. lepidulum* into montane catchments in the Southern Alps of western Canterbury, New Zealand. This thesis builds largely upon a foundation established by a previous thesis, which by surveying the catchments found evidence to suggest that there exist significant differences in the establishment and abundance of H. lepidulum in different habitats (Miller 2006). The spatial configuration of the habitats within the landscape appear to play a central role in determining how the invasion unfolds; an intact forest of *Nothofagus* spp., which is thought to be relatively resistant to invasion by H. lepidulum, currently appears to be acting as a barrier, preventing the invasion from reaching the alpine habitats which exist at higher elevations. However, stream corridors which dissect the catchment appear to be quite suitable to invasion, and may be contributing to the spread of the invasion by acting as a vector which allows the invasion to bypass the relatively inhospitable forest habitat and reach the higher elevation alpine habitats. The scale of these habitats is such that homogeneous areas are generally large enough to contain all but the furthest dispersal events of H. lepidulum, and therefore their size and configuration are highly influential to spread.

The previous work has provided much of the foundation necessary to complete this thesis. This includes data collection from field surveys, which provide an estimate of current H. lepidulum abundance in the different habitats. Additionally, the initiation of a seed sowing experiment provided replicated recruitment trials at different densities in each habitat; the continued monitoring of these experiments has provided demographic data that has been vital to this thesis. Additional demographic data was obtained from monitoring tagged individuals and seed burial experiments. Seed dispersal trials were also performed; although they were not originally designed with the intention of simulating dispersal, they have proved quite an excellent data source for such a purpose.

Collectively, the existing sources of demographic data permit me to develop a set of detailed demographic models which I use to project the population growth of *H. lepidulum*. These projections allow me to examine differences in susceptibility to invasion of the different habitats that comprise the study landscape. In addition, I develop a mathematical kernel that describes the dispersal distances of individual *H. lepidulum* seeds. These two elements are employed in a custom-scripted simulation software package that combines them into a spatial-demographic model, which I use to simulate the growth and spread of the invasive population. These simulations are then used to investigate invasion dynamics across a range of virtual landscapes in an effort to examine the influence of landscape heterogeneity on invasion success.

1.3 Modelling Context

The concept of quantifying the spread of organisms has been around for quite some time. but it has more recently begun to move more to the forefront of ecological research. Fisher's (1937) examination of the application of diffusive processes to the movement of genes along a singular dimension and Skellam's (1951) subsequent application of the diffusion solution to a two-dimensional examination of mammalian spread established the reaction-diffusion approach as the standard method to describe spread, and are still compared against quantitative models of organism spread that are developed today. These works provided an elegant solution, where spread was represented as a traveling wave, expanding at a constant rate outward from the initial introduction point. This singular expansion rate results from the cumulative effect of the dispersal distances of many individuals being described using a Gaussian distribution, as in Brownian motion (Skellam 1951; Okubo & Levin 2002). While the applicability of the Gaussian kernel to describe dispersal was questioned early on (Bateman 1950; Wallace 1966; Taylor 1978), the reaction-diffusion model was still widely applied to describe and quantify spread (i.e., Okubo 1980; Kareiva 1983; Andow et al. 1990). It remained the only approach incorporating both demography and dispersal until research began to highlight the influence and frequency of relatively rare long distance dispersal events (Shigesada et al. 1995; Liebhold et al. 1992), and the application of other kernels began to be explored in concert with

demography to model spread (Neubert et al. 1995; Kot et al. 1996; Clark 1998; Higgins & Richardson 1999).

One of the most important advancements from this line of research was the recognition that these relatively rare long-distance dispersal events have a disproportionate effect on overall spread rates (Moody & Mack 1988; Neubert & Caswell 2000; Nathan & Muller-Landau 2000; Nehrbass et al. 2007). As a result, research began to examine the frequency of these events more closely. Before long, it was observed that leptokurtic dispersal kernels (those with positive kurtosis) reflect a distribution with a flatter peak and fatter tails than Gaussian dispersal, which in turn results in a higher probability of extreme or longdistance dispersal events, and lead to increased rates of spread (Kot et al. 1996). Although properly parameterising these functions can be challenging (Nathan 2001; Nathan et al. 2003), studies have shown that the frequency of long distance dispersal events are typically better represented by these leptokurtic distributions, which increases the frequency of these of those highly influential long-distance events (Wallace 1966; Kot et al. 1996; Clark 1998; Clark et al. 1999).

Concurrently, the relative importance of the interactions between demographic processes and spread rates was also beginning to gain ground (van den Bosch et al. 1992; Higgins et al. 1996; Neubert & Caswell 2000). Early applications of diffusion models incorporated a simple per-capita reproductive rate (Fisher et al. 1937; Skellam 1951). The spread rates estimated using this model were relatively insensitive to changes in the demographic parameter(s), suggesting that the role of demography is relatively inconsequential in determination of spread rates compared to that of the dispersal processes. However, more recent investigations found that with the application of leptokurtic dispersal kernels, the relative influence of demography on spread rates increased (Higgins et al. 2003). In addition, research has revealed the existence of an interdependency between demographic processes and the spatial distribution of individuals (or groups of individuals), where dispersal influences demography, and in turn, demography influences dispersal (Hanski 1991; Neubert & Caswell 2000; Jongejans et al. 2008). This recursive feedback between the two processes highlights how an accurate depiction of demographic processes can be just as critical as dispersal mechanisms when attempting to achieve accurate and useful projections of population spread.

As the complexity of the processes involved in modelling invasive spread increases, more flexible approaches are required to integrate them into predictive models. Not until the application of integro-difference equations (IDEs) did it become relatively easy to link different demographic sub-models with a wide array of dispersal sub-models in a succinct form (Kot et al. 1996; Hastings et al. 2005). This approach can be very elegant as it is typically analytically tractable, extremely flexible, and can be used to produce estimates of spread velocities (Caswell et al. 2003; Neubert & Parker 2004). However, in this dissertation I strive to simulate the movement of an invasion over a heterogeneous landscape represented as a cellular (raster) structure, using a discrete population model. In such an application, IDEs can be difficult and computationally intensive to apply, limiting their potential extent and/or resolution (Westerberg & Wennergren 2003). Instead, I utilise a slightly different approach which applies population growth via a stage-structured matrix population model, and implements dispersal of individuals as separate processes. Both these processes are applied within a geographic information system (GIS) framework. This approach is similar to an IDE in how the population growth and dispersal elements are combined to predict spread, but applying the processes independently within the GIS framework provides an intuitive approach that is easier and less computationally intensive to implement. In addition, this approach makes it relatively simple to implement stochastic variation in demographic parameters, which can have a significant effect on the accuracy and usefulness of any predictions derived from the model (Clark 2003; Buckley et al. 2005; Hooten & Wikle 2008).

1.3.1 Heterogeneous environments

While many of the approaches described above have been used successfully, the level of detail examined is often inadequate for real world situations. Populations spreading across a landscape are destined to encounter variations in their environment that modulate their success. While propagule pressure and climate appear to be primary factors limiting population movement at large (continental) scales, spatially explicit measures of habitat suitability and traversability can explain a great deal of variation at smaller scales (Dobzhansky et al. 1979; With 2002; Chytry et al. 2008). This variation can depend on a number of characteristics, including nutrient availability (Huenneke et al. 1990; Davis et al. 2000), community structure (Burke & Grime 1996; Wiser et al. 1998; Bulleri et al. 2008), disturbance (Tilman 1997; Gross et al. 2005), or interactions between these characteristics (Diez et al. 2009). In addition, the patterning and magnitude of these types of heterogeneity can have marked impacts on the movement of a population (With 2002). In this thesis, I attempt quantify the differences in demography and dispersal between the clearly identifiable vegetation communities that exist within a study landscape in order to assess their influence on the growth and spread of an invasive population. By independently parameterising models of both demographic and dispersal processes for each habitat, I am able to examine how these processes are operationally different in the various habitats, and use this information to examine how the spatial arrangement of habitats affects spread across a landscape.

1.3.2 Use of Bayesian methods

For much of the demographic modelling performed in this thesis, I use a hierarchical Bayesian approach to quantify parameter values. This approach has a number of advantages to modelling invasive spread. Although there are philosophical arguments regarding the tradeoffs between traditional frequentist hypothesis testing approach and Bayesian approaches (see Ellison 2004; Clark 2005; Stephens et al. 2007), my decision to use Bayesian approaches for some analyses was largely pragmatic. First, this approach streamlines the analysis of available data. These data contains an inherently complex nested structure, and would otherwise be cumbersome to analyse in a more traditional frequentist framework (i.e. Diez et al. 2009). Second, the hierarchical model framework allows me to explicitly define and approximate the uncertainty in the parameter estimates, which helps to isolate parameter estimates from the asymptotically declining confidence intervals associated with increasing sample size (Clark 2003). This provides estimates of uncertainty in the parameter values, and less a function of the number of observations. Lastly, the specification of models in the Bayesian hierarchical framework provides a straightforward approach to model data using distributions other than the normal distribution, permitting additional flexibility during the model specification.

The use of the approximations of parameter uncertainty (obtained from the hierarchical Bayesian estimation technique) to define the potential sample space during the simulations is also beneficial in a number of ways. First, the output from this approach provides parameter estimates in the form of posterior distributions, which define the distribution of parameter estimates as a vector of estimated values. These posterior distributions are easily incorporated into a simulation framework by constructing a method to sample the resultant vector. Additionally, as covariance between parameters can be specified in the model structure, utilising the estimates from the vectors which are simultaneously estimated will inherently account for this covariance without having to explicitly include it in the simulation. This is implemented by drawing from the same position in those vectors for each iteration of the simulation. Using this approach, once the parameter estimates are calculated, the incorporation of parameter variability within the simulation is relatively robust and straightforward.

1.4 Goals of the Thesis

This thesis is divided into two sections. In the first section, I develop the components necessary to simulate invasive spread, and describe the development of demographic models (Chapter 2), dispersal models (Chapter 3), and the software necessary to integrate them (Chapter 4). In the second section, I show how components of the first three chapters can be combined to simulate the spatial dynamics of invasive spread; first by using a small-scale simulation to examine the spatially dependent aspects of population growth (Chapter 5), and then by examining how the spatial configuration of habitats can influence invasive spread (Chapter 6). I then conclude with a final chapter to summarise the work and look ahead. In Chapter 2 I focus on examining how the demographic success of the invasive population is influenced by the surrounding community. This is achieved by developing detailed demographic models based on the life cycle of the invader while incorporating the appropriate mechanisms regulating population growth. These demographic models are then parameterised using data collected in each of the different habitats that together make up the heterogeneous landscape. This approach allows me to then use these models to make realistic projections of population growth for each of the individual habitats. I can then use these projections to examine how the potential for invasion success varies across the landscape. This is a critical component in analysing the effect of landscape heterogeneity on invasive spread, as it provides a robust method for quantifying the variation in population-level success between the different habitats, and allows me to evaluate how and to what variation between habitats influences the success of the invasive population.

Chapter 3 focuses on quantifying seed dispersal. The pattern of seed dispersal plays a large role in determining the rate at which a plant invasion advances. In order to evaluate seed dispersal, I fit a range of dispersal kernel forms in order to determine which provide the best fit to the data. I then examine how some of the model forms differ, and the implications of these differences for describing dispersal. In addition, I use habitatspecific model parameterisations to examine how dispersal varies from one habitat to another, and what the potential implications are for variation in dispersal between the different habitats.

The third step (Chapter 4) focuses on developing a platform where the demographic and dispersal models from the first two steps can be integrated in a spatial simulation. This platform builds upon a pre-existing simulation software package that has been developed to simulate spread. I develop a new module for the existing software that permits demographic models to be incorporated, expanding the existing dispersal functionality. While the primary goal of this module is to implement the demographic models specific to this thesis, a good deal of effort was expended to assure that the functionality of the module is flexible enough to accommodate a wide range of applications.

Finally, I integrate all three of these components into a series of spatial simulations which utilise the demographic models and the dispersal models to investigate invasion dynamics, both at a relatively local 30x30m homogeneous landscape to investigate implications of model structure (Chapter 5), and in a larger 3x3km landscape to examine the effects of habitat heterogeneity on spread (Chapter 6). As noted earlier, the inclusion of both the demographic and dispersal processes in a simulation is an important step, as neither process operates in isolation of the other. Their interaction is what ultimately determines the 'success' of the invasion, in terms of abundance and spread rate. As implementing the full demographic and dispersal models is computationally intensive, the simulations run at smaller scale in Chapter 5 are used to determine the range of population trajectories in the different habitats. This information is then used to implement the simulations across a larger landscape in Chapter 6, which allows me to examine the implications of landscape structure over a spatial and temporal range that would not be possible using traditional field-based observation or manipulation approaches.

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Chapter 2

Using demographic projections to infer invasibility in different habitats

2.1 Introduction

Quantifying the inherent invasibility of a system with regard to a specific organism can be accomplished by determining how likely an invasive population is to persist in that system. Observational data can tell us if a species is currently present or not, but evaluating the demographic processes that underlie the population-level dynamics can provide additional information about the persistence and severity of the invasive population. These processes can be investigated through the development and application of traditional life cycle models, which are typically developed using observational demographic data. These models can be used to produce both estimates of the probability of population persistence and of the population-level growth for a specific species. The analysis of these models can also reveal more subtle dynamics within the population, such as if it is self-sustaining, or reliant on supplemental propagule influx from outside sources. Understanding such dynamics can have a significant impact on options for successful management. Similar applications of demographic models are used in population viability analysis (PVA), which assesses the extinction risk posed to populations of threatened species (Boyce 1992; Burgman et al. 1993; Meekins & McCarthy 2002). Although less common, similar principles can also be used to predict the susceptibility of different environments or community assemblages to invasive species. Once the demographic models are developed, they can be used to estimate population-level metrics such as growth rates, population size, and reproduction rates which in turn can be used to project the long-term potential of an invasive population (Parker 2000; Caswell 2001; Burns 2008).

Historically the simplest demographic models predominately utilised linear models of population growth, which describe growth as a constant rate that can be approximated using a minimum of observations (Groenendael et al. 1988). This simplification can be useful to describe short term trajectory of the population in order to identify if the population is in immediate danger of going extinct or threatening to become invasive. However, it has been known for some time that as populations continue to develop, growth rates will not remain constant, but will typically decline as the population approaches a maximum size limit (Pearl & Reed 1920; Verhulst 1838). The assumption of a constant growth rate therefore quickly becomes invalid when projecting population growth. In reality, population growth is regulated by a number of processes, including density-dependence, environmental feedback, sex ratios and proportional membership in the different lifestages (Caswell 2008). These processes constantly provide feedback to the system, resulting in a growth rate that is continually changing (Parker 2000; Freckleton et al. 2003; Koons et al. 2005). Incorporating these types of processes into demographic models allows us to develop projections of population growth which are more realistic and more informative than a static linear response.

Just as it is important to incorporate how regulatory processes affect population growth, it is also important to recognise that many of these processes respond differently to different environments. At a landscape scale, it is often possible to delineate different habitats as a relatively coarse measure of change in environmental conditions or community assemblages. Such heterogeneity at the landscape scale has been shown to explain a large portion of the variation in demographic responses (Horvitz & Schemske 1995; Koop & Horvitz 2005; Maron & Kauffman 2006), as well as having a direct influence on the success and spread of invasive species (With 2002; Hastings et al. 2005; Christen & Matlack 2006; Melbourne et al. 2007). In this chapter, I develop the framework of a demographic model for a particular invasive species, and then parameterise the model independently for the six different habitat types found in a landscape currently under threat of invasion. I then use these models to simulate population growth in the different habitats, and use the results to identify habitat-specific differences in invasibility. A perturbation analysis is then performed on the parameterised models to examine the sensitivity of the models to changes in the different parameters. Traditionally these analyses focus on incrementally modifying one parameter at a time to observe the resultant change in population growth rates (Heppell et al. 2000; Caswell 2008). However, the demographic models explored here incorporate population regulation via density-dependent effects, which means that the growth rate is subject to change as a function of the current state of the population. Because of this, it is more informative to examine the sensitivity of the equilibrium population size to changes in parameter values, instead of the growth rate (Grant & Benton 2000; Caswell et al. 2004). The differences between the habitat-specific parameterisations of the demographic models and their sensitivities to various parameters are explored, which allows me to identify those parts of the life-cycle of the invader that are affected by habitat, and which of these stages are most critical to population success. This information is then used to identify which life stages and/or transitions might be targeted to refine management options in an effort to improve their effect and economy.

In addition to being influenced by regulatory processes and landscape heterogeneity,

stochastic behaviour in the population can have a marked impact on the population trajectory (Sebert-Cuvillier et al. 2007; Keith et al. 2008). Demographic models based on mean parameter values can provide an average trajectory, but incorporating stochasticity into the projections of the population can add an additional dimension by allowing us to not only explore the average outcome, but also develop an estimate of how much variability to expect in those outcomes. Understanding this variability helps us to estimate how certain we can be in the predictions, and just how much potential variation exists in the system (Buckley et al. 2005; Melbourne & Hastings 2008). How this stochasticity is incorporated into the models can be important; using a bottom-up approach and quantifying the stochasticity in lower-level processes of population behaviour (such as reproduction and mortality) can provide a more robust and informative depiction of variability at the population level, as opposed to directly assessing the variability of the higher-level population response (Melbourne & Hastings 2009). Incorporating this variability as stochastic behavior at these lower levels while simulating population trajectories can provide a clearer picture of how the specific sources of variation propagate through the system, and what the cumulative effects of that variation might be. The projections then have the potential to provide a more accurate assessment of the population-level behaviour (Tenhumberg et al. 2008) as well as the magnitude and source of variability within in the system (Regan et al. 2002; Calder et al. 2003).

In this chapter I apply these concepts in an effort to investigate the invasion of *Hieracium* lepidulum (Stenstroem) Omang (Asteraceae) (a European native) into mountain stream catchments in the Southern Alps of New Zealand. H. lepidulum is an aggressive invader which is often associated with decline in native communities or pasture productivity in New Zealand (Rose et al. 1995; Radford et al. 2007; however see Meffin et al. 2010). Recent surveys identify *H. lepidulum* as becoming established to varying degrees in the different habitats that make up these catchments (Miller 2006). The catchments typically range from approximately 800 to 2000m above mean sea level (AMSL), and are typified by two major vegetation types; mountain beech forest (Nothofaque solandri var. cliffortioides) is the dominant vegetation up to approximately 1400m, where it gives way to a mixture of sub-alpine scrub and tussock grasslands. The forest matrix at lower elevations consists of an almost pure monoculture of mountain beech which forms a dense canopy, resulting in an open understorey. Within the forest, openings caused by stream corridors and occasional treefall gaps typically support more vegetation on the forest floor (Wiser et al. 1998). At higher elevations, the alpine communities are primarily a matrix of tussock grassland (dominated by *Chinochloa* species) interspersed with patches of low-growing scrub and dissected by alpine creek habitats. These alpine areas support a relatively rich assemblage of species, making them a priority for conservation. Below approximately 800m the catchments flatten out into larger river basins which consist primarily of an anthropomorphically modified landscape, largely dominated by pastoral areas and interspersed with roads.

Previous survey work (Miller 2006) suggests H. lepidulum is invading upslope from the modified landscape at lower elevations and moving towards the alpine areas, where it is feared it will negatively impact the native flora. These same surveys also indicate that H. lepidulum densities are currently quite low underneath the intact beech canopy. This suggests that the intact forest may be inhospitable to populations of H. lepidulum, and could be acting as a natural barrier to the invasion. In contrast, the stream corridors in these catchments tend to have higher densities of H. lepidulum, suggesting that this habitat is more invasible. Based on these observations, it is hypothesised that the invasion may be utilising these stream corridors as an invasion vector to bypass the (presumably less invasible) forest habitat, and spread to the alpine areas.

In an effort to test this hypothesis, a seed sowing experiment was initiated in one of the catchments to compare the recruitment rates of H. lepidulum in different habitats, as a way to quantify their differential invasibility. Successful recruitment of H. lepidulum in the alpine habitats (alpine creek, scrub, and tussock) during these sowing trials suggest that they are susceptible to invasion, even though the survey data indicates they currently exhibit relatively low levels of occupancy of H. lepidulum. In addition, at least some level of recruitment occurred in all three of the lower elevation habitats, albeit significantly less in the intact forest compared to the forest creek or gap habitats (Miller 2006). While these results help to explain observed differences in abundance between the forest habitats, it suggests that the intact forest and forest gap habitats are not completely resilient to invasion by H. lepidulum.

Based on the survey data and the hypothesis that stream corridors are serving as the primary vector for the invasion, control efforts could selectively target populations within the stream corridors, and potentially cut off the population's access to the alpine habitats. However, given the evidence that recruitment does occur in the forest and forest gap habitats, control efforts targeting only the stream corridors may be not be as effective as previously thought. Unfortunately the results from the seed sowing trials only reflect the initial recruitment of H. lepidulum, and the germination of individuals from seed in these habitats does not necessarily translate to the establishment of a viable population. Given the available data, it remains unclear if the levels of recruitment observed from these trials would lead to persistent populations.

In order to further explore the ability of populations of *H. lepidulum* to persist, I develop a series of demographic models in this chapter which I use to assess the long-term viability of populations in the different habitats. Independent parameterisations of the model are used to project population trajectories in each habitat into the future, and thus determine in which habitats the invasion will be successful. In this case the demographic processes are represented using a matrix population model, with the individual transition probabilities within the matrix estimated from field data. Where sufficient data exists, regulatory processes such as density dependence have been incorporated into the sub-models used to estimate the individual transition probabilities within the matrix, providing more realistic

projections of population growth. Ideally, data for parameterising the model would be obtained by monitoring a population from inception until it reaches a stable equilibrium; unfortunately, plant populations can take an extremely long time to fully develop and occupy all available growing space (up to hundreds of years or more; Pyšek & Jarošík 2005). As an alternative, I have adapted more of a bottom-up approach to constructing the model, where data are collected from individuals in a range of conditions (densities and habitats), and parameters estimated from these data are then used to obtain populationlevel projections. This permits a more rapid development of population-level projections, which can then be used to examine the plausibility of the hypothesis that the stream corridors are serving a vector for invasion.

Successfully assessing the invasibility of the different habitats and understanding the full range of potential outcomes requires an accurate description of the uncertainty and variability present in the different components of the system. In order to properly quantify that uncertainty, I have utilised a Bayesian hierarchical fitting procedure to estimate model parameters. This approach allows me to quantify the uncertainty associated with each parameter, providing parameter estimates in the form of posterior distributions as opposed to a singular static value. These estimates can then be incorporated into the simulated projections by using the posterior distributions to define the sample space for stochastic parameter behaviour. The results of these projections then reflect the propagation of variability from relatively low level processes up to the final estimates of population size. I also employ a sensitivity analysis to examine which parts of the life cycle are critical to the persistence of the population, and if these critical stages are different for different habitats. This information is then evaluated to determine if control measures can be refined to target specific vulnerabilities in the life cycle of H. lepidulum.

2.2 Materials and Methods

2.2.1 Study species

H. lepidulum is a perennial herb, native to northern and central Europe where it is commonly found in high elevation meadows. First recorded in New Zealand in 1941 (Wiser et al. 2000), it has become a prolific weed in New Zealand, invading a wide range different habitat types (Duncan et al. 1997; Wiser et al. 1998). Concern over the presence of this invader stems from its association with the decline of a number of native communities (Rose et al. 1995; Wiser et al. 2000), although a recent investigation failed to find a direct link between its presence and any decline in native species (Meffin et al. 2010). The juvenile and adult growth forms of *H. lepidulum* are easily distinguished; in the juvenile stage, the plant exists as a low-growing individual no more than approximately 5cm in height, typically with two leaves. Upon sexual maturation (marked by the presence of flowering) the plant bolts and produces a distinct central stem, typically to a height of
10cm or more. On this stem the plant produces additional cauline leaves as well as one or more flowers. The seeds of *H. lepidulum* are relatively small (approximately 3x0.5mm) and have a 6-7mm pappus with plumose bristles (Webb et al. 1989). These characteristics make the seed ideally suited to dispersal by wind, and their apomictic nature permits viable seed to be produced without pollination (Chapman et al. 2003).

2.2.2 Data collection

The data used in this study was collected from the Southern Alps of Canterbury, New Zealand. The study area consists of two adjacent stream basins (Broken River and Craigieburn) within the Craigieburn range, located at approximately 43.13° S 171.71° E. Six primary habitats have been identified in these catchments; forest, forest creek, canopy gap (treefall gaps), alpine creek, tussock grassland, and scrub. The forest, forest creek, and forest gap habitats occupy lower elevations within the stream catchments, generally ranging from approximately 800 to 1400m AMSL. These three habitats coexist in a matrix which consists primarily of forest habitat. The forest habitat is typified by a dense canopy of mountain beech (N. solandri), and is interspersed with occasional windfall gaps (forest gap habitat), typically caused by the loss of a single tree or small group of trees. The forest creek habitat reflects the more open conditions which occur adjacent to the creeks which dissect the catchment, and is comprised largely of stream banks or open gravel. Above approximately 1400m, the catchment is dominated by tussock grasslands, which consist primarily of long-lived *Chionochloa* species with a mixture of alpine herbs and grasses that occupy the inter-tussock spaces. Intermixed with the tussock grassland are patches of scrub habitat, dominated by low-growing (approximately 30-100cm) woody shrubs. The alpine creek habitat are those areas directly adjacent to the creeks that dissect these upper reaches of the catchment, and are also comprised largely of stream banks and open gravel.

Four field experiments were performed to obtain demographic data on H. lepidulum. These data were used to parameterise the models which describe the probability of a H. lepidulum individual transitioning between different stages of its life cycle. These field experiments included 1) a field survey of existing H. lepidulum distribution, 2) monitoring of tagged individuals of H. lepidulum, 3) a seed sowing trial, and 4) a seed burial experiment. These experiments were initially established by Alice Miller as part of her PhD thesis (Miller 2006); subsequent years of data collection were performed by myself and others. The use of multiple data sources allowed for the demographic model to reflect the full life cycle of H. lepidulum; however, this approach also introduced a few shortcomings. Observations of adult mortality did not account for the density or size of conspecifics, and therefore does not incorporate the density-dependent regulatory mechanisms which are included in the models of juvenile survival. In addition, the seed sowing experiments from which the observations of juvenile survival collected from were even-aged cohorts and did not

produce adults until the final two years. As such, the density-dependent mechanisms incorporated into the models of juvenile survival reflect the influence of similarly sized individuals. In application, the models of juvenile survival account for the total number of individuals present in a cell across all life stages, but assume that they have similar influences, as opposed to attributing a larger influence to the adult individuals. This effectively results in a conservative estimation of the density dependent mechanisms by downplaying the influence of adult individuals.

Field survey

Survey data were collected for a previous investigation in the austral summer of 2003/04 to describe the distribution and abundance of *H. lepidulum* in these catchments (Miller 2006). Ten (10) randomly chosen creeks from two adjacent catchments within the Craigieburn Range were chosen for survey. Transects were placed perpendicular to the creek every 100m (side chosen at random) until the creek was no longer identifiable, and extended into the adjacent habitats for 100m. Five 2x3m plots were located randomly along the transect and surveyed for *H. lepidulum* abundance. Counts of abundance were performed at six 1x1m subplots within each plot. Mean abundances across these subplots are used to estimate density per m^2 , and summarised by the six habitat types for analysis. Measurements reflecting the number of individuals present were recorded for a total of 1068 plots.

Tagged individuals

Five patches of H. lepidulum in each of the six habitats were randomly selected from those identified during the field survey. In each patch 40 flowering individuals were selected for monitoring. Four of the patches contained less than 40 individuals; in these patches all of the plants were monitored. Overall, a total of 1355 individuals were tagged and monitored. These individuals were surveyed in January 2004 and then again the following year. During each survey the number of flowers on each individual were counted, seed production was estimated from a subset of mature flowering heads, and any mortality was recorded.

Seed sowing trial

Additional demographic data were obtained from a seed sowing experiment established in the Craigieburn basin in 2003. Sowing density treatments consisted of a control with no seed addition, and seed addition at rates of 25, 125, 625, 3125 and 15625 seeds per 30x30cm plot. Each treatment was replicated three times in each block, and each block was replicated six times in each habitat. Blocks were located a random distance up the catchment's primary creek; forest creek and alpine creek blocks were located directly adjacent to the creek, forest and tussock habitats were randomly located between 20 and 200m from the creek, and forest gap blocks were located at a gap greater than $25m^2$ nearest to a randomly located point between 20 and 200m from the stream. Scrub habitats were randomly selected from all scrub patches within the catchment. The entire experiment was replicated the following year, with the new blocks sown adjacent to those from the previous year, resulting in a total of 1512 individual sowing trials. Seed was collected in the field immediately prior to sowing from the lower reaches of the Avoca River, close to the study area. Seed was collected from a single location to minimise potential variation in seed viability. These plots were revisited annually through 2008 to survey the number of individuals recruited from seed and to record any occurrences of flowering over that five year period. This resurveying provided size years of data for one replicate their influence.

Seed burial

In addition to the seed sowing, seed burial trials were performed at each of the blocks to determine the viability of the seed bank after one year, and how this varied among habitats. The survival of seed in the soil in each block was assessed by burying 100 seeds in mesh bags at a depth of 3 cm. Bags were buried at a random location within three metres of the plot, and were removed after 1 year. Seed survival was assessed by counting empty and filled seeds on exhumation, and determining the proportion of filled seeds which germinated by placing them on moist filter paper.

2.2.3 Demographic model

This model simulates the number of individuals present in three primary stages of development; seed, juvenile (non-reproductive), and adjust (reproductive). The data collected was used to construct a demographic model for *H. lepidulum* that is similar to a stagebased non-linear projection matrix model (Cushing 1998) and describes the development of individual plants in one year time steps. This approach generally applies death and reproduction simultaneously, so that adult individuals have the chance to reproduce in the year in which they die. Five juvenile stages were included in the model; this was designed to reflect the variable length of retention in this stage, as all individuals remained juveniles for at least one year, with some individuals still in the juvenile stage after five years. Replication of model stages and implementing a minimum stage membership duration in this manner is similar to the approach used by Buckley et al. (2005). This also allows our model to reflect how the probability of survival and transition into adulthood changes as individuals accumulate time spent in the juvenile stage.

This demographic model is constructed of a number of *stage transition models* that describe the probability of an individual transitioning from its current state (Figure 2.1). Various stage transition models were used to describe the mechanisms of survival, maturation, and fecundity. Each transition probability was modelled using a unique parameterisation of these stage transition models (described in detail below). The stage transition models include density-dependent effects where data were available. This densitydependence serves as the primary regulatory mechanism limiting population growth. A number of the features incorporated into the modelling process (specifically the recruitment function and the integer-based projections; see below) required adjustments to the strict matrix modelling approach; the demographic models were therefore projected by evaluating a system of equations that did not strictly adhere to a matrix structure.



Figure 2.1: Life cycle diagram for the population model for *H. lepidulum*. The seed bank is modelled by retaining a portion of those seed that do not germinate to the following year. There are five juvenile stages (J) representing age classes 1 through 5. Membership in juvenile stages 1 through 4 each lasts a single year, while individuals are permitted to remain in the final juvenile class indefinitely. Age-specific probabilities of transitioning into the adult stage (T_{JA}) and different survival probabilities (S) are estimated individually for each stage x habitat combination by the stage transition models. Details of the stage transition models can be found in the text.

2.2.4 Parameterising stage transition models

The stage transition models are those models used to calculate the probability of transitioning between stages in the demographic model. These stage transition models are parameterised using a hierarchical Bayesian approach, which provides a number of practical benefits. First, the flexibility of model specification makes it much easier to account

for the complex nested structure in the data I used (e.g. seed sowing plots nested within blocks, nested within habitats, replicated in two different starting years) compared to using a frequentist approach. Secondly, the use of the hierarchical Bayesian approach affords some additional flexibility with model specification. Instead of estimating the parameters directly, this approach estimates 'hyperparameters'; these hyperparameters define a distribution, which in turn describes the parameters of interest. The effect of this is twofold; first, this approach effectively isolates the parameter estimates from being subject to the reduction in variability associated with increased sampling intensity. Instead, the variability reflected in the parameter estimate (in the form of the posterior distribution) more accurately reflects the actual level of variation present in the observed responses (Clark 2003, 2005). Secondly, by incorporating another hierarchical level in the form of an additional 'hyperprior' distribution (that describes the distribution of the hyperparameters), I can specify a higher habitat-level of organisation in the model structure. This way the observed data is described by a function, the parameters within that function are described by distributions, and the distributions are parameterised using the hyperparameters. On top of that, these hyperparameters can be drawn from another distribution which describes the relationship of parameters across habitats. Incorporating these linkages specifies the interrelatedness of the observations (i.e. although observations come from different habitats, we assume habitats may share some commonalities) instead of assuming that they are completely independent of each other. Lastly, the data used to parameterise the stage transition models contained some inherent correlation between parameters, both spatial and non-spatial. The hierarchical Bayesian approach allows me to incorporate parameter covariance by explicitly specifying the correlation within the model structure. Using this approach, covariance between parameters is accounted for during the simulations by using parameter estimates that were produced during the same iteration of the model fitting procedure. This way the covariance does not have to be explicitly stated when applying the stage transition models in the simulations.

Parameters within the stage transition models were estimated using a Markov chain Monte Carlo (MCMC) method, employed using the OpenBugs v3.0.2 package (Lunn et al. 2009) in R 2.8 (R Development Core Team 2009). Burn-in periods varied in length according to each particular model's convergence dynamics; typically these lasted approximately 10,000 iterations or less. After burn-in, a further 10,000 iterations were performed which were used to construct the posterior distribution for each parameter. Three chains of parameter estimations with different random starting values were produced for each parameter and inspected for convergence. Convergence was assessed visually by inspecting mixing of chains (vectors) while also calculating the potential scale reduction factor, or PSRF (Gelman & Rubin 1992; Brooks & Gelman 1998); the convergence results of specific models are detailed below. The following sections describe the data and model structures used to estimate each of the transition probabilities within the demographic model. For simplicity, I have only included the lowest level of these models, the parameters of which are estimated using a hierarchical structure that includes hyperparameters at the habitat level and an overarching hyperprior describing the interaction of the different habitats. While the use of prior distributions to inform the behaviour of these observations is debated to add a subjective element to the parameter estimation process, I had no information on which to base such priors, and instead used priors which were largely uninformative. By specifying them as large and relatively uniform, these priors imposed a minimal constraint on the parameter estimations, as the potential parameter space defined by the prior and explored by the parameter range, and the priors were primarily used only to reflect the scale of measurement (i.e. discrete or continuous).

There are six different stage transition models which are used to calculate the individual elements within the transition matrix that represent the probability of individuals moving from one stage to another. These models describe the probability of juvenile survival, transitioning from juvenile to adult, adult survival, seed production, recruitment of seed, and survival of seed in the seedbank (Figure 2.1). The models of juvenile survival and transition probabilities are reparameterised for application to the different juvenile stages. The whole contingent of stage transition models are also reparameterised independently for each habitat. The application of the models in the simulation is described below.

Juvenile survival

The probability of juvenile plants surviving is parameterised using data which reflects successive annual counts of the seed sowing plots over a five year period. Trajectories of seed sowing trials at each of the sowing densities (25, 125, 625, 3125 and 15625 seeds per 30x30cm plot) were used to fit the data; this provided age-specific data reflecting survivorship at different density levels. Because of this, I was not able to collect data reflecting the survivorship of 'older' individuals (i.e. five years) at the highest sowing densities (1000 or more individuals per plot), as by the time they reached this age the density had been dramatically reduced. However, the data that was collected covered the full range of age and density combinations that were encountered in the simulations, and were therefore considered to be representative of the necessary range of conditions. The probability of survival for each juvenile stage is modelled as a binomial process

$$r_{JS,hab,y} \sim Dbinomial(S_{J,hab,y}, a_{JS,hab,y-1})$$
 (2.1)

where r_{JS} = the number of juveniles present in a given year, a_{JS} = the number of juveniles in the previous year's survey, and $S_{J,y}$ is the estimated probability of survival of the *y*th stage. A logistic function was used to estimate the density-dependent probability of survival for each habitat:

$$S_{J,hab,y} = \log\left(\frac{b_{0,JS,hab,y} + b_{1,JS,hab,y} * a_{JS,hab,y-1}}{1 - (b_{0,hab,y-1} + b_{1,hab,y-1} * a_{JS,hab,y-1})}\right).$$
(2.2)

The priors for b_0 and b_1 were initialised using a relatively uninformative prior which was normally distributed with a mean of zero and variance of 100. The use of a logistic function ensured that the survival probability estimates were confined to the interval [0,1]without the need to constrain the MCMC fitting procedure to a truncated parameter space, as would be necessary if a decay model were used (Pacala & Silander Jr 1985). This type of function also assures that density-dependent effects can be expressed in the response; the function can take either a linear or a sigmoidal response to describe how (or if) survival changes according to the number of individuals present $(a_{JS,hab})$. The degree and variability in the strength of the density dependence observed in the data will then be reflected in the model by the stochastic parameter values. In the simulations, both juveniles and adults are reflected in this count; however, since the survival response is informed only by the results from the seed sowing trials, the observed densities $(a_{JS,hab})$ reflect predominately juvenile individuals, and therefore reflect a relatively conservative measure of density dependence in the presence of a large number of adults. When applied in the simulations, no individuals in the first four juvenile stages are retained in the stage; surviving individuals either proceed to the next juvenile stage, or a proportion progress to adult status (with probability $T_{\rm JA}$). Once the final juvenile stage (J_5) is reached, individuals are retained within the stage until they die or advance to the adult stage.

Juvenile to adult transitions

The probability of a juvenile transitioning into the adult (flowering) stage was modelled as a function of the current juvenile stage, habitat, and the density of conspecifics. The habitat-specific transition values are modelled as a binomial process, specified as:

$$r_{f,hab} \sim Dbinomial(T_{JA,hab}, a_{JA,hab})$$
 (2.3)

where r_f is the number of successful flowering events, a_{JA} = the total number of juveniles in the previous year, and T_{JA} is the probability of transitioning from a juvenile to adult stage. The variable of interest, T_{JA} , is modelled as time variant, using a logit link function:

$$T_{JA,age,hab} = log\left(\frac{b_{0,JA,age,hab} + b_{1,JA,age,hab} * age}{1 - (b_{0,JA,age,hab} + b_{1,JA,age,hab} * age)}\right)$$
(2.4)

where age is the number of years since the initial sowing of the plot (equivalent to the current juvenile stage) and $b_{0,JA,age,hab}$ and $b_{1,JA,age,hab}$ are initialised with a minimally informative prior reflected by a Gaussian distribution with a mean of zero and variance of 100.

Adult survival

Estimates of adult survival are derived from the observations of the tagged individual plants. Survival is also modelled as a binomial process, specified as:

$$adults_t \sim Dbinomial(S_A, adults_{t-1})$$
 (2.5)

where $adults_t$ are the number of surviving adults in the current year, compared to the number of adults in the previous year $(adults_{t-1})$, and S_A is the probability of adults surviving. Estimates of survival rates are calculated for each of the habitat types, again using a Bayesian hierarchical approach. No density- or age-specific relationships were available from the dataset for estimating this parameter, so the model consisted of an intercept-only form, using a logit transformation to restrict the parameter to the interval [0,1]:

$$S_{A,hab} = \log\left(\frac{b_{0,SA,hab}}{1 - b_{0,SA,hab}}\right).$$
(2.6)

The $b_{0,SA,hab}$ parameters are initialised with a Gaussian prior with a mean of zero and a variance of 100.

Reproduction

Estimates of the reproductive ability of individuals were obtained via a combination of estimating plant level seed production (Fec in Figure 2.1) in the field, and then using a previously developed recruitment function (Duncan et al. 2009) to determine the proportion of those seeds that germinate and establish to become new juvenile individuals. Seed production is modelled in two parts. First, the number of flowers on each plant was modelled as a Poisson process using flowering data from the tagged individuals. As there was no age information associated with the individuals from which the flowering success was modelled similarly across all adults; this is in contrast to the probability of transitioning from the juvenile to adult life stage $(T_{JA,age,hab})$, which is age-dependent. Production of flowers is a prerequisite for membership of the adult stage class; as such, there were no adults monitored that had zero flowers. While it is potentially possible for adult plants to skip flowering for a year and remain in a vegetative state, this was not observed in the data collection and is therefore not reflected in the demographic model. As the Poisson distribution used to model the number of flowers on adults will always have some probability of a zero value occurring, I performed a n-1 transformation on the observed number of flowers which allows me to model it as a Poisson process:

$$Flowers_{hab} - 1 \sim DPoisson(\lambda_{flowers,hab}) \tag{2.7}$$

where $Flowers_{hab}$ is the number of flowers produced by a plant which is distributed as a Poisson process with a mean of $\lambda_{flowers,hab}$. This is a simpler approach than implementing a zero-truncated Poisson distribution in the confines of the OpenBugs model specification. A n+1 transformation is then performed on the predicted values to construct the posterior distribution. Once seed had set, a subsample of seedheads were collected to estimate seed production at the individual flower level as a Poisson process:

$$Seed_{f,hab} \sim DPoisson(\lambda_{seed,hab})$$
 (2.8)

where $Seed_{f,hab}$ is the number of seed modelled as a Poisson distribution with a mean of $\lambda_{seed,hab}$. Habitat specific estimates of seed production at the plant level (Fec_{hab}) were then calculated by multiplying the number of flowers by estimates of seed production per flower:

$$Fec_{hab} = (\lambda_{flowers,hab} + 1) * \lambda_{seed,hab}.$$
(2.9)

Recruitment function

In order to calculate the proportion seeds produced that germinate and recruit into the population, I used the recruitment function

$$rec = bn \left[1 - \frac{\omega^{\omega}}{\left(\omega + \frac{S_{tot}}{n}\right)_R^b} \right]$$
(2.10)

developed by Duncan et al. (2009). This function estimates three parameters that describe the number of microsites in a plot (n), the proportion of those microsites that are available for occupation (b_R) , and their size heterogeneity (ω) . Parameter values for this function are obtained from other work which developed habitat-specific parameterisations of the function, estimated using data from the same seed sowing experiments (Miller et al. unpublished). This function approximates the amount and distribution of sites within a cell that currently exist $(n \text{ and } \omega)$ and the proportion of those sites that are not occupied by the preexisting community $((b_R))$, and are therefore available to *H. lepidulum*. This function is used to calculate the proportion of seed (rec) that germinate and produce first year juveniles (in stage J_1). The seed input (S_{tot}) is equivalent to the total number of seed from the seedbank (SB; see below) with the total amount of seed production from the current year, calculated as a product of the fecundity rate (Fec) and number of adults (*A* from Figure 2.1). The number of seed is then multiplied by *rec* to determine the number of individuals in J_1 .

Seed bank

The proportion of seed that are produced but do not germinate (1-rec) enter the seedbank stage. The probability of these seed surviving to the following year (ϵ) is estimated by modelling the response from a seed burial trial as:

$$\epsilon_{hab} \sim Dbinomial(SB_{hab}, seed_{sown})$$
 (2.11)

where ϵ_{hab} is the observed number of seed which germinated after one year, SB_{hab} is the estimated proportion of seed that are able to germinate in a given habitat after being buried for one year, and $seed_{sown}$ is the number of seed that were sown in each trial (in this case, each trial was performed with 100 seed). Sixteen burial trials were performed in each habitat, for a total of 96 trials. As with the adult survival estimates, there are no explanatory variables; only the different factor levels (habitats) for which the probability of survival is estimated. Estimates of these probabilities are confined to the interval [0,1] using a logit transformation:

$$SB_{hab} = \log\left(\frac{b_{0,hab}}{1 - b_{0,hab}}\right) \tag{2.12}$$

which provides an estimate of seed survival after one year. The variable b_0 was initiated with a non-informative prior distribution with a mean of zero and a variance of 100.

2.2.5 Simulating populations

A total of 100 replicates of population projections were simulated for each habitat. Each of these replicates was run for 2000 annual timesteps. Each replicate began with an initial seeding using one of the seed input levels from the seed sowing experiment (25, 125, 625, 3125 or 15625 seeds) as the starting point. Using a Bayesian approach to estimate parameters from the stage transition models described above produces a posterior distribution for each parameter in the stage transition models in the form of a vector of potential parameter values. At each application of the demographic model, parameter values were drawn from these vectors in order to calculate the required transition probabilities. In addition, covariance between parameters within the same stage transition model was accounted for by drawing values for each parameter estimated at the same iteration of the MCMC sampler.

During the simulations the fate of each plant was determined by using Bernoulli trials for each individual, allowing me to maintain a discrete count of individuals. The benefit of this approach is that it permits the unambiguous extinction of populations, as opposed to using a continuous estimate of population size. In a declining population, the use of a continuous measure of population size would result in the population size asymptotically approaching zero, resulting in the existence of a partial (<1) individual which could persist indefinitely. As the demographic processes in the simulation are stochastic, the existence of a partial individual could potentially serve to initiate a revival of the population within a cell where it is effectively extinct. The discretisation of the population into individuals allows me to eliminate the possibility of such biologically unrealistic phenomena.

Environmental stochasticity

The uncertainty in the parameters of the models used to estimate the probabilities of stage transition reflects variability in the data, which is a result of either measurement error or the inherent variation in plant responses. By using the posterior distribution to define the sample space for the parameters, I discount the measurement error and assume that the variation is representative of the true variation in plant behaviour. This stochasticity then accounts for variability in both biotic and abiotic conditions without having to specify them explicitly, similar to implementing process noise (Dennis et al. 2006). By drawing different samples from the posterior distributions at each iteration of the simulation, this uncertainty was incorporated into the simulations as latent environmental stochasticity. This provides a novel approach to incorporating realistic estimates of variability (which are inherent in a natural system) into the projections.

Demographic stochasticity

Demographic stochasticity was implemented in the simulation by performing individual Bernoulli trials to determine the fate of each individual during each time step of the simulation. For each individual in the population, the probability of survival was calculated using a random draw from posterior distributions to parameterise the appropriate survival model described above. A number was drawn from a uniform probability on the interval [0,1], and compared against the probability of stage transition to determine if that individual survived. For surviving juveniles, another similar trial was performed to determine if the individual remained in its current stage or transitioned to a new stage. Adult individuals do not transition to later stages; they are only subject to the survival trials. These trials are repeated for each individual in the population; a random draw equalling or exceeding the probability value was considered a success, and the number of successes tallied to obtain the resultant number of individuals. Surviving adults each produce a randomly generated number of seed (*Fec*, described above). Similar approaches have been used before, such as in the PATCH simulation software (Schumaker 1999).

Model Check

The first five years of simulated population sizes were compared against the five years of the available seed sowing data to assess if the simulations produced realistic outcomes. Visual inspection of the distributions of observed population sizes in each year were compared with the simulated data. In addition, a two-sample Komolgorov-Smirnov test was used to test if the distribution of observed data was significantly different than the simulated values over these five years (Conover 1999). Ideally a full validation would be performed using resampling methods; however, this demographic model consists of a number of component sub-models which are parameterised using different data sets, making a traditional validation not only much more difficult to employ, but also less directly informative. Instead, this approach is intended to serve as a 'sanity check' to validate that the structure of the model is correctly employed.

Population equilibrium

The amount of time required for the populations to reach a stable equilibrium was approximated by simulating population growth using deterministic (non-stochastic) versions of the stage transition models in each of the six habitats. This allowed me to approximate the amount of time necessary for the invasions to reach a steady state population size, and evaluate the range of population sizes at that time produced by the stochastic simulations. This provided a way to approximate an equilibrium population size using the stochastic projections which is otherwise inherently difficult to identify (because of their stochastic nature). These deterministic simulations used the mode of each parameter vector (akin to a least-squares fitting approach) to calculate transition probabilities using the same stage transition models described above. Simulations were run in each of the six habitats from six different initial starting densities reflecting the the seed input levels from the seed sowing experiment (25, 125, 625, 3125 or 15625 seeds). The time required to reach an equilibrium condition (t_{eq}) was identified by locating the time at which simulations within a habitat of all initial densities converged (within 0.1% of each other) on a stable population size. Typically stable equilibria are identified by their derivative being equal to zero; however since these deterministic projections will only asymptotically approach zero change, the cutoff of them converging to with 0.1% of each other was considered sufficient to identify convergence to a stable state.

Comparing simulated populations with field abundances

As the amount of time the field populations have had to develop is unknown, it is impossible to choose a corresponding time point in the simulated population growth that I could use for a direct validation. Instead, I used projections of population growth obtained from the simulations at two different time intervals to provide a context in which to assess the development progression of the invasion. This gave me a context to understand how far along the invasion had already progressed, and what it was likely to do in the future. For this I chose to project population sizes from the stochastic simulations at both 20 years since establishment and at the t_{eq} point. Comparing populations after 20 years of

development is a largely arbitrary timeframe; however, this amount of time provides a reference to the degree of population development a person is likely to observe in their lifetime, and also provides a reference point that should reflect a relatively early stage of invasion. In contrast, the population size at the (t_{eq}) point is intended to represent the eventual stable population size the invasion is capable of given enough time to fully develop. Mann-Whitney tests (Hollander & Wolfe 1999) were used to compare the medians of the simulated vs. observed populations, and a Kolmogorov-Smirnov test (Chakravarti et al. 1967) was used to determine how well the distribution of abundances from the two sources matched. Using the two test provides a highly sensitive comparison of the central location of the two samples (Mann-Whitney) and a comparison of the overall distribution of data (Kolmogorov-Smirnov). As the field surveys were conducted in a somewhat random fashion without the context of where *H. lepidulum* had previously occurred, it is impossible to determine if locations currently devoid of *H. lepidulum* had previously been exposed to invasion pressure or not. For this reason, the same two comparison tests were also performed using censored versions of the abundance data, reflecting only non-zero counts. This restricts the comparison to only abundance at locations where *H. lepidulum* has successfully established, and compares the growth of established populations without the additional complexity of predicting the establishment or persistence of a population.

Perturbation analysis

A perturbation analysis was performed to examine the sensitivity of the population-level performance to change in the various parameters within the stage transition models. The analysis was performed by systematically altering individual parameters within the deterministic version of the simulation by multiplying them by a perturbation constant (P_c) , running the simulation, and observing the change in the stable population size (calculation described above above). This range of adjustment constants provides an approximation of expected model behaviour if the parameter is removed $(P_c = 0)$, if the parameter is reduced to a fraction of its original value ($P_c = 0.1$ or 0.5), remains constant ($P_c = 1$), or is increased $(P_c = 2 \text{ or } 5)$. Where necessary, individual parameters were constrained to avoid non-sensible values (i.e. survival probability does not exceed 1). The parameters are altered one at a time while the others remained at their modal value as described above, resulting in a total of 144 simulations, replicated in each habitat. Each projection utilised the same starting conditions (625 seeds); the choice of this starting value was largely arbitrary, but the projections from the deterministic model suggest that the start point is irrelevant, as the lack of any ergodic effects means the populations will reach the same stable size regardless of the initial value. Trajectories were simulated until growth rates fell below 0.001, at which point they were assumed to have reached an equilibrium state. Once this point was reached, the number of plants was recorded for comparison against the unperturbed projections. Traditionally perturbation analyses typically evaluate the change in growth rates as a function of the perturbation. However, due to the incorporation of regulatory mechanisms in these demographic models, population-level growth is self-regulating, and the growth rates always approaches zero. As a result, this analysis focuses on changes in the overall stable population as the basis to compare the effects of parameter perturbation.

2.3 Results

2.3.1 Parameter estimates

The hierarchical Bayesian fitting procedure using an MCMC sampling algorithm produced three independent vectors (chains) of parameter estimates for each individual parameter within the stage transition models; each chain consists of 10,000 individual parameter estimates, resulting in a total of 30,000 parameter estimates for each parameter x habitat combination. Together these vectors represent the posterior distributions which describe the variability and uncertainty in each parameter. Visual inspection (graphing) of these chains indicated that there was convergence of the chains for all of the parameters, indicating that the three independent estimations reflected consistent parameter estimates with each other. A more quantitative assessment of convergence was also performed by calculating the potential scale reduction factor (PSRF); values at or below 1.2 indicate sufficient convergence of the chains (Gelman et al. 1995). PSRF values of nearly all estimated parameters were below 1.2, with the only exception of one habitat-specific parameter estimation exceeding the cutoff with a value of 1.22. However, visual inspection of the distributions produced from the individual chains were nearly indistinguishable, and the individual chains appeared to mix well, indicating that the MCMC sampler was fully exploring the parameter space and returning consistent results. Given these results, all parameter estimates were assumed to be well estimated.

These posterior distributions are used to define the sample space for stochastic behaviour within the simulation. For simplicity only one of the three chains was sampled during the simulations (as convergence diagnostics suggested they were effectively interchangeable); values were randomly drawn from the vector to populate the stage transition models with parameter values (Figure 2.2), which are then in turn used to calculate the transition probabilities (individual matrix elements) for each iteration of the population matrix (e.g. Figure 2.3). Examining the full range of uncertainty in modeled responses (via the total response envelope presented by the dotted lines in Figure 2.3) reveal that the range of uncertainty was relatively small at lower versus higher densities; this held across all relationships. For stage transition models with multiple parameters, parameter values were drawn from corresponding positions within the vectors; this assures that each parameter was estimated at the same time, and accounts for the potential of any covariance that might be present.



Figure 2.2: Values for the different parameters of the models (equations 2.1 to 2.12) used to simulate the life cycle of *H. lepidulum*. The modal values of parameters used in the deterministic simulations to evaluate equilibrium conditions are denoted by the diamonds, while the bands represent the density of observed values obtained from the MCMC parameterisation technique (darker parts of the bands represent a higher number of observations). Extent of the graphs was limited to the 90th percentile of parameter values, and may therefore not reflect the range of extreme values.



Figure 2.3: Probability that a first-year juvenile will survive, as a function of *H. lepidulum* density. The parameter estimates reveal a wide range of responses from strong density dependence (where survival declines sharply with increasing density of conspecifics) to negative density dependence (where survival increases with increasing density). Mean responses (solid lines) indicate that in the majority of situations, this relationship is negative. The minimum and maximum responses (dotted lines) depict the corresponding extreme values from the posterior distributions, and denote the boundaries of the sample space used for the J_1 transition value when implemented in the simulation. The same approach was used to define all transition values within the matrix population model.



Figure 2.4: Comparison of observed abundances from the seed sowing data (both 2003 and 2004 replicates averaged) with simulations of the demographic model for the first five years after sowing. Location of the mean for each distribution is indicated by the vertical lines. Using a Kolmogorov-Smirnov test to compare the predicted and observed values reveals that significant differences exist between the observed and predicted abundances, but removal of the zero-class negated most of those differences (see text).

2.3.2 Model Check

Visual comparison of the observed population sizes from the seed sowing plots with the first five years of simulated population growth suggests that the demographic model provides reasonable estimates of population sizes during this time frame. The mean population size of the simulated populations was particularly consistent with the observed population sizes (Figure 2.4). As the distribution of the projected population sizes were heavily skewed (i.e. not normally distributed, see Figure 2.4), I used a Kolmogorov-Smirnov test to examine if there were significant differences between observed and projected population sizes for the different year x habitat combinations. As the data were counts of individuals in the population, a small amount of random noise was added to the population size estimates to approximate a continuous response, and eliminate the potential for ties, which would invalidate the test. These tests indicated that in terms of size, the majority of simulated populations were significantly different to those observed in the field (Table 2.1). However, the comparison was heavily influenced by the number of simulated populations which went extinct, and inflate the zero class (approximately 88% of the projected populations, and 46% of observed). When populations of size zero were removed and the

test was applied only to the distribution of sizes of successful populations (≥ 1 individual), the simulations matched the observed data much more closely, and only three of the factor combinations (forest habitat at year five, and scrub habitat at years three and five) showed significant differences between the observed and projected values (Table 2.1).

2.3.3 Survey data

A pairwise comparison of the abundances of H. lepidulum in the different habitats observed during the field surveys was performed using a Mann-Whitney test to identify habitatspecific differences in population success (Table 2.2). Although five of the six habitats had median abundance values of zero, there will still some significant differences, suggesting that some of the habitats differed in their level of invasibility. Abundance was the lowest in the tussock habitat, which was significantly distinct from the other groups. There was a great deal of overlap between abundances observed in the forest, forest gap, alpine creek, and scrub habitats. The forest creek habitats contained the greatest abundance, and was also significantly distinct from the other habitats. Removing the zero values and repeating the comparison provided a comparison in abundances only where H. lepidulum was present (Table 2.2). In this comparison, the forest creek still contained the highest densities, but was indistinguishable from the scrub habitat. Again, the remaining habitats were largely similar; forest, forest gap, and scrub habitats were indistinguishable, forest gap and alpine creek were similar, and alpine creek and tussock were similar.

2.3.4 Simulation output

The results of simulating populations of *H. lepidulum* showed that there is a great deal of variation in population success (measured in terms of abundance of individuals and persistence of populations) between the different habitats. The deterministic simulations showed that the amount of time for the simulated populations to reach a relatively constant size (defined as (< 0.1% change from the previous year) was quite variable (t_{eq} , Table 2.2). The equilibrium criteria were reached most quickly in the forest habitat, followed by the tussock. The population in the scrub habitat was next, followed by those in the forest gap and forest creek habitats, which were quite close to one another. The population in the alpine creek took the longest to converge, over twice as long as in the next closest habitat.

Persistence of populations (the proportion still surviving) in the different habitats are compared at two time references; after 20 years and at the t_{eq} point (Table 2.2). Twenty years provides a useful time frame for comparison that provides an estimate of what the progression of the invasion will achieve in a relatively near future. The t_{eq} , although variable, denotes the point in the development process where the population achieves a stable (and presumably sustainable) size. This size represents the population's final potential,

		· · · · · ·				ive, and may projection
not match the observed data. The Yee	e top section shows o ur Forest Creek	comparisons usi Forest	ng all data, while Gap	e the bottom com Scrub	pares distributions Alpine Creek	<u>without zero-values.</u> Tussock
All observations						
1	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
2	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
ω	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
4	< 0.001	< 0.001	< 0.001	0.009	< 0.001	0.002
Сл	< 0.001	0.055	< 0.001	0.388	0.020	0.024
Zero truncated dist	ributions					
1	0.711	0.100	0.715	0.317	0.148	0.570
2	0.120	0.070	0.142	0.478	0.938	0.810
లు	0.811	0.153	0.328	0.005	0.188	0.274
4	0.779	0.153	0.320	0.091	0.384	0.840
CJ	0.814	0.025	0.440	0.017	0.326	0.551

	0.024	0.020	0.388	01
4	0.002	< 0.001	0.009	01
12	< 0.001	< 0.001	< 0.001	01
	< 0.001	< 0.001	< 0.001	01
	< 0.001	<0.001	<0.001	TO

and can be used to compare population performance independently of ergodic effects or population growth rates which affect the amount of time required for the population to reach this point. After 20 years, the majority of populations in the forest and forest gap habitats go extinct; out of 100 simulation runs in each habitat, 14% of populations persist in the gap habitats, while only 1% remain in the forest. More populations persist in the tussock landscape (38%), but still less than half. Simulations in the forest creek and scrub habitats indicate higher persistence, with a greater proportion surviving to 20 years (53% and 68% respectively); but the populations in the alpine creek have the highest persistence after 20 years (76%). Persistence of populations at the projected equilibrium point (t_{eq}) are in general reduced compared to the 20 year point, but the relationship of the different habitats follows roughly the same pattern; all populations in the forest gap habitat have gone extinct, and only 3% remain in the forest and tussock habitats. Populations in the forest creek habitat don't fare much better, with only 7% still in existence. The proportion surviving in the alpine creek has dropped significantly, but 30%still remain. Populations in the scrub habitat appear to be the most successful, with 49%of the simulations still existing at this point.

Comparing the abundances observed from the field surveys to the projected population sizes (after 20 years and at the t_{eq} point) using the Kolmogorov-Smirnov tests revealed that all abundance measures from field data are significantly different than their projected population sizes at either time reference (Table 2.2). The same comparisons using a Mann-Whitney test produced nearly the same results, with the exception that the simulated population in the alpine creek habitat was indistinguishable from the survey data at the t_{eq} point. The same comparisons were repeated using only observations from field abundances and simulated population sizes that were ≥ 1 . This comparison produced largely the same results; only simulations in the forest creek habitat produced results after 20 years that were indistinguishable from the abundance data using the Mann-Whitney test, and the simulated and observed abundances in the forest habitat were indistinguishable at either reference times (Table 2.2). In nearly all cases the simulated populations were larger than the observed population sizes, except those in the forest habitat, and in the forest gap habitat which are extinct at t_{eq} .

Graphing the distribution of current abundances provides a more intuitive visual assessment of the simulated vs. observed abundance (Figure 2.5). The simulated population sizes at t_{eq} represent the eventual potential of populations in each habitat; this graph serves as a way to compare the distribution of observed abundance values in each habitat to the distribution of simulated potential values. It is clear from the graph that the observed abundances of *H. lepidulum* in the lower elevation forest habitats (forest, forest creek, and forest gap) are closer to their projected potential than in the upper elevation alpine habitats (alpine creek, scrub, and tussock).

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a Kolmogorov-Smirnov test	*) and i	ted by	e denc	wher	except	≤ 0.05	nt at p	gnifica	were si	ences .	ı (differ	ocation	upare lo	o com	r test t	hitney	unn-Wł	g a Ma	a usin
et or zero-truncated) survey	ll datase	ing (fu	spond	corre	inst the	ed agai	compar	were	and t_{eq}	years :	s at 20	ndance	ed abui	mulate	05. Sir	$p \leq 0.0$	ed at p	e denot	erence
with the significance of the	ey test v	Whitne	Mann-	ng a l	ned usi	perform	were I	arisons	comp	these	letters;	script	^r super	ted by	e denot	ces are	Indance	ed abu	survey
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	Forest Creek	Forest	Forest Gap	Alpine Creek	Scrub	Tussock
t_{eq}	386	5	347	850	244	108
Proportion Persisting @ 20 yrs	0.53	0.01	0.14	0.76	0.68	0.38
Proportion Persisting @ t_{eq}	0.07	0.03	0.00	0.30	0.49	0.03
All Observations						
Surveyed Abundance	$5.4^A (64.9)$	0^B (31.3)	$0^{B,C}$ (8.2)	$0^{B,C}$ (10.1)	0^{C} (24.8)	0^D (10.3)
Simulated @ 20 yrs	3.3(63.2)	0(0.33)	0(26.8)	11.7 (42.4)	6.7(39.0)	0(55.8)
Simulated @ t_{eq}	0(96.2)	0 (0.6)	0 (NA)	0^{*} (236.6)	0 (80.6)	0 (56.6)
Persisting populations (≥ 1	individual)					
Surveyed Abundance	$9.3^A \ (69.7)$	5.0^B (52.4)	$3^{B,C}$ (11.3)	$1.7^{C,D}$ (15.0)	$3.5^{A,B}$ (34.6)	0.7^D (20.1)
Population Size @ 20 yrs	10.0^{*} (79.41)	$3.33^{*\dagger}$ (NA)	58.3(44.4)	20.0(44.9)	28.3 (41.0)	$10.0 \ (86.2)$
Population Size @ t_{eq}	266.7(168.61)	$3.33^{*\dagger}$ (0.00)	0 (NA)	$350.0\ (265.0)$	130.0(54.1)	213.3(236.0)



Figure 2.5: Comparison of the distribution of observed current abundances of *H. lepidulum* compared to the distribution of expected potential population sizes estimated from simulation predictions. Darker locations along the bar indicate a higher density of observations at that population size.

2.3.5 Perturbation analysis

The perturbation analysis revealed that the populations of *H. lepidulum* in different habitats respond differently to perturbation of parameters (Figure 2.6). While this analysis focused on the final equilibrium size of the population, it is important to note that changes in these parameters may also affect the speed at which this equilibrium population size is reached. As this analysis was concerned with only the potential population size as a measure of invasibility, I ignored variation in the rate at which these sizes were reached. There were a few commonalities between habitats, however; manipulating of the first term (b_0) in the stage transition model that relates the probability of transitioning from a juvenile to the adult stage to current density of individuals (Equation 2.4) consistently had a substantial effect on the population size (Figure 2.6). Decreasing this parameter effectively increased the y-intercept of the function, which in turn increases the probability that an individual juvenile will transition to the adult stage, given a low density of conspecifics. Manipulating the second term (b_1) in the same equation had a similar effect, although the population size was positively correlated with this parameter. The magnitude of the response from manipulating these parameters was not consistent (Figure 2.6); in the tussock habitat manipulation of the first parameter for any juvenile stage appeared

to have an effect, while the perturbing the second parameter had no perceivable effect. In other habitats, manipulating both parameters seemed to have an effect (forest creek and forest gap), in others neither seemed to matter (scrub). The effect of perturbing these parameters was so strong that in some habitats it even revived populations that were otherwise approaching extinction (i.e. the forest and tussock habitats).

Other responses observed during the perturbation analysis were not as consistent across the different habitats. Reducing the single parameter used in the calculation of adult survival (Equation 2.5) reduced population sizes, but there didn't appear to be an effect of increasing the parameter value. Manipulation of seed supply and recruitment affected a number of habitats. Increasing seed production tended to increase the population size, but decreasing seed production appeared to have a stronger negative effect. The recruitment function (Equation 2.10) was most sensitive to changes in the *b* parameter (representing the proportion of sites available for colonisation) and the ω parameter (the size heterogeneity of available sites). Manipulations of juvenile survival had intermittent effects in the forest creek and alpine creek habitats, but did not appear to substantially influence the population size in other habitats. Variation in seed production appeared to be another consistent influence, producing a marked effect across all of the habitats. Manipulating the survival of seed in the seed bank had a minimal influence.



Figure 2.6: Relative change in estimated population size, testing the sensitivity of the simulation model to changes in the different parameters. Each parameter was multiplied by a perturbation constant ($P_c = 0, 0.1, 0.5, 1, 2, \text{ or } 5$). The horizontal lines represent the change in simulated population size using modified parameters, with the size of the vertical line indicting the magnitude of perturbation (taller and thicker lines represent larger values of P_c).

2.4 Discussion

2.4.1 Predicting invasion

The initial impetus for this investigation was to re-evaluate the hypothesis that the forest creek habitat was more suitable to invasion by *H. lepidulum* than the surrounding forest, and that in the current landscape configuration these creek corridors represent a vector which the invasion is utilising to breach the impermeable forest habitat. This hypothesis was developed using only the recruitment data, and this investigation was intended to examine if that hypothesis held in light of a more complete understanding of the invader's life-cycle. The projections from the demographic models suggest that the forest and forest gap habitats found in the lower elevations of the catchment are largely incapable of sustaining viable populations of *H. lepidulum* in perpetuity. This finding reconfirms the conclusion reached using just the recruitment data, that these habitats are relatively uninvasible to *H. lepidulum*. In contrast, the simulated populations in the forest creek habitat persist indefinitely, and suggest that even relatively small introductions can reach the point of becoming self-sustaining (Table 2.2). This is also supportive of the original hypothesis; while *H. lepidulum* appears to perform relatively poorly in the lower elevation landscape matrix (consisting of forest and forest gap), it appears to do well in the stream corridors, reaffirming that the riparian corridors may be critical to the progression of the invasion into the upper elevation habitats.

These results highlight that the corridors not only have the potential to provide a conduit for seed dissemination, but perhaps more importantly provide suitable habitat for population establishment, providing a foothold to the invasion in an otherwise largely inhospitable matrix. Similar dynamics have been observed in other systems where invasions utilise available habitat provided by linear features to bypass inhospitable habitats (Parendes & Jones 2000; Christen & Matlack 2006; Andrew & Ustin 2010). Without the refuge provided by the stream corridors in the Craigieburn landscape, H. lepidulum would have to rely on long-distance or non-standard dispersal of propagules to reach the higher elevation alpine habitats (Nathan et al. 2002; Higgins et al. 2003). Observations of other members of the Asteraceae family suggest that wind disseminated seed similar to *H. lepidulum* have a relatively low probability of traveling far enough to bypass the forest habitat altogether (Soons et al. 2004; Tackenberg 2003), especially considering the uphill movement required to extend into the catchment. However, given the fecund nature of *H. lepidulum* and its ability to reproduce apomictically, there is still a marginal chance that a single long distance dispersal event could result in the establishment of a population in the higher elevation habitats. Correspondingly, it should be noted that even the most effective control measures within the stream corridors may prove futile if long-distance dispersal events are successful at transporting even a small proportion seed to the alpine habitats. Still, without any intervention, the results of these simulations

suggest that the invasion is able to effectively utilise the forest creek habitat as a corridor to bypass the forest habitat, and to do nothing would almost assuredly result in the invasion reaching the higher elevation habitats. Overall, these conclusions largely support the hypothesis formed using only the recruitment data that suggested that the forest creek habitats provide a vector which allows the invasion to permeate the barrier posed by the forest matrix.

While these results make it clear that the forest creek habitat is facilitating the invasion of H. lepidulum, they also suggest that once it arrives, the invasion is likely to do quite well in the alpine habitats. Surprisingly, the tussock habitat (which reflected the highest initial recruitment) appears to be the least likely of the alpine habitats to sustain populations of H. lepidulum in the long term. Nevertheless, the projections suggest that a substantial proportion (38% on average) of populations in this habitat can survive to at least 20 years. This could be long enough to establish a local presence and seed source that could spread elsewhere, and could even be long enough to have a negative impact on the existing community and ecosystem (although this work is not designed to directly address such impacts). In contrast to the tussock habitat, projections will survive to 20 years, and a substantial proportion (49 and 38% on average, respectively) will survive indefinitely. Compared to the lower elevation forest habitats, it appears that the upper elevation alpine habitats are much more susceptible to invasion by H. lepidulum.

2.4.2 Comparing survey data

The pairwise comparisons reveal that there is very little agreement between the simulated abundances of *H. lepidulum* and those observed in the field in the first five years of invasion (Table 2.1). However, when the zero values are removed, agreement between predicted and observed abundances increases substantially. This suggests that the mechanisms for determining the establishment of a population are fundamentally different than the mechanisms which determine abundance (i.e. Diez et al. 2009), and that these simulations more accurately describe the latter. However, comparisons of population establishment are confounded by the fact that we have little contextual data for the field observations, such as what (if any) propagule supply a location has been subject to, how long the population has been present, and if the the absences of *H. lepidulum* reflects a failed establishment (as in the simulations) or simply a location which the invasion has not yet reached. These are important caveats to note when using field observations to validate projections.

If we compare only estimates of abundance between the simulated and observed populations, it suggests that the established populations of *H. lepidulum* in the forest creek habitat are currently at or near the population size expected at t_{eq} , suggesting they are nearing the full extent of their development. This is not surprising given the relatively short development time required for the population to reach equilibrium in this habitat (five years; Table 2.2). The non-zero observations of abundance from the field surveys (intended to represent only locations which are occupied) in the forest creek habitat appear to match the projected abundance at 20 years, but still hasn't reached the maximum abundance observed in the simulations (Table 2.2). This suggests that the age of the invasion is closer to 20 years than the estimated nearly 400 years required for the projections to converge on a steady state, which roughly aligns with the first report of *H. lepidulum* in this area occurring in 1941 (Wiser et al. 2000).

The current abundances in the alpine habitats also appear to be currently well below the steady state condition as projected by the simulations, and appear to be capable of supporting much larger populations. This supports the initially hypothesised invasion progression; H. lepidulum appears to approaching the capacity of available space in the lower elevation habitats (particularly the forest creeks), and is only beginning to establish in the alpine habitats. I can conclude from the simulated projections performed in this chapter that the relative rarity of *H. lepidulum* in the higher elevations is not a function of differential resistance to invasion in the habitats, but instead that these habitats are highly invasible, and a lack of propagule pressure is the only thing keeping H. lepidulum from increasing in abundance. Unfortunately, the survey data reveals that while levels of *H. lepidulum* abundance in the alpine areas are currently well below their capacity, there are some individuals already present, suggesting the invasion process is already underway. Controlling spread through the natural bottleneck of the stream corridor may be achievable, but additional efforts would be required to remove individuals that have already established in these alpine habitats. While it is possible that control efforts in the alpine areas could slow invasion, complete eradication of invasive species is often an extremely difficult task, and is unlikely to be feasible for *H. lepidulum* (Mack & Lonsdale 2002).

2.4.3 Perturbation analysis

The perturbation analysis helped to identify a number of demographic processes that are particularly influential to populations of *H. lepidulum*. The transition from the juvenile to adult stage was the most consistently sensitive transition in the life cycle. Increasing the probability of transitioning had a positive effect on overall population size, as individuals in the adult life stage have a much lower probability of mortality, as well as contribute new propagules to the pool. Increasing recruitment into the adult stage even tipped some of the some populations from unsustainable to sustainable (forest and tussock habitats; Figure 2.6). Reducing the probability of transitioning to the adult stage really only influenced overall population size when applied to the older age classes; this is predominately because the proportion of younger juveniles transitioning to adult is effectively none, and reducing this probability has very little effect. The overwhelming majority of individuals that reach the adult stage do so after three or four (or more) years in the juvenile stage, so reducing the probability of transitioning to adult from these age classes effectively cuts deeper into the normal supply of recruits to the adult stage. Unfortunately this doesn't help to focus management efforts very much; it is already obvious that controlling the plants before they become reproductive is potentially beneficial. One useful aspect of this finding is that aside from a very small number of individuals, the vast majority of *H. lepidulum* will take at least three to four years to reach maturity. If an approach that eliminated all individuals at once (i.e. fire or broadcast herbicide treatment) then reapplication of the treatment would only have to occur every two to three years until the seedbank was exhausted, as individuals are highly unlikely to mature in such short an interval to resupply the seed bank.

Aside from the transition from juvenile to adult stage, there were other sensitive life stages, although they were less consistent across the different habitats. The availability of recruitment sites was influential in a number of the habitats, but this is largely an attribute of the existing landscape and is difficult to actively influence, save for an attempt to minimise disturbance and promote the expansion of existing vegetation to occupy all available sites. Seed production also appeared to be a constant point of vulnerability in the life cycle, and substantial reductions in seed production appeared to severely impact the viability of the population. This suggests that release of a highly effective seed predator could potentially impact population success, although levels of seed predation are often too low to be effective (Shea & Kelly 1998; McFadyen 1998).

2.4.4 Modelling approach

The use of the hierarchical Bayesian methods to estimate parameters for the models of transition probabilities provided a number of benefits to this analysis. Some of these are primarily pragmatic; first, the way the model can be specified in the hierarchical Bayesian method allows me to account for the complex hierarchical nested structure of the data obtained from the seed sowing experiments. While the structure of the experimental design could certainly be analysed using frequentist approaches, the hierarchical Bayesian approach provides a simplified and more streamlined method which facilitates the decomposition of the process into different levels (Clark 2005).

Secondly, the parameter estimates provided in the form of empirical posterior distributions provide an ideal avenue to define the stochastic sample space in the final model. Because of this, the final projected abundances are able to reflect the full range of uncertainty (Figure 2.5 and Table 2.2) propagated up from the original data all the way to the final population estimations. This approach frees the final output of the simulations (estimates of population size) from being restricted to a preconceived population-level error structure (i.e. Gaussian) (Clark 2003) which would clearly not fit the predicted population sizes (Figure 2.5).

Finally, utilising the Bayesian/MCMC procedure to parameterise the density-dependent models provides a unique avenue to allow the magnitude and variability of the densitydependent relationships to vary as defined by the available data. Using the Bayesian hierarchical approach when parameterising the stage transition models allows us to define the uncertainty in the parameters in a way that does not attempt to distinguish between the exogenous and endogenous mechanisms shaping the regulatory process, which are notoriously difficult to isolate (Grenfell et al. 1998; Higgins et al. 1997; Buckley & Metcalf 2006). Instead, both are incorporated as a latent processes, reflected in the uncertainty of the parameter estimates, and by extension the direction and magnitude of the different relationships. While specifying the endogenous and exogenous processes independently would provide a better understanding of the mechanisms behind the process, the uncertainty associated with our parameter estimates reflect the observed variation in the data. In this form the range of the potential strength of the regulatory processes can be easily incorporated into the demographic models and then used to project the full range of population behaviour.

2.5 Conclusion

Variation in population potential across heterogeneous landscapes can have a profound effect on landscape-level spread. In the case of H. lepidulum, analysing the demographic performance in different habitats reveals that stream corridors provide refugia in an otherwise inhospitable forest matrix. While we cannot conclude from this analysis that a continuous tract of forest would provide an absolute buffer against invasion into the alpine areas, it is clear that the population of H. lepidulum is able to exploit the relatively small proportion of stream habitat. At the very least the stream habitat provides a foothold for additional seed sources in closer proximity to the alpine areas than would be found otherwise. These results suggest that management efforts directed at keeping the population from spreading into the alpine areas should prioritise the forest stream habitats, although the potential influence of transient populations in the forest and forest gap habitats has not been fully assessed.

Unfortunately the sensitivity analysis provides little information that can help to direct control efforts; H. lepidulum appears to be be well adapted for invasion. At this stage, even if weaknesses in the lifecycle were identified, it is still not clear to what extent these habitats are subject to seed input from distal sources. The threat posed by long distance dispersal from either within the landscape or even from from more distant sources cannot be certain without separately assessing seed dispersal for the species. However, we can conclude from the demographic models that if seed are able to reach the alpine areas, those habitats are invasible, and will provide fertile ground for establishment of a population. To further compound the threat, the apomictic nature of H. lepidulum means that a single wayward seed has the ability to provide the impetus for a full scale invasion.

Although parameterising the demographic models used here to assess habitat invasibility can be quite data intensive (perhaps prohibitively so; Coulson et al. 2004; Ramula & Buckley 2009), strides are being made to explore how the use of hierarchical Bayesian approaches can maximise the knowledge gained from what data is available (Clark 2003). Even though the level of detail necessary for a full demographic analysis may not be available for all control efforts, this example has demonstrated that increasing the fidelity of demographic models by incorporating features such as habitat heterogeneity, density dependence, stochasticity, and temporal variation can have a significant impact on the resultant population-level projections, and can be essential to provide a clear picture of the dynamics which drive the invasion.

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Chapter 3

Quantifying wind-dispersed seed rain of *Hieracium lepidulum* in heterogeneous environments

3.1 Introduction

Since the majority of plants are sessile, dispersing seed away from the parent helps to mediate several factors that can be detrimental to survival of the offspring, such as intraspecific competition or predation by enemies (Harper 1977; van der Pijl 1982; Nathan 2001). The vast majority of these dispersal events typically result in progeny remaining close to the parent plant and are relatively easy to document (Cain et al. 2000). However a fraction of these seeds often travel much further. These long distance dispersal events can be loosely defined as the relatively small proportion of seed (typically represented by the furthest 1% or so of the seed dispersal; Cain et al. 2000) that are disseminated considerably further than the rest and result in different ecological or evolutionary consequences (sensu Nathan et al. 2003). With regard to population spread, these relatively rare events typically impose a disproportionately large influence on the overall spread rate (Clark 1998; Nathan 2006).

Quantitative models of dispersal traditionally represent the relocation of seed by using a probability density function describing the likelihood of a dispersal event traveling a given distance from the parent plant. This function, known as a dispersal kernel, typically takes the form of a positively skewed probability distribution. These distributions describe the majority of seed deposition occurring at relatively short distances from the parent plant, with the proportion of seeds deposited inversely related to distance from the parent (Cain et al. 2000). The occurrence of long distance dispersal events is represented in the tail of the curve; subtle changes in this portion of the function can play a critical role in determining the overall rate of the spread of an advancing population (Clark et al. 1999; Nehrbass et al. 2007). Unfortunately, the rarity of events at these distances

means that there is a general paucity of data available for accurately fitting this portion of the curve (Nathan 2006). The combination of the rarity of this type of data along with its disproportionate influence on spread rates compounds the difficulty in accurately estimating these kernels, and subsequently producing accurate estimates of invasion speed. For this reason, even though great care is taken in determining the correct kernel form and parameterisation, there is inherent uncertainty in the predictions developed here, as the highly influential long distance events are (inevitably) estimated by extrapolation of the kernel beyond the range of the observed data.

Throughout this chapter I focus on parameterising empirical dispersal functions as opposed to mechanistic forms to describe the dispersal of *Hieracium lepidulum* (Stenstroem) Omang (Asteraceae). There are a number of reasons an empirical approach was chosen over a mechanistic approach; the first of which is an attempt to match the data collection method with an appropriate analysis. In this investigation the data were collected using seed traps, which generally describe the patterns that result after collecting a multitude of observations over a period of time. The alternative is to use a seed tracking approach, where the dispersal of individual seeds is monitored. The seed tracking approach is ideal for the development of mechanistic models, which typically rely on two primary data inputs; the terminal velocity of seed, and data describing the wind behaviour during seed flight (Greene & Johnson 1989; Nathan et al. 2002; Tackenberg, Poschlod, & Bonn 2003). While tracking an individual, all of the relevant variables that affect that one dispersal event can be recorded in the same instance as the dispersal occurs, and attributed to that singular event. In contrast, seed traps reflect the resulting outcome from a large number of dispersal events. A retrospective analysis could be used to reconstruct mechanistic dispersal data from the seed traps, but if the traps are left out for any significant amount of time, it becomes difficult to reconcile the individual dispersal events with explanatory data at an appropriate resolution necessary to provide a useful insight. For example, many mechanistic analyses of wind-dispersed seed suggest that instantaneous measures of both the horizontal and vertical wind behaviour at the time of seed release dictate the dispersal distance (Nathan et al. 2002; Tackenberg, Poschlod, & Kahmen 2003; Soons et al. 2004). This type of information is practically impossible to match up to collections made in seed traps. The second reason for selecting an empirical approach is that the goal of this investigation is to assess the options for dispersal models to be implemented into a spatial simulation. Empirical kernel forms are not only more straightforward, but are also much less computationally intensive to implement in comparison to a mechanistic model (Katul et al. 2005). While mechanistic models can be integrated to form a less computationally intensive kernel for use in simulations (Nathan & Muller-Landau 2000), the resolution and corresponding advantages of the mechanistic approach would be lost. Lastly, while a appropriately developed mechanistic models are typically more robust to being applied beyond the range for which they were initially developed, the potential advantage in this situation would still be limited by the difficulty in accurately recreating the appropriate frequency of the underlying mechanisms, due to their relative rarity. The long distance events are most likely driven by relatively rare wind conditions, are arguable just as difficult (if not more so) to observe.

In this chapter I focus on identifying dispersal kernels that are best able to recreate the dissemination of wind-dispersed seed from H. lepidulum. To accomplish this I have assembled a variety of potential dispersal kernel forms, each of which is fit to available dispersal data. These different kernel forms are then compared to determine which kernel best describes the observed dispersal of H. lepidulum seeds. While similar approaches have been employed in a number of other investigations, in this investigation I have taken the additional step of parameterising the kernels for specific habitats in which H. lepidulum occurs. Using this approach I am able to assess how the shape and form of the dispersal kernel changes according to different environmental settings.

3.2 Methods

3.2.1 Data collection

The dispersal data used to parameterise the kernels was collected in a range of different habitats that exist in a montane catchment in the Craigieburn forest park in the mid-Canterbury region of the Southern Alps, New Zealand. This data was collected as a part of Alice Miller's thesis work (Miller 2006); however it was initially used solely to identify differences in dispersal between habitats. By assessing the fit of a range of dispersal kernels for each of the habitats in which data were collected allows me to identify which kernel provides the best fit, and compare how the dispersal behaviour changes in the context of the existing community structure. The distribution of habitats in this catchment is representative of catchments throughout the range, and can be broken into two primary groups; below approximately 1400m above mean sea level (AMSL) the catchment is comprised primarily of mountain beech (Nothofaqus solanderi var. cliffortioides) forest, while higher elevations consist of a sub-alpine mixture of scrub and tussock grassland dominated by *Chinochloa* species. The Mountain Beech forest is subdivided into intact forest, forest treefall gaps, and forest creek habitats. The sub-alpine areas are subdivided into tussock, scrub, and alpine creek habitats, although logistical constraints prevented dispersal trials from being located in the scrub habitat. Greater detail about these habitats can be found in Chapter 2.

Locations for the dispersal trials were chosen to maximise accessibility so that the maximum number of trials could be run in a single day and to minimise variation in wind behaviour. The dispersal trials took place in five habitats; forest, forest creek, forest gap, alpine creek, and tussock grassland. Five replicates were performed in each habitat, and each replicate was repeated for five subsequent days, providing a total of 125 replicates.

All replicates in the forest habitats were run on the same five days, while the trials in the sub-alpine habitats were run on a separate set of five days, as it was logistically impossible to run trials in all habitats at the same time. All stems of *H. lepidulum* within a 50m radius of plot centre were removed prior to setting up the experiment in order to remove confounding seed sources. At each site, dispersal data were collected by setting up an experiment where 240 flower stems of H. lepidulum were inserted into a 10 x 30cm block of horticultural sponge. This setup yielded a seed source of approximately 38,000 seeds (Miller 2006). Although the process was not modelled directly, using seeds still in the flower ensured that the force necessary to remove the seed from the capitula was incorporated, an important element which is often overlooked in seed dispersal studies. These seed sources were placed in the centre of a 50x50cm square of plastic sheeting, with four sampling strips of plastic extending 10m from the source at 90° angles. These strips were covered with an adhesive coating to trap seeds following dispersal from the source. Seed dispersal occurred over a period of approximately six hours, at which point the sampling strips were removed and stored for later analysis. Each trial was begun with a new seed source and clean sampling strips. The number of dispersing seeds were counted on each of the sampling strips and grouped into 30cm distance classes. The 30cm resolution was selected in order to match the resolution of the density-dependent demographic mechanisms described in Chapter 2, in order that they can later be combined in a spatial simulation (see Chapter 5).

3.2.2 Empirical dispersal kernel forms

A large array of potential formulae exist for describing the dispersal of seed (Clark et al. 1999; Bullock & Clarke 2000; Levin et al. 2003; Nathan 2006). For simplicity, the majority of these applications (including my own) limit their investigation to dispersal in a single dimension, removing or ignoring any anisotropic effects. While the data collected here reflect dispersal in four directions, there was not sufficient data collected to identify the mechanisms behind anisotropic effects (nor implement them in the subsequent simulations) so the direction data was ignored and counts at each distance averaged across the four directions. I have included a description below of those kernel forms that I use to describe the *H. lepidulum* dispersal data. These particular kernel forms were selected as they have previously been used in empirical descriptions of wind dispersed seed; some not only to describe the probability of dispersing a given direction, but in some cases also to describe observed counts at different distances (Cousens et al. 2008). In addition, they are relatively simple models (three parameters or less) that typically define the probability density function of common distributions. While this is not an exhaustive set of potential kernels, this list provides an excellent starting point when exploring which options are available for fitting a probability density function to dispersal data. The variables x(dispersal distance in terms of the number of 30 cm units), and y (the model response,

in terms of the probability of dispersing to that distance) are consistent across all of the formulae; however, parameters within the kernels are generally not directly comparable between the different equations.

Cauchy

The Cauchy distribution is a leptokurtic distribution that can be used for modelling the dispersal of seeds (Shaw 1995; Skarpaas et al. 2005). It is often considered an alternative to the exponential function when a greater proportion of long distance events are required (Paradis et al. 2002). The functional form of this distribution is

$$y = \frac{1}{\pi \alpha [1 + (\frac{x - \beta}{\alpha})^2]}.$$
 (3.1)

Two versions of this kernel were fitted to the data; a two-parameter version which fit both the scale (α) and location (β) parameters, and a second version which omitted the location parameter, forcing the peak of the distribution to occur at x = 0.

Weibull function

This density function was initially developed to be highly flexible (Weibull et al. 1951) and has been previously applied to modeling seed dispersal (Clark et al. 1998). It is flexible enough to provide a range of curves using two parameters:

$$y = \frac{1}{N} \exp\left[-\left(\frac{x}{\alpha}\right)^c\right]$$
(3.2)

where α is a dispersion parameter, c is a dimensionless shape parameter, and N is a normalisation constant (Clark et al. 1998). For a one-dimensional model

$$N = \frac{\Gamma\left(\frac{1}{c}\right)\alpha}{c} \tag{3.3}$$

where Γ is the gamma function (Pitt 2008). The shape parameter allows this function to be quite flexible; values of c less than or equal to one are concave at the source and have fatter tails. When c is equal to one, the function is the same as a one-parameter exponential function; and as c approaches zero, the kurtosis of the function approaches infinity (Clark et al. 1999). As c increases beyond one, the shape of the kernel becomes convex at the source, the kurtosis decreases, and at c = 2 the function is identical to a Gaussian distribution (Clark et al. 1998). Unfortunately, parameterisation of these models becomes unstable if both the α and c parameters are fitted at the same time; it is therefore necessary to assume a value of one of them and fit the other (Clark et al. 1999). As both a Gaussian and an exponential function are fit to the data separately, I parameterised this kernel using values of c = 0.5 (Kot et al. 1996; Clark 1998) and c = 3 (Ribbens et al. 1994) in order to approximate both a fatter-tailed function and one that is more convex at the source, respectively. In addition, both of these kernels were fit twice; once where both occurrences of the α value were constrained to be equal, and a second where these values were allowed to vary independently. This resulted in a total of four versions of this kernel being fit to the data.

Gaussian

The Gaussian function is probably the most well known option, however the lack of excess kurtosis means that it does not often provide an adequate fit to the leptokurtic shape commonly observed in dispersal events (Levin et al. 2003; Nathan 2006). However, the Gaussian function can provide a good estimate of local dispersal (Buckley et al. 2005; Clark et al. 2005), and it's shape can be used to reproduce the high concentration of seed often found directly below an overhanging canopy (Clark et al. 1999; Ribbens et al. 1994). The Gaussian kernel takes the form

$$y = \frac{1}{\sqrt{2\pi\alpha^2}} e^{-\frac{(x-\beta)^2}{2\alpha^2}}.$$
 (3.4)

In my analyses, two versions of the Gaussian kernel were fit; a two-parameter version which included a location parameter (β) which adjusted the location of the mean, and a single parameter kernel where the location parameter was omitted, restricting the mean of the distribution to a value of zero.

Log-normal

The log-normal distribution is designed to represent variables whose logarithm is normally distributed, and are described by the function

$$y = \frac{1}{x\sqrt{2\pi\alpha^2}} e^{-\frac{(\log(x)-\beta)^2}{2\alpha^2}}.$$
 (3.5)

The log-normal is a unimodal and strongly leptokurtic distribution (Russo et al. 2006). This function provides a 'fatter-tailed' option compared to the standard Gaussian form. Two forms of this kernel were also fit; one which included the location parameter (β), and another where the location parameter was omitted, forcing the peak of the distribution to occur at one.

Power

The power function

$$y = \alpha x^{-\beta} \tag{3.6}$$

equates to a linear fit on a log-log plot. This feature makes it relatively easy to fit and correspondingly popular, and has been used to describe seed dispersal in a number of studies (Okubo & Levin 1989; Laman 1996; Bullock & Clarke 2000). This function produces a strongly leptokurtic distribution, which typically provides fatter tails (and therefore more long-distance dispersal events) than the Gaussian or negative exponential functions. The power function however has an infinite density at zero, which makes it's use as a dispersal kernel difficult (Nathan & Muller-Landau 2000). Normalisation of the function requires bounding the function, which is useful in order to restrict it to the range of the data (Clark et al. 2005). A second, less common one-parameter version of this kernel was also fit as

$$y = \beta x^{-\beta}.\tag{3.7}$$

Negative exponential

The negative exponential function has been employed in many instances to describe seed dispersal distances (Bullock & Clarke 2000; Clark et al. 1999; Russo et al. 2006; Martínez & González-Taboada 2009). The basis of this function is that the response variable decreases at a rate proportional to itself. This function is useful in that it provides a more leptokurtic distribution, with a larger proportion of events occurring in the tail compared to a Gaussian distribution (Clark et al. 1999). However, the tail of this distribution may not be 'fat' enough (accommodate a high enough proportion of events) to accurately recreate many observed dispersal patterns (Levin et al. 2003). It's simplest form uses a single parameter α , which determines both the intercept (or initial quantity) and the rate of decay away from that quantity

$$y = \alpha e^{-(\alpha x)}.\tag{3.8}$$

There is also a version of the exponential model that utilises two variables, by shifting the origin of the distribution. This is accomplished by introducing a location parameter β into the exponent of the function

$$y = \alpha e^{-\alpha(x-\beta)}.\tag{3.9}$$

The same effect of including the location parameter can be obtained by fitting separate intercept and decay parameters (Sit & Poulin-Costello 1994)

$$y = \alpha e^{-(\beta x)}.\tag{3.10}$$

where γ determines the intercept and α the rate of decay. Both the first and last versions of this function were fit to the dispersal data.

Student's t

The student's t distribution can also used to model seed dispersal, and can be quite useful as it allows a fatter tail than either a Gaussian or exponential model form. This fatter tail increases the probability of distal dispersal events, which in turn results in an overall faster spread rate (Clark et al. 1999; Levin et al. 2003). The kernel form

$$y = \frac{\Gamma\left(\frac{b+1}{2}\right)}{\sqrt{b\pi}\Gamma\left(\frac{b}{2}\right)} \left(1 + \frac{\left(\frac{x}{b}\right)^2}{b}\right)^{-\left(\frac{b+1}{2}\right)}$$
(3.11)

follows the one-dimensional form; other applications often use a two-dimensional form ("2Dt"), which can be used to describe the resultant seed density per unit area as it includes an arc-wise integration of the circular area (Clark et al. 1999).

3.2.3 Model fitting procedure

Data conversion

Counts of seeds were performed for every 30cm section of the plastic strips used to collect dispersed seed. In order to fit the kernels to the dispersal data, these counts had to be converted to reflect the proportion of seed that were dispersed at each distance interval. This conversion was performed by first calculating the mean density of seed at each 30cm interval for each trapping replicate. At each interval, the size of the segment was equal to the width of the strip (0.5m) by the depth of the interval (0.3m), producing a trap area at each distance of $0.15m^2$. There were four seed trap strips at each replicate, which equates to four replicates of $0.15m^2$ trap segments at each distance for each dispersal replicate. These four segments were used to calculate a mean density at each distance for each replicate. The calculated density was then used to project the total number of seed dispersed to that distance interval.

In reality, the total number of seed dispersed each distance would fall not into the discrete segments, but be distributed within an annulus (a ring-shaped feature represented by the area between two concentric circles) that occupied the same distance intervals as the segment. In order to project the total number of seed at each distance, I converted the number of seed at the segment level to the number of seed in the total area of the annulus, calculated as

$$A_{annulus} = \pi (R^2 - r^2) \tag{3.12}$$

where r is equal to the diameter of the inside circle (or the distance of the nearest edge of the trap segment from the seed source) and R is equal to the diameter of the outside circle (the distance of the furthest edge). The width of the annulus is defined by the width of the distance interval, and is always 0.3m, but as r increases, the area of the annulus increases.

The mean observed density (N(x)) at a distance (x) from the seed source is converted to a corrected seed count $(N_c(x))$. This corrected count represents the total number of seed projected to be deposited within the annulus. The conversion was performed by multiplying the mean seed count at the individual segment level by the area of the annulus at that distance, and then dividing by the area of the trap segment using the equation

$$N_c(x) = \frac{N(x) \cdot \pi (R^2 - r^2)}{0.15}.$$
(3.13)

This value was then converted to reflect the proportion of seed that are deposited at each distance so that the data could be used to fit a probability density function (pdf), representing the probability that a given seed would disperse to that distance (P(x)). For this operation the distance for each trapping segment was set to the furthest distance represented by the segment; for example, the first distance value was 0.3, and represented those seed that fell between zero and 0.3 metres from the source. The zero value was not included as the number of seeds that did not disperse were not accounted for. To convert $N_c(x)$ to P(x), I first calculated the total number of seed dispersed within the radius of the seed trapping $(N_{c,tot})$ as

$$N_{c,tot} = \sum_{x=0.15}^{10} N_c(x) \tag{3.14}$$

and then divided the amount represented by each trap segment by the amount represented by the entire trapping sheet

$$P(x) = \frac{N_c(x)}{N_{c,tot}}.$$
(3.15)

The kernels were then fit to reflect the proportion of seed P(x) as a function of the distance (x).

Parameter estimation

The different kernel functions were fit by determining the least-squares parameter estimates using the nls algorithm in the R statistical software language (R Development Core Team 2009). The kernels were first fit to the complete pool of data, ignoring any habitat information; this allowed me to fit the functions using a greater number of points, making the procedure less sensitive to starting values. Using this approach to fit the different kernels to the dispersal data required the selection of appropriate starting values. For some of the kernel forms, estimating starting values was relatively straightforward; estimates for the Gaussian parameters α and β were obtained by calculating the mean and the standard deviation (respectively) of the raw data. The log-normal kernel was fit using the same starting values as the Gaussian kernels. The negative exponential kernel has an intercept term, which was visually estimated from a graph of the data for a starting value of the one-parameter kernel; the resulting parameter value was then used as a starting point for the two-parameter kernel. For the power kernel, the *a* parameter can be interpreted as the response at x = 1 (when the equation reduces to y = xa), which was visually estimated from the data. As with the negative exponential kernel, the parameter estimate from fitting the one-parameter power kernel was used as starting values for the two-parameter power kernel. For the single-parameter Cauchy kernel, the amplitude of the function can be calculated using

$$\text{Amplitude} = \frac{1}{\pi\gamma}; \tag{3.16}$$

this was re-arranged to calculate a value for γ that provided an amplitude of 0.5, which in this case was equivalent to an intercept value (similar to the negative exponential model). The fitted parameter estimate from the one-parameter Cauchy kernel was used as the starting values for the two-parameter kernel. Starting values for the Student's t distribution were chosen by exploring a range of possible values and selecting one that approximated an appropriate intercept for the data. The Weibull kernel has a special case where it is equal to the negative exponential kernel (c = 1). I was therefore able to use estimates from the fitted negative exponential kernels as starting values for these kernels. An informal examination of the sensitivity of the starting values revealed that the starting values were robust as long as they were within an order of magnitude of the appropriate parameter value. The parameters for the pooled models were then used as the starting values for parameterising the habitat-specific kernels.

Model selection

Akaike's information criterion (AIC) values were calculated for the pooled kernels and each habitat-level kernel estimate to allow for comparison of the fit of the different kernels. This approach provides a standardised technique to compare the deviation of fitted models from the actual data in order to determine which of the models provides the best approximation (Burnham & Anderson 2001). This approach also imparts a penalty for each additional model parameter in order to discourage the over-fitting of models. AIC values were calculated using the formula

$$AIC = 2k - 2ln(L) \tag{3.17}$$

where k is the number of parameters estimated, and L is the likelihood of the fitted kernel. Models with AIC scores that differ by less than 2 are considered equally as plausible, 4 to 7 are considerably less equally plausible, and > 10 suggests they are substantially different (Burnham & Anderson 2002).

Each kernel was evaluated to determine the proportion of dispersal events which are predicted to extend beyond the 10 metres reflected by the observed data. This proportion was estimated by using partial integration to calculate the amount of area under each fitted function on the interval [0, 10] (the range reflected by the data) and [10, 100000] (the extrapolated range). This was calculated as

$$P_{tail} = \frac{\int_{10}^{100000} f(d)}{\int_{0}^{10} f(d) + \int_{10}^{100000} f(d)}.$$
(3.18)

3.3 Results

3.3.1 Pooled kernels

Based on the AIC scores, the two-parameter Cauchy kernel provided the best fit to the pooled data (Table 3.1). A score difference of 4.5 suggests that this kernel form is more plausible (although minimally) compared to the Student's t kernel, which provided the second-best fit. The Student's t kernel returned a score which was virtually identical to the 3rd rank kernel, which was a two parameter version of the Weibull model where s = 0.5 (AIC difference < 1). After this there was a significant difference in score (21.9) to the next best kernel, which was a two-parameter negative exponential. The similarity of the fit of the two-parameter Cauchy kernel and the second best student's t kernel can be observed by examining the plotted response of both functions (Figure 3.1). The proportion of dispersal events in the tail showed a large range of variation, but in general tended to be smaller in the kernels with better AIC scores.



Figure 3.1: The two-parameter Cauchy kernel and the Student's t kernel after being parameterised using the data pooled from all habitats. The modelled responses are plotted against the observed data.

Table 3.1: Parameter values of the kernels fitted to the pooled data in order of decreasing AIC values, along with the proportion of events predicted to occur in the extrapolated range beyond the observed data (P_{tail}). The AIC values are used to determine which function best describes the observed seed dispersal, with the lowest score indicating the best fit.

Kernel Form	No. of Parameters	α	β	AIC	$\mathbf{P}_{\mathrm{tail}}$
Cauchy	2	0.805	0.021	-883.0	0.052
Student's t	1	0.368	N/A	-878.5	0.194
Weibull $(s=0.5)$	2	0.7653	0.271	-877.8	0.016
negative exponential	2	3.424	0.986	-855.9	< 0.001
power	2	0.078	0.945	-842.4	0.398
Gaussian	2	-0.867	1.779	-825.5	< 0.001
Weibull $(s=3)$	2	6.034	1.372	-767.6	0
Cauchy	1	1.473	N/A	-725.6	0.073
Weibull (s= 0.5)	1	3.347	N/A	-595.8	0.484
Guassian	1	6.839	N/A	-580.0	0.383
negative exponential	1	19.45	N/A	-536.1	< 0.001
power	1	0.034	N/A	-522.7	.999
Weibull $(s=3)$	1	36.16	N/A	-518.0	0
log-normal	1	0.582	N/A	-482.9	0.001
log-normal	2	0.013	1.398	-464.0	0.674

3.3.2 Habitat-specific kernels

In addition to fitting the data pooled across all habitats, in four of the five cases the Cauchy kernel also provided the lowest AIC scores when fit to data from the individual habitats. In two of these habitats (forest and forest creek) the two-parameter Cauchy kernel was virtually indistinguishable from the student's t kernel in terms of the AIC scores (Table 3.2). In the forest gap and tussock habitats, this distinction was clearer; the AIC values indicated a distinct advantage of the 2-parameter Cauchy kernel over the second best score returned by the two-parameter negative exponential kernel. Only in the alpine creek habitat did a different kernel form return the best AIC value; the two-parameter power and Student's t kernels both provided AIC scores which were lower than the two-parameter Cauchy , which was separated from the lowest (best) score by just over six points. The plotted responses reveals that the best-fit power kernel produces a slightly shallower curve (fatter tail) than the two-parameter Cauchy kernel, suggesting a slight increase in the proportion of dispersal events travelling longer distances in this habitat (Figure 3.1).



Figure 3.2: Plot of the habitat-specific parameterisations of the two parameter Cauchy kernel against the observed data in each of the habitats. The Cauchy kernel (red lines) reflected the best-fitting kernel in each habitat based on AIC values, except in the alpine creek habitat where the two-parameter power kernel (broken line) fit better. Both kernels are plotted in this habitat to illustrate their similarities.

Habitat specific parameter estimates for the two-parameter form of the Cauchy kernel were compared to identify habitat-specific differences. The Cauchy kernel form was used as it provided a standard comparison, even though it was not the best fitting function in the alpine creek habitat. 95% confidence intervals were calculated around each parameter by assuming they are normally distributed, and then calculating the interval as $\bar{x} \pm$ 1.96SE, where the standard error was calculated as $SE = \frac{sd}{\sqrt{n}}$. These confidence intervals were then used to perform a multiple comparison test by examining if there was any overlap between the 95% confidence interval of the parameters. This test permitted me to identify the habitat-specific differences in dispersal kernels (Table 3.2). The results of these comparisons revealed that the scale parameters (α) fell into two groups, with the forest and forest creek habitats having effectively the same value, while the forest gap, alpine creek, and tussock habitats were indistinguishable from one another. Differences in the location parameter were more complex, with overlap found between the forest and forest creek habitats, forest and alpine creek habitats, and the alpine creek and tussock habitats. The location parameter in the forest gap habitat did not overlap with any of the other habitats. These comparisons suggest that forest and forest creek habitats had very similar kernels, as did the alpine creek and tussock habitats.

3.4 Discussion

The dispersal range reflected in this model is relatively short (10m), as others have developed kernels describing dispersal of herbaceous species up to 80m (Bullock & Clarke 2000) and even further (see Willson 1993 for an extensive review). However, given the paucity of data at the extremes of the transects, I can be relatively confident that the approach used here captures the vast majority of dispersal events, and provides a good trade-off between collecting representative data and the benefit to accuracy achieved by increasing the sampling intensity, especially considering the time and logistical difficulty in collecting observations at further distances. Available data on other *Hieracium* spp. suggest the genus has relatively short dispersal distances; for example, the maximum dispersal distance observed for *Hieracium aurantiacum* was <2m (Stergios 1976). Unfortunately, this means I have to rely on extrapolating the kernel beyond the observed data in order to predict dispersal events beyond 10 metres. While these long distance events are known to have a disproportionate effect on overall spread rates (Clark 1998; Nathan 2006), I can be relatively sure the more local dispersal processes (i10m) will be accurately reflected, and it is these more localised dispersal events that will influence the demographic interdependency and exchange of propagules between local populations.

Table 3.2: AIC values derived from fitting various functions to describe the seed dispersal of <i>H. lepidulum</i> in different habitats. The AIC values are use
to determine which function best describes the observed seed dispersal, with the lowest score indicating the best fit. The three lowest AIC scores for eacl
habitat are denoted by bold font, and the superscript reflects their specific ranking.

AIC values are used	AIC scores for each		ck
	ee lowest		$Tuss_{i}$
	best fit. The three		Alpine Creek
TSALOL II. iepiuuiuni	score indicating the		Forest Gap
napa ang	ith the lowest	ic ranking.	Forest
	seed dispersal, w	lects their specif	Forest Creek
	t describes the observed s	t, and the superscript ref	No. of parameters
le 3.2: AlC values derived	etermine which function bes	tat are denoted by bold fon	Kernel Form

	1			4	4	
Cauchy	1	-154.2	-158.4	-136.2	-139.7	-149.1
Cauchy	2	-181.9^{1}	-193.8^{1}	-220.6^{1}	-189.4^{3}	-217.3^{1}
Weibull $(s=0.5)$	1	-135.2	-133.5	-99.8	-123.0	-110.3
Weibull $(s=0.5)$	2	-163.4	-168.4	-159.7	-152.2	-160.5
Weibull (s=3)	4	-117.3	-114.6	-82.2	-107.1	-94.4
Weibull (s=3)	2	-163.4	-168.4	-159.7	-152.2	-160.5
Gaussian	4	-125.5	-125.0	-114.4	-115.3	-110.6
Gaussian	2	-171.8	-182.5	-183.2^{3}	-165.4	-183.9
log-normal	4	-106.2	-104.2	-79.3	-97.1	-88.4
log-normal	2	-99.9	-97.6	-73.8	-93.1	-83.5
power	1	-118.5	-115.8	-83.0	-108.1	-95.3
power	2	-166.3	-174.6	-179.5	-195.3^{1}	-193.6
negative exponential	1	-121.9	-119.3	-85.4	-111.0	-97.8
negative exponential	2	-176.8^{3}	-188.1^{3}	-209.0^{2}	-173.4	-199.0^{2}
Student's t	,	-179.5^{2}	-191.6^{2}	-169.6	-190.6^{2}	-188.6^{3}

3.4.1 Pooled kernel

The two functions fit to the pooled dispersal data with the lowest AIC scores produced very similar responses when compared graphically. However, the two-parameter Cauchy kernel represents an increase in fit across a number of metrics (including the residual sum of squares, log-likelihood, and AIC), suggesting this kernel provided a better representation of the data compared to the Student's t kernel. A close examination reveals that the Cauchy kernel predicts a slightly thinner tail; a close examination of the tail of the dispersal using integration techniques reveals that the best-fit Cauchy kernel predicts approximately 5% of dispersal events occurring beyond 10 metres; this value is much closer to what is expected compared to the next best fitting Student's t model, which predicts almost 20% of events occurring beyond 10m. Unfortunately, any of the estimates of dispersal beyond 10 metres are entirely speculative based on extrapolation of the fitted models. Given the rarity and difficulty in observing dispersal events at these distances, it is not usually practical to validate this level of extrapolation, even those these relatively long distance events can have a disproportionate effect on spread rates. The discrepancy in the significance of the tail between the two best fitting kernels (and between all kernels; 3.2) exemplifies what a significant impact the selection of the kernel form can have on dispersal characteristics and subsequent estimations of spread rates.

An important aspect of the Cauchy kernel providing the best fit to dispersal is the fact that it is exponentially unbounded; such kernels which have 'fatter' tails than an exponential distribution are able to continue to accelerate over time (Clark 1998). This is a significant divergence from the constant spread rates which are characteristic of the reaction-diffusion models often used to characterise spread, which utilise a bounded Gaussian dispersal kernel (Skellam 1951; Kot et al. 1996). The use of a bounded kernel (either inherently via a reaction-diffusion approach or specified explicitly in an integro-difference model or otherwise) would undoubtably underestimate the dispersal of H. lepidulum; such issues with appropriate kernel selection have been identified as one of the primary reasons rates of spread are underestimated (Andow et al. 1990; Hastings et al. 2005). However, it is important to note that while kernel shape has a decidedly significant impact on invasion rate, it is only part of the invasion process; once dispersed, demographic processes determine the success of that seed, and can therefore also have a significant impact on the final spread rate of a population (Clark et al. 2001).

3.4.2 Habitat-specific kernels

The AIC values of the habitat-specific kernel fits reveal that the two-parameter Cauchy distribution provides the best representation of seed dispersal in the forest creek, forest, forest gap, and tussock habitats (Table 3.2). Only in the alpine creek habitat does this pattern deviate, where the power function provides the best fit. While comparison of AIC values suggest that the power function provides a significant increase in fit over the Cauchy

in the alpine creek habitat, the two-parameter Cauchy kernel still provides a better fit in the alpine creek habitat than it does in the other habitats in terms of minimising the sum of squared residuals (Table 3.2). Plotting the responses of the power and two-parameter Cauchy kernels suggests that they are quite similar, their difference manifesting as a subtle shift in the proportion of short- to long-distance dispersals (Figure 3.2). If I relax the constraint of selecting only the model with the best AIC score and assume that the twoparameter Cauchy kernel provides a sufficient representation, I can then utilise a set of pairwise comparisons to infer differences in patterns of dispersal across all of the habitats.

I initially expected that dispersal distances in the intact forest habitat would tend to be smaller as a result of winds being buffeted by the surrounding trees. I presumed this effect would be lessened in the more open environments of the forest gap and forest creek habitats, and that the open conditions of these and the alpine creek and tussock habitats would result in more seed traveling further distances. What these results show is almost exactly the opposite; the kernels parameterised in the alpine creek and tussock habitats (whose parameterisations are statistically equivalent; Table 3.2) disperse a greater proportion of seed near the source compared to the shallower response seen in the forest and forest creek habitats, which are also equivalent (Table 3.2, Figure 3.2). Forest gaps had the greatest proportion of dispersal events occurring directly adjacent to the source.

Explanations for these observed differences are only speculative; since the forest habitats were measured on different days than the alpine habitats, the different kernel responses could be attributed to day to day variation in wind patterns; however the forest gap habitat (measured on the same days as the other forest habitats) seems to contradict this. Wind data collected during the trials indicated that horizontal wind speeds were variable across days and habitats during the dispersal trials (ranging from 0 to over 6 m/s), but was not a significant predictor of the dispersal fit (Miller 2006). Another potential explanation is that wind movement below the canopy is less restricted, and better able to disperse seed. In this case, the co-dominant position that H. lepidulum occupies in the relatively low vegetative canopy of the alpine habitats may be more sheltered by surrounding vegetation than the sub-canopy position that H. lepidulum occupies in the forest habitats, which has little other vegetation (pers. observation). Although studies that examine sub-canopy wind velocities are rare, conditions have been described where a relatively bare understorey beneath an intact canopy may be subject to higher wind velocities than within the canopy itself (Landsberg & James 1971; Miller et al. 1991). In addition, wind flow over canopy gaps in a similarly structured forest has been shown to create variable conditions at the surface level within the gaps, with eddies forming on the leeward side, and relatively low wind velocities across the surface (Miller et al. 1991) which may explain the relatively short dispersal distances observed in the forest gaps. However more conclusive answers can only be found by more closely examining wind behaviour and seed positioning within the different canopies at the time of release.

Although the parameterisation of the two-parameter Cauchy kernel suggests equivalency

in the alpine creek and tussock habitats, the fact that the power kernel provided a better AIC score in the alpine creek habitat suggests that dispersal in these two habitats may exhibit fundamentally different patterns. The plotted responses suggests that the power function produces a slight increase in the proportion of dispersal events travelling longer distances compared to the Cauchy kernel (Figure 3.1). This variation in the pattern of dispersal distance may be due to a difference in the physical structure of the vegetation in the riparian areas of the alpine creek, although there was no data collected to reflect this. The overall magnitude of the difference between the Cauchy and power kernels is also unclear; visually the two kernels fit to the dispersal data in that habitat appear nearly identical, and may be qualitatively very similar to one another aside from the increased probability of long-distance events encountered when employing the power function.

Surprisingly, the confidence intervals around the parameter estimates revealed that the parameterisation of the forest and forest creek habitats were not significantly different from one another; my *a priori* expectation was that the dispersal conditions in the forest habitat would result in significantly shorter dispersals due to the presumed decrease in wind speed. However this was clearly not the case, as the two habitats had virtually identical parameter values. Although corridors are often associated with invasive spread (i.e. van Dorp et al. 1997; Wangen et al. 2006; Hoyle 2007 and others), the mechanisms by which the corridors influence spread are somewhat unclear, and researchers are beginning to question if the primary benefit of these corridors in fact lies in their ability to provide suitable habitat as opposed to acting as a conduit to increase seed transport, particularly for wind-dispersed seed (Christen & Matlack 2009; Andrew & Ustin 2010). The finding here that dispersal does not differ between the intact forest and the forest corridor, along with the increased demographic response seen in this habitat (Chapter 2), suggest that this may be the case for *H. lepidulum*.

Assuming that dispersal is the primary determinant of the overall rate of spread of the invasion, these results suggest that we would expect to see the invasion of *H. lepidulum* progressing the fastest through the forest and forest creek habitats, with a reduced rate of spread once it reaches the tussock and alpine creek habitats. Spread through the gap habitats would be the slowest, although this habitat tends to occur in small patches and an invasion front would presumably tend to find a path around them through the adjacent forest. Again, however, dispersal is not the only mechanism affecting invasive spread, and the influence of demographic processes can significantly influence these presumed invasion trajectories. While this research helps to identify exactly where and how dispersal differs between the habitats examined, it also suggests that a thorough analysis of how a range of existing vegetative structure can affect wind patterns, and subsequently the dispersal patterns of wind-dispersed seed, could provide valuable insight to how heterogeneous landscapes can affect invasive spread.

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Chapter 4

PopMod: A software module for incorporating demographics into spatial simulations

4.1 Introduction

The benefits of modelling a species at the level of the population have been recognised for some time. The modern application of the demographic model began in the 1940's when the idea of applying survival and fertility rates to age classes surfaced in the literature a number of times (Bernardelli 1941; Lewis 1942; Leslie 1945). Leslie's work was the first to consider the problem in a matrix format, which lead to the development of what we know today as matrix population modelling. Later, the work of Lefkovitch (1965) and Usher (1966) helped to make these techniques more accessible to ecologists by applying the concepts to stage-structured populations (as opposed to age-structured format used previously) and paralleling their usage with life tables, a more easily accessible data source for most researchers. Since then, matrix population models have been applied to investigate the life cycles of a vast range of organisms and address a broad spectrum of research questions (Crouse et al. 1987; van Mantgem & Stephenson 2005; Schwarzkopf Kratzer et al. 2009; Morris et al. 2011).

While matrix population models have proven an extremely useful tool for investigating the behaviour of populations, one shortcoming of their application is that they are typically employed as a closed system (Hixon et al. 2002), incorporating neither immigration or emigration of individuals or propagules. At approximately the same time as the matrix models were being developed, researchers began to look into the interaction of individual populations and their collective behaviours as metapopulations. This was largely stimulated by McArthur and Wilson's initial work on island biogeography (1963; 1967) and has since been furthered by a diverse array of applications (Hanski 1991; Wells & Richmond 1995; Wiens 1997; Freckleton & Watkinson 2002). Recently, modern demographic investigations are beginning to blur the distinction between metapopulation and population-level modelling, and incorporate elements of both approaches in order to develop a more holistic method for investigating the dynamics of species abundance. This hybridisation typically leads to the incorporation of a spatial context within which the demographic processes operate, creating a form of 'spatial population dynamics' (Jongejans et al. 2008). One of the most straightforward implementations of this concept is to model demographic processes at a local scale (population-level modelling), and provide links between the local populations via the modelling of dispersal processes (metapopulation modelling). This allows the modelling of demographic processes that determine population success and growth to occur on a local scale, while maintaining the linkages that connect populations at a landscape or regional level. Due to the complex spatial interactions necessary for implementing such approaches, specialised tools such as geographic information systems (GIS) are often employed to assist with the handling and processing of large amounts of spatial data. As the processes being modelled do not occur independently of the surrounding biotic and abiotic conditions, incorporating landscape details often increases the accuracy of prediction (Brown et al. 2008).

There currently exist a variety of tools which have been developed to employ this approach of incorporating demographic processes in a spatial context (Possingham et al. 1995; Akçakaya et al. 2004; Sebert-Cuvillier et al. 2010). While these examples are all useful and informative in their own right, there was a general lack of a highly flexible and powerful tool that was generic enough to be used in a wide variety of applications. With that goal in mind, I have developed PopMod, a modular interface that expands the already useful toolset made available by the MDiG software (Pitt 2008) to include demographic processes. MDiG was designed to integrate the modelling of temporal and spatial dynamics in a raster-based landscape using a pre-existing GIS package (GRASS) as a foundation. The MDiG software achieves this by performing two basic functions; 1) implementing modules that are used to calculate and modify cell values within rasters and 2) organising and storing the series of rasters after the calculations are applied. The software works by creating a sequence of rasters, representing the state of the population in the landscape at each time step. New rasters layers representing subsequent time steps are calculated on an individual cell basis, performed by implementing the necessary modules in a predetermined order. These modules can be custom scripted, and added or removed as needed. Additional detail can be found on the MDiG website, available at http://fruitionnz.com/mdig/. Currently existing modules focus primarily on dispersal of organisms to simulate dispersal (Pitt 2008). This system has successfully been applied to describe the spatial patterning of an invasion of argentine ant (*Linepithema humile*) across a heterogeneous landscape in New Zealand (Pitt et al. 2009).

In order to extend the utility of the MDiG software, I have developed an extension module (PopMod) that provides a flexible and powerful option for integrating matrix population

models into MDiG's existing dispersal and simulation functionality. PopMod was written using the Python programming language, primarily chosen due to it's approachability and flexibitiliy. Python is a natural fit, as its simplicity makes it easy to learn, easy to implement interoperability with other languages (including GRASS scripting in this instance), and there is a well developed suite of computational tools readily available, particularly SciPy (Jones et al. 2001). The flexibility of implementing the PopMod module lies in how the transition matrix is specified; it allows the user to to specify a range of options from simple static transition models to spatially-explicit, density-dependent stochastic models. This allows anyone to apply matrix-based population models to a cellular landscape in combination with MDiG's existing customisable method for modelling dispersal.

4.1.1 Matrix population modelling

PopMod's primary function is the application of a matrix population model. This modelling approach organises members of a population into the different stages of the lifecycle, denoted through the use of a population vector B_t . Each element in the population vector represents the number of individuals that belong to the corresponding stage at time t. The delineation of stages is independent of the model application; they can be determined in any way desired by the researcher, but are typically either classified by age or the developmental stage of the individuals. This population vector is then multiplied by a transition matrix (M) to obtain a new population vector (B_{t+1}) , representing the number of individuals in each respective lifestage at the following timestep (Figure 4.1). The transition matrix is critical to determining the outcome of the population, as the values within the matrix (termed transition values) represent the probability of transitioning between stages, and therefore determine the fate of the individuals.

$$B_{t} = \begin{bmatrix} S_{t} \\ J_{t} \\ A_{t} \end{bmatrix}$$
$$M = \begin{bmatrix} P_{SS} & P_{JS} & P_{AS} \\ P_{SJ} & P_{JJ} & P_{AJ} \\ P_{SA} & P_{JA} & P_{AA} \end{bmatrix}$$
$$B_{t+1} = \begin{bmatrix} S_{t+1} \\ J_{t+1} \\ A_{t+1} \end{bmatrix}$$

Figure 4.1: The matrix B represents the distribution of individuals of a population in the different lifestages (S=Seed, J=Juvenile, A=Adult), at time t and time t+1. The transition matrix (M) is made up of the probabilities of transitioning from one stage to the next; the specific transition reflected at each position in the matrix is signified by the first letter of the subscript representing the stage from which the individual originates, and the second letter the stage it transitions to.

4.1.2 Representation of the population

PopMod utilises a series of rasters to represent the population of the organism of interest. Each timestep in the simulation contains a number of rasters, each of which represents the number of individuals in a particular lifestage of the organism. The individual cells in a raster represent the membership of the lifestage at that corresponding spatial location. PopMod assembles the population vector (B_t) by querying all of the rasters at a specific location. This vector is then multiplied by the transition matrix to calculate the quantity in each lifestage at that location, represented by B_{t+1} . This process is then iterated for each cell location in the landscape, and the resulting cell values are combined to develop a new set of rasters that represent the landscape at the following timestep (Figure 4.2). PopMod can theoretically handle an unlimited number of stages in the lifecycle, but as additional stages (and associated rasters) accumulate, processing time and memory requirements quickly escalate.

4.2 The PopMod module

4.2.1 Defining expressions

One of the most powerful features in PopMod is the flexibility with which the transition matrix can be specified. Each transition value within the transition matrix is produced by evaluating a user-defined expression. This expression is evaluated for each iteration of the transition matrix (defined as individual cell x timestep combinations), so that any stochastic elements of the matrix will be re-drawn for each cell in each timestep of the simulation.

In the simplest application, each expression in the transition matrix can evaluate to a single value, resulting in a static matrix that is exactly the same in every cell across the raster layer at every timestep. This static population model applied across a homogenous landscape will result in identical growth trajectories in each cell. In this case, any differentiation between results in individual cells will be completely dependent on either starting values or immigration/emigration processes that result from dispersal of individuals.

More complex applications can incorporate variation in the transition matrices between different cells. One way to incorporate that variation is to include environmental stochasticity into the expressions, implemented as variation in the parameter values (Caswell 2001). In PopMod this stochasticity is defined by specifying a distribution for each stochastic parameter, which serves to define the sample space from which the parameter values are drawn. Values are then drawn from this distribution at random, and are then substituted into the expression when the model is applied. Currently, this sample space can be defined using any of the 35 standard distributions currently utilised by Python's numpy extension, providing a wide range of possibilities (Appendix A).



Figure 4.2: Diagram describing how PopMod integrates matrix population modelling into the the MDiG framework. Beginning at the top of the diagram, three different rasters represent three different lifestages (S, J, and A) at time t. At this point other modules available through MDiG can be applied; in this example, the dispersal module is applied to only individuals in the 'seed' stage, as established plants (J and A stages) are sessile. The lifestage vectors are assembled by querying the different lifestage rasters at a particular cell location (c) to construct the population vector for that location at time t, represented by the 3x1 matrix in the lower right. A transition matrix is then generated using a range of potential data sources. The population vector at time t+1. This process is reiterated for all cell locations and then rewritten to a new set of rasters, which record the count of individuals in each stage at each location across the entire landscape. Variable definitions are the same as in Figure 1, with the addition of the location specificity (c).

In addition to using standard distributions to define the sample space, PopMod has the ability to utilise the posterior distributions produced by hierarchical Bayesian modelling obtained from BUGS software (Lunn et al. 2000). These posterior distributions are used to represent an estimated variable, and are produced in the form of a vector of estimates. The benefit of using a hierarchical Bayesian approach for parameter estimation is that a properly formulated model will produce a result where the confidence interval is not influenced by increasing sample size, as is the case with many traditional frequentist approaches. Instead, the distribution better reflects the uncertainty in the parameter value (Clark 2003), providing a more realistic sample space for simulation behaviour. PopMod

is currently set up to process posterior estimates in the form of the files produced by the BUGS software. The output from other MCMC sampling software can be incorporated, but it must be modified to match the BUGS output format. In addition, multiple factor levels in the posterior distribution can be referenced through the the indexing of parameter levels (see below). PopMod draws values for parameters in the same expression from the same position in the chains in order to account for any covariance between simultaneously estimated parameters.

Parameter values can also be sourced from additional rasters, allowing them to reflect spatial variability across the landscape. Any data raster can be used to provide the parameter values as long as it has the same extent and resolution as the population rasters. This approach allows the user to incorporate any spatially explicit environmental data, such as moisture availability, light levels, nutrient availability, or any other relevant spatial data. In addition to environmental variables, this approach can be used to query previous population rasters, which are also stored and accessed as a raster format. This feature allows the number of individuals in the previous time step to be used as a parameter in the expression, providing an ideal avenue for implementing density-dependent regulatory processes. As each lifestage is assigned to a unique parameter in the expressions, their influence can even be weighted according to the lifestage they currently occupy. This would allow, for example, adults to have a greater influence on density-dependent processes than seedlings (or vice-versa).

Lastly, differences in the expressions for parameter values can be implemented through an indexing feature. This feature works by classifying the landscape into a finite number of classes. Each cell of the index raster is assigned an index integer, analogous to a factor level. This index is then used to determine which of multiple possible parameter definitions is used to source the parameter value to be implemented into the expression. The indexed parameters can be as similar or different to each other as desired; it may be different static values, represent an alternative parameterisation of a distribution for a stochastic parameter, or even contain a mix of stochastic and static parameter sources, which are dependent on the physical location. This indexing function provides an excellent option for integrating coarser delineations of the landscape such as habitats or biomes into the analysis.

4.2.2 Periodic matrix modelling

PopMod includes the functionality to implement multiple transition matrices during a single time step in a periodic approach to matrix modelling. This allows the transitions of a single timestep to be partitioned across a number of transition matrices (Figure 4.3). There are three direct benefits to this approach; first, applying matrix modelling to project plant populations contains a logistical dilemma; incorporating a seed stage inherently introduces a dormant year when the matrix is applied in annual increments (Caswell 2001).

Utilising the periodic approach allows one matrix to specify the recruitment of seed from the previous year, while a second can specify the production of seed. This allows seed that are produced in one year the opportunity to recruit to a plant stage the following year, as opposed to serving a timestep in the dormant seed stage. Secondly, while a demographic model could incorporate fecundity as a single step, separating seed production and recruitment provides an opportunity to enact a dispersal process on individuals in the seed stage. This is an important step as germination probabilities are more likely to be influenced by conditions the seed experiences after dispersal, as opposed to conditions at its origin. Incorporating the differential response to the seeds eventual location in a single function would require accounting for all possible destinations, creating a function which is both unwieldy and ineffective. Lastly, separating the seed production and recruitment processes provides an opportunity to incorporate one or more seedbank stages, which can be important and influential aspect of plant success at the population level (Anderson et al. 1996; Lonsdale et al. 1988).

$$\begin{bmatrix} S_t \\ J_t \\ A_t \end{bmatrix} \times \begin{bmatrix} P_{SS,a} & P_{JS,a} & P_{AS,a} \\ P_{SJ,a} & P_{JJ,a} & P_{AJ,a} \\ P_{SA,a} & P_{JA,a} & P_{AA,a} \end{bmatrix} \times \begin{bmatrix} P_{SS,b} & P_{JS,b} & P_{AS,b} \\ P_{SJ,b} & P_{JJ,b} & P_{AJ,b} \\ P_{SA,b} & P_{JA,b} & P_{AA,b} \end{bmatrix} \times \begin{bmatrix} P_{SS,c} & P_{JS,c} & P_{AS,c} \\ P_{SJ,c} & P_{JJ,c} & P_{AJ,c} \\ P_{SA,c} & P_{JA,c} & P_{AA,c} \end{bmatrix} = \begin{bmatrix} S_{t+1} \\ J_{t+1} \\ A_{t+1} \end{bmatrix}$$

Figure 4.3: Example of a periodic matrix application where instead of a single transition matrix, multiple transition matrices are utilised in the calculation of the population vector at t+1.

4.3 Implementation of PopMod

4.3.1 Specification via xml file

All of the details necessary for the implementation of PopMod are submitted via a transition file. The transition file is an xml file specified following the dispersalML format (Pitt 2008). This format is intended to be a cross-platform standard for the specification of dispersal models. The file structure contains two main sections; the first defines the data source for parameters, and the second applies the parameters in an expression which is evaluated to calculate the individual transition values.

Parameters

PopMod can process a virtually unlimited number of parameters, each of which is defined using the following syntax:

```
<ParameterValue>
```

```
<parameterName></parameterName>
<source></source>
<index></index>
<distribution></distribution>
<values>
<d>></d>
<d>></d>
<d>></d>
</values>
</values>
</values>
</values>
</values>
</values></values></values>
```

Each element in the statement begins with a opening tag (<element_name>) and is closed with a closing tag (</element_name>). Arguments for each element are placed between the opening and closing tag (see example, below). Only the elements with the opening and closing tags on the same line receive arguments; the others are to organise those elements that receive arguments. Arguments for the different elements are defined as follows:

- <parameterName>: Defines a string (name) used to identify the parameter in the expression (see below).
- <source>: Determines how the parameter is derived; can take the values 'static' (a single floating point value), 'map' (a raster to be queried for values), 'random' (randomly drawn from a standard distribution), or 'CODA' (derived from a hierarchical Bayesian approximation).
- <index>: Specifies which corresponding value in the <indexMap> is associated with this particular <ParameterValue>. Can also be specified as the path to an index file associated with a CODA file from a Bayesian estimation using BUGS. If the definition of the parameter is global (i.e. not indexed) this can be left blank.
- <distribution>: Name of the distribution if the value is derived from a standard distribution (see appendix), otherwise 'None'.
- <values>: Associated parameter values. Can take the form of either a static number, the parameters necessary for implementing a standard distribution, or the path name to a chain from a Bayesian fitting performed in BUGS.

Expressions

An expression must be specified for each position in the transition matrix. These take the form of a mathematical function which can (but does not necessarily) incorporate parameters defined as above. Expressions are specified using the following syntax:

```
<expression>
    <position></position>
    <formula></formula>
  </expression>
```

The **<position>** tag specifies which transition value is defined by the corresponding **<formula>**. Position is determined by numbering each position in the matrix left to right and top to bottom, starting at zero. For example, the positions in a 3x3 matrix are as follows:

0	1	2
3	4	5
6	7	8

The <formula> tags contain the right side of a mathematical equation that determines the value of the transition value. The <formula> can incorporate static values, parameters defined earlier by referencing their parameterName>, or query lifestage rasters using the syntax "MAP_[lifestage name]". As PopMod is written in the Python programming language, it will understand the majority of standard mathematical operators (i.e. +,-,*,/). For more complex operations Python's built-in math module can be called, further expanding the capabilities of the PopMod module.

Example: fecundity

This example describes a hypothetical situation where the objective is to simulate the production of new plants. For simplicity, I will only describe the fecundity transition, a single transition element in the transition matrix. In this example, fecundity is modelled as a two-stage process where seed production and recruitment are combined to determine the number of new individuals. Both seed production and germination are modelled as random processes, with seed production being represented as a Poisson process with a lambda value of 35

$$SeedProduction \sim DPoisson(35). \tag{4.1}$$

This distribution can be assigned to a parameter named "SeedProduction" in order that it is randomly sampled at each iteration of the simulation to generate a new value. This is specified in the transition file as:

```
<ParameterValue>
<parameterName>SeedProduction</parameterName>
<source>random</source>
```

```
<index></index>
<distribution>Poisson</distribution>
<values>
<d>35</d>
<d>35</d>
<d></d>
<d></d>
</values>
</ParameterValue>
```

Note that there is no index specified, and that only one parameter value is expected for the Poisson distribution. The probability of germination for these seeds is modelled as a beta distribution. In this hypothetical situation, there are two different parameterisations of the germination function, corresponding to germination in two different habitats. The probability of germination in the two habitats is modelled as

$$P_1(germination) \sim Dbeta(2,2)$$
 (4.2)

or

$$P_2(germination) \sim Dbeta(2,5)$$
 (4.3)

which are assigned to a parameter 'Germination' in the transition file, specified as

```
<ParameterValue>
    <parameterName>Germination</parameterName>
    <source>random</source>
    <index>1</index>
    <distribution>beta</distribution>
    <values>
        <d>2</d>
        <d>2</d>
        <d></d>
    </values>
</ParameterValue>
<ParameterValue>
    <parameterName>Germination</parameterName>
    <source>random</source>
    <index>2</index>
    <distribution>beta</distribution>
    <values>
        <d>2</d>
```

```
<d>5</d>
<d></d>
</values>
</ParameterValue>
```

Note that the two different specifications of germination are assigned to the same <parameterName>, but are differentiated by their <index> values. Finally, the incorporation of both the seed production and germination processes into the calculation of the transition value is performed by multiplying them together so that

Seedlings produced per flowering plant = SeedProduction $\times P_h(germination)$ (4.4)

which is reflected in the transition file by the specification of the expression

```
<expression>
<position>1</position><sup>1</sup>
<formula>SeedProduction*Germination</formula>
</expression>
```

PopMod is then able to use this information to employ the appropriate transition value where necessary. All transition values within a matrix are specified in the same context, and within the same transition file. In the case of multiple matrices in a periodic matrix application, each matrix is specified with an individual transition file.

4.4 Applications

The PopMod module was developed to integrate the demographic models of *Hieracium lepidulum* (Stenstroem) Omang (Asteraceae) described in Chapter 2 of this thesis with the dispersal function described in Chapter 3 in a spatial context in order to simulate the spatial dynamics as the species invades. However PopMod's greatest strength lies in its generality and the flexibility with which it can be applied. Using PopMod, matrix-based demographic models of a wide range of complexity can easily be applied in a spatial context, ranging anywhere from a simple static two-stage lifecycle, to a spatially- and density-dependent stochastic demographic model that incorporates a periodic matrix approach. In the next two chapters I will apply MDiG and PopMod in concert with one another to combine the demographic model of *H. lepidulum* growth developed in Chapter 2 with the dispersal kernels developed in Chapter 3. I will first use this combination

 $^{^1 \}rm For$ simplicity this example assumes a 2x2 transition matrix, and places this transition value in the upper right position

in Chapter 5 to explore the local dynamics of interacting populations of H. lepidulum, and explore how propagule exchange between adjacent locations affects demographic dynamics, and see how these relationships change depending on the landscape context. In Chapter 6 I will then use this modelling framework in conjunction with a coarser approximation of the dispersal and demographic mechanisms to project how the invasion H. lepidulum will interact with various configurations of a heterogeneous landscape.

While the application in this thesis focuses on describing the invasive spread of a plant, this module could just as easily be applied to animal species. In addition, while this application focuses on using the module to assess the threats posed by non-native species, it also has the potential to be a very useful tool to explore population dynamics of desirable species, providing an excellent framework to perform analyses such as population viability analysis of endangered or threatened populations of both plants and animals. My hope is that this module (along with MDiG) will serve as a useful tool for a wide variety of spatial demographic analyses in the future.

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Chapter 5

Incorporating spatial dynamics into model structure at a local population scale

5.1 Introduction

Demographic models have become an invaluable tool for the analysis and forecasting of biological populations. These models can be applied across a range of applications, from determining the viability of relatively rare and potentially threatened populations (Boyce 1992; Beissinger & Westphal 1998; Keith et al. 2008), to examining the potential threat posed by undesirable invasive pest species (Neubert & Caswell 2000; Buckley et al. 2003; Burns 2008). The complexity of these models varies dramatically, from the application of a single function to describe population-level growth (Verhulst 1838; Tsoularis & Wallace 2002; Martinez et al. 2008), to matrix population models which describe the transitions between different ages or stages in an organism's life cycle (Caswell 2001; Neubert & Parker 2004; Ramula et al. 2008), to higher-order nonlinear functions describing the interaction of multiple populations (Holt & Pickering 1985; Vucetich et al. 2002; Reichenbach et al. 2006). As our understanding of these systems becomes more sophisticated, the critical evaluation of different modelling approaches becomes increasingly important. Understanding the underlying characteristics and features of the multitude of potential modelling approaches can help to evaluate the suitability of a particular approach for certain applications, and at the same time help to ensure that the approach properly reflects the mechanisms of the system under study.

In addition to the level of complexity, the wide variety of demographic models currently available can also be classified by using a few simple criteria that describe how they operate at different scales. *Closed* systems are those models which use a single function or process to describe all of the individuals within a population of interest. As such models are inclusive of all individuals, their spatial scale is inherently defined by the extent of the population. These systems are largely autonomous, and immigration and emigration processes have little or no influence on the population trajectory (Hixon et al. 2002). This is in contrast to an *open* system which typically consist of a single or series of 'local population(s)'. In these open systems, demographic processes operate at the 'local' scale, while immigration and emigration connect the local populations to one another at a larger scale. This connection permits the transfer of individuals between locations, which can significantly influence the dynamics of population growth at both the local and global levels. In these systems, a portion of the propagule supply to any local population can potentially originate from a different location. As such, not all of the propagule input to a local population is necessarily influenced by local processes, as it would be in a closed system (Johnson 2005). This potential for externality and independence in the source of propagule pressure is an important defining characteristic of the open system. Metapopulations are a commonly used example of an open system (Hanski 1994; Hanski & Ovaskainen 2003; Fahrig 2007).

In addition to being open or closed, populations can be represented using either a *complete* or *incomplete* structure. *Complete* systems are those models where the origin and fate of all individuals are accounted for. The closed model described above is typically employed as a complete system, where there is only a single population and immigration and emigration are effectively nonexistent. The majority of population models represented by a single equation or function fall into this category. However, complete systems can also be represented by a group of open populations interlinked via immigration and emigration, similar to a metapopulation structure (Fahrig & Merriam 1985; Hixon et al. 2002). *Incomplete* systems also incorporate immigration into the dynamics of local populations, but the external supply of immigrants is derived independently of the primary demographic processes; i.e. assuming a constant seed rain from an external unspecified source. The result is that this supply of immigrants is not a result of the dynamics of local processes. This approach is most commonly utilised when it is difficult or impossible to precisely determine the external source of propagules, typically due to the large scale of dispersal, as in marine systems (Roughgarden et al. 1985; Hixon 1998).

The overall structure of the model (open or closed, complete or incomplete) can influence how well the model is suited to its intended application. The absolute decoupling of the immigration source from demographic processes in an incomplete system results in a model that is relatively poorly suited for examining the persistence of a population, as the propagule supply is typically unabated even in the case where the number of reproductive individuals is extremely limited (Gaines & Lafferty 1995). The incomplete structure is therefore not ideally suited for examining the self-sufficiency of isolated populations, either desirable or undesirable. The decoupling of propagule supply and demographic processes in this type of model make it difficult to recreate the unique conditions of extreme low density populations such as Allee effects (Stephens et al. 1999). Instead, incomplete models typically incorporate a relatively constant influx of propagules, which can create a persistent obligatory sink where the establishment of a population is bolstered and/or sustained via the supply of propagules from an external and unspecified source. Such a model structure would not accurately reflect the diminishing propagule supply experienced by a declining population. Under such conditions, a complete model structure (composed of either a single large closed model, or multiple interlinked open models) typically represents a better option to investigate the probability of a population persistence, as it provides a more detailed accounting of propagule supply.

While the philosophical underpinnings of the different approaches can be used to determine appropriate model structure, this decision is not always considered ahead of time. More often, the decision between an open or closed model structure is determined *post hoc* and dictated as a pragmatic decision, driven by a combination of the scale at which field measurements are collected and the dispersal characteristics of the particular organism in question. However considering the model structure before hand may help to ensure that the level of complexity contained within the model is sufficient to answer the question posed. While not all questions require the highest level of modelling complexity to address them (and indeed, parsimony is desired), consideration to this point *a priori* can help to focus the investigation. Addressing this ahead of time may also help to direct data collection, and can be done so relatively easily; for example, if the scale of the process in question is such that dispersal is likely to move individuals beyond the bounds of the area investigated, then an open model structure is more appropriate (Hixon et al. 2002).

The desire to incorporate density-dependent regulatory processes in the model can also have a strong influence on the scale of measurement chosen for data collection, and in turn the appropriate model structure. Modern demographic models often include regulatory processes that provide feedback to the model, constantly modulate growth rates, and often limit the overall size of the population (Freckleton et al. 2003; Koons et al. 2005; Caswell 2008). These regulatory processes typically operate at relatively small scales in close proximity to the individual; the absolute measure of this scale varies depending on the organism, but these processes typically represent direct interaction with other organisms (Ray & Hastings 1996; Gunton & Kunin 2007). One of the primary (although not exclusive) functions of dispersal is to allow progeny to escape the regulatory effects of competition in proximity to the parent, and potentially reach more favourable conditions that increase the likelihood of successful establishment and growth (Howe & Smallwood 1982; Ronce 2007). For this mechanism to be effective, propagules must be dispersed beyond the range where those local density-dependent effects can severely limit their success. As such, there exists the potential for conflict when attempting to model density-dependent regulatory processes using a closed-system population model, as both density-dependent effects and dispersal are often incompatible within the same scale. Because of this limitation and the importance of accurately depicting population viability as described above, I have applied a combination of an open and complete model structure to investigate the spatial demographic dynamics of an invasion of *Hieracium lepidulum*, a herbaceous

perennial plant. This allows me to utilise the approach of modelling density-dependent processes at a local scale using an open model structure, while interlinking the local populations through dispersal to create a complete model structure. This approach is much like a traditional metapopulation structure, except that in this application the local populations occur in a continuous landscape, whereas a metapopulation by definition requires that the local populations exist as spatially discrete (Wells & Richmond 1995; Freckleton & Watkinson 2002). The result of this is that the exchange of propagules in my application relies on the distribution of seed using a less rigorously defined approach using a dispersal kernel to simulate the distribution of individual seeds in space, where exchange between local populations in a metapopulation analysis are determined by defining the edges of a network. Still, the two approaches share a great deal in common, and much of the work done on metapopulation dynamics can be applied to this type of system as well. For example, the concept of rescue effects has been examined in the framework of metapopulation models (Brown & Kodric-Brown 1977; Hanski 1991; Jongejans et al. 2008), and can also be applied in this context.

The catchments which are under threat by *H. lepidulum* contain a range of habitats, typified by Nothofagus solandri var. cliffortioides (beech) forest at the lower elevations, and a mixture of tussock and sub-alpine scrub at higher elevations (above approximately 1400m above mean sea level). The lower-elevation forest areas are comprised of three distinct habitats, which include closed-canopy forest, forest gaps, and forest creek. The higher elevation alpine areas can be further classified into scrub, tussock, or alpine creek habitats. Each of these habitats provide conditions that result in unique demographic trajectories of *H. lepidulum*. In Chapter 2, I developed a small-scale (30x30cm) closed demographic model to characterise *H. lepidulum* growth in the different habitats. The closed structure was appropriate to that application, as immigration to the sites was controlled during the seed sowing experiments (by removing all potential seed sources within a 50m radius), and the scale allowed me to characterise the density-dependent processes. However, in this chapter I build upon that work by switching to an open model format by applying the small scale demographic model to individual cells within a rasterised landscape. Using this new approach, these small scale processes are interlinked at a larger (30x30m) scale using an individual-based dispersal function. This approach creates a nearly complete structure by allowing the dissemination of individuals between cells to occur as a function of the dispersal kernel developed in Chapter 3. The system is only 'nearly' complete, as the bounds of the spatial extent are absorbing, and propagules leaving this area are lost to the simulation (i.e. Pacala & Silander Jr 1985).

In this chapter I compare and contrast the simulation H. lepidulum populations using two different model structures; the first approach uses the aspatial demographic models developed in Chapter 2 to project population growth from a specific starting condition. The results are then compared against a second open and complete approach described above, in which I utilise the PopMod extension (Chapter 4) in the MDiG simulation software (Pitt 2008). This software allows me to integrate the stochastic demographic model from Chapter 2 with the dispersal kernels developed in Chapter 3 to create a spatially explicit simulation of H. *lepidulum* populations. Both approaches are employed to simulate and project population-level growth in each of the habitats found in the Craigieburn catchments. The results are then compared to examine how the incorporation of spatial dynamics affects the dynamics of population growth. Specifically, the behaviour will be analysed to examine the following questions regarding the development of the H. *lepidulum* population;

- 1. How does the incorporation of a spatial component influence predictions of *H. lep-idulum* invasion compared to the aspatial projections?
- 2. What do projections reveal about the dynamics of *H. lepidulum* invasion in this landscape, and how do these dynamics vary among the six habitats?
- 3. What implications can the choice of model structure have for management decisions?

In addition to selecting the appropriate structure and scale for projecting population behaviour, dealing with the inherent uncertainty in the estimation of biological parameters can also affect the final utility of any projections or estimations provided by the model (Buckley et al. 2005). Incorporating parameter uncertainty at a basic level in the model propagates the uncertainty throughout the projections, and in the end, should more accurately convey the breadth of potential population-level responses. This provides a realistic assessment of just how stochastic the outcome can be, and provides a quantitatively assessment of prediction precision (Melbourne & Hastings 2008; Tenhumberg et al. 2008). Such uncertainty is incorporated into the projections explored in this chapter by utilising three different sources of stochasticity; demographic stochasticity (random trials to determine the fate of each individual), environmental stochasticity (defined as parameter uncertainty (Caswell 2001) derived from the Bayesian hierarchical estimation of parameters described in Chapter 2), and stochasticity in the dispersal of individuals (obtained by randomly sampling an appropriate dispersal kernel fitted to empirical data in Chapter 3). Incorporating these sources of stochasticity across multiple iterations of simulating population growth provides an approximation of the range of potential population trajectories expected from the invasion.

5.2 Methods

The simulation approaches used to forecast the success and growth of H. lepidulum both employ the previously developed demographic models (Chapter 2). The aspatial model simply replicates those demographic models across all cells within the landscape. The open and complete structure utilises the demographic models in concert with one of the dispersal kernels fit to *H. lepidulum* dispersal data (Chapter 3). These are interlinked using the MDiG modelling software (Pitt 2008) in concert with the PopMod module (Chapter 4) to create an open and complete system that captures both small scale density-dependent effects (via the demographic processes) with larger scale exchange of individuals (via the dispersal process). This process is outlined in the previous chapter; an overview is available in Figure 4.2. Both simulation approaches are performed using habitat-specific demographic models in order to reflect the different conditions that constitute the landscape of the study area.

5.2.1 Demographic models

In order to simulate the local population-level dynamics of H. lepidulum, I utilised an eight-stage stochastic matrix model to simulate annual changes in population structure. The lifestages represented in the model include a seedbank stage, a seed stage, five juvenile stages, and one adult stage. These stages reflect the observed life cycle of H. lepidulum (Chapter 2, Figure 2.1). The distribution of the population in these lifestages at any location at time t can be described by the matrix

$$P_{t} = \begin{bmatrix} seedbank_{t} \\ seed_{t} \\ J_{1,t} \\ J_{2,t} \\ J_{3,t} \\ J_{4,t} \\ J_{5,t} \\ A_{t} \end{bmatrix}$$
(5.1)

where seedbank stage (seedbank_t) consists of those seed that did not germinate during the previous year, and now lie dormant in the soil, and the seed stage (seed_t) represents new seed produced during the previous timestep. The juvenile stages ($J_{\alpha,t}$) represent those individuals of age α which are not yet reproductive; five juvenile stages are employed in order to represent an age structure within the non-reproductive state. Adult individuals (A_t) are distinguished as those capable of reproducing. Transitions between the different lifestages are then calculated by using a periodic matrix application (Caswell 2001), where the the population matrix is multiplied by a series of three transition matrices to calculate the population distribution at the following timestep. The specific details for the calculation of the transition values are outlined in Chapter 2. The first transition matrix

$$A = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ SB & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$
(5.2)

determines the proportion (SB) of seeds in the *seedbank*_t stage that are viable, and then pools these with the seed in the *seed*_t stage. All the other lifestages remain unchanged by this transition matrix. The second transition matrix

uses the pooled seed count from the previous step to calculate the proportion of seed (Rec) that recruit to the first juvenile stage (J_1) . The proportion of seed that do not recruit (1-Rec) transition to the seedbank stage. All other stages remain unchanged by this matrix. The third and final matrix

contains the majority of the activity in the life cycle; juveniles in the first stage (J_1) either survive with a probability $S_{J,1}$ or die. Individuals in the remaining juvenile stages also have a probability of survival $(S_{J,2-5})$, but those that survive have two possible fates; they either mature to a reproductive adult form with probability $T_{JA,2-5}$ or remain a juvenile and move on to the subsequent juvenile x age lifestage with probability $1 - T_{JA,2-5}$. Those individuals that begin the timestep in the fifth juvenile stage (J_5) and survive but do not advance remain in the J_5 stage.

This approach to applying the matrices means that individuals will enter the flowering stage in the year prior to actually producing offspring, which is in conflict to the definition of 'adults' given in Chapter 2. However, this shortcoming is overlooked in the interest of keeping all maturation of individuals contained within a single matrix; otherwise individuals would have the opportunity to advance multiple stages in a single year. In addition, the use of this approach means that it is possible for populations to go completely extinct, and recolonize from seed the following year. While this can create some very short lived invasion episodes, I feel that this approach most accurately represents the process of germination of seeds in many areas followed by failed establishment.

Benefit of periodic matrix approach

Utilising a periodic matrix modelling approach permitted me to integrate into the simulation a number of biologically important processes that affect population growth that would not otherwise be possible using a more traditional single matrix model. First, the use of the periodic matrix application allows the incorporation of a seed stage. The single matrix approach is incompatible with the use of a seed stage, as individuals entering this stage would not be allowed to germinate until the second timestep following their production (Caswell 2001). This also permits both seed production and recruitment to act as spatially-dependent processes in potentially different locations; i.e. seed production may be influenced by conspecifics in one location, while recruitment of that seed may be subject to different competitive effects at a different location.

The second benefit of the periodic matrix approach is that it allows me to include a seedbank stage while retaining compatibility with the recruitment function. Members of this stage must be kept separate from the new seed at the end of each timestep, as only the new seed are relocated by the dispersal function, while the seedbank is assumed to be immobile. The first transition matrix A functions to combine the viable seed from the seedbank with the new seed that were produced in the last timestep into a total seed pool. It is critical that the size of the seed pool is calculated prior to the application of the second matrix, B (see Chapter 2 for details). Using this estimate of recruitment, the total number of seed recruiting into the first juvenile stage can be calculated using the third transition matrix, C. Overall this approach differs from the approach in Chapter 2, which a) implemented stage transitions as a system of equations as opposed to a periodic matrix multiplication approach (although they are functionally equivalent) and b) implemented density-dependency in the same way, but did not reflect the possibility of a seed recruiting

in a location other than its origin.

Incorporating stochasticity

Similar to the one-dimensional projections of population growth described in Chapter 2, this model incorporates both environmental and demographic stochasticity. Just as in the one-dimensional application, environmental stochasticity is incorporated by randomly drawing parameter values from a vector which describes the potential sample space. These vectors were derived from using hierarchical Bayesian techniques to estimate those parameter values (Chapter 2). Demographic stochasticity was incorporated by performing a trial for each individual to determine their fate. This is accomplished by generating a random number from a uniform distribution between zero and one, and comparing that number to the transition value in the matrix. If the random number is lower than or equal to the transition value, then the transition occurs. This is only employed for those transition values with a value ≤ 1 ; in the case of seed production, there is no demographic stochasticity.

5.2.2 Simulations

Populations of *H. lepidulum* were simulated in a 100 by 100 cell landscape to examine how the inclusion of dispersal between the cell-level local populations affects demographic performance of the species. Both dispersal and demographic models were parameterised for each of the six habitats (except dispersal in the scrub habitat, see below), which allows me to examine if there are any patterns or unique elements of population spread and/or growth which are habitat-specific. Each cell in the simulated landscape represents a 30x30cm area, matching the scale at which the demographic data were collected. Two different sets of simulations were run; the first (the 'Model Structure Comparison') was designed to compare the differences in projected population behaviour when using a closed versus a complete modelling approach. The second set of simulations was designed to model the expected behaviour of *H. lepidulum* in the different habitats after an initial introduction using a spatially-explicit approach ('Population Growth' section).

Model structure comparison

The first set of simulations is designed as a paired comparison to examine how differences in model structure influence the demographic performance of *H. lepidulum* at the local (individual cell) level by comparing the output from a closed model structure (similar to that used in Chapter 2) with that from an open and complete structure (incorporating propagule dispersal between cells). First, a series of closed model runs were performed using the PopMod module in MDiG (Chapter 4), where immigration and emigration were disallowed by disabling the dispersal feature in MDiG, forcing all propagules to remain in their parent cell. This effectively makes each cell an individual replicate of a closed demographic model. It was necessary to run these independently of those examined in Chapter 2 in order to match appropriate initial conditions for the open/complete simulations. The second set of simulations utilised a complete model structure, achieved by allowing the individual local populations (cells) to interact via dispersal. This dispersal function was implemented stochastically, with dispersal distances being randomly generated using the appropriate kernel (below). Initial conditions for both sets of simulations reflected three different starting densities; 1, 10, and 50 adults per cell. Simulations were run for 100 timesteps (1 timestep = 1 year) in each habitat.

Population growth

The second set of simulations were designed to model the growth of *H. lepidulum* populations at the 30x30m scale in the different habitats using the spatially-explicit complete model structure. To achieve this, 10 replicate simulations were run in each of the six different habitats for a total of 60 simulation runs. Each simulation was run for 100 timesteps, where each timestep was equal to one year. Initial conditions in these simulations consisted of the four central cells being populated with 10 adult individuals each. This initial value is sufficient to ensure the persistence of the population, assuring that the resultant dynamics are not a result of inadequate initial propagule supply. Additionally, this helped to make sure processing time was used as efficiently as possible, as simulating populations that go extinct immediately would require similar processing time while contributing little to understanding the expected population trajectory. Each iteration of the simulations typically required just over three hours to run on a 3.0 GHz Pentium P4 desktop computer with 2560 MB of RAM.

Dispersal

The dispersal kernels fitted in Chapter 3 served as the basis for the incorporation of a kernel to describe the dispersal of *H. lepidulum* in these simulations. In order to be employed within the simulation software, the kernels needed to describe dispersal distances in terms of the number of landscape cells traveled. As the simulated landscape is represented using a 30cm cell size (dictated by the scale of the density-dependent mechanisms specified in the demographic models developed in Chapter 2), the dispersal kernels had to be rescaled to match. Unfortunately, unlike a linear function, many of the dispersal kernels did not have a dedicated rate or slope parameter that could simply be adjusted to reflect the change in scale. Instead, the original data were rescaled to reflect the observed dispersal distances in the dispersal trials (Chapter 3) in terms of 30cm units instead of metres, and the kernels re-parameterised to fit the rescaled data. ¹ This was performed using the

 $^{^{-1}}$ As a fictional example; consider that the dispersal events averaged 10 metres, and their distribution around that mean was best described using a poisson distribution (with lambda equal to 10). This

nls algorithm in the R statistical software language (R Development Core Team 2009). The reparameterisation of these kernels resulted in a change in the measure of fit for each kernel; each kernel was therefore re-evaluated, and the best fitting kernel reflecting the new scale selected for implementation.

When implemented in the simulation, dispersal distances for individual seeds were obtained by generating a random number from a uniform distribution on the interval [0,1], and then using the cumulative distribution function of the dispersal kernel to relate the number to a corresponding dispersal distance (Pitt 2008). The seed is dispersed in a random direction originating from the centre of the parent cell. As dispersal events originated at the centre of the cell, a random value from a uniform distribution on the interval [0,0.5] is added to the dispersal distance in order to approximate a random origin between the centre and edge of the cell. As a note, the MDiG software does not currently contain the functionality to define the dispersal kernel parameter values as stochastic variables in the same was as in the demographic model. As such, the dispersal kernel must be specified using set (static) parameters, but the kernel itself is randomly sampled to calculate each dispersal distance.

5.2.3 Simulation analyses

Model structure comparison

The comparison of the two different model structures examined differences at the level of the individual cell; the 100 by 100 cell landscape provided a total of 10,000 replicates of each combination of habitat, initial condition, and model structure, for a total of 36 simulated landscapes. I examined the results for habitat-specific differences and general trends that indicate the projected trajectory of the population. I also included some aggregate measures of performance across the entire landscape, which includes the proportion of occupied cells and the population size across the entire landscape. Since each landscape was simulated once, there is no replication of these aggregate measures, and statistical comparisons are not possible. All indices of population performance (density, occupancy (proportion of cells with one or more plants in the juvenile or adult stage), and total population size) were calculated using only the adult life stage, as this is a better indication of invasion success than the more transient juveniles.

distribution would describe a dataset with a standard deviation of approximately 3.16 metres. Now, consider the same data needed to be converted to cm; the mean distance could be easily converted (10 metres = 1000 cm), but simply replacing the lambda value in the Poisson function creates a distribution with a standard deviation of 31.59 cm, a full order of magnitude smaller than when using metres as base units. Because of this type of behaviour and the interaction of terms within the probability density functions used to describe dispersal, changing the units of the scale at which dispersal was measured required re-parameterisation of the kernels and a re-assessment of their fit.

Population growth

The second set of simulations were performed to model population growth following introduction, and focused on the same indices as the comparison of model structure. This included the total number of individuals, the proportion of cells that were occupied (one or more plants in the juvenile or adult stage), and the density of individuals within occupied cells. As in the comparison of model structures, these indices were calculated using only the adult life stage. However, these simulations reflected an initial introduction (consisting of a small proportion of cells) spreading into a largely unoccupied landscape; as such, the performance at the level of the entire landscape was more the focus here, as opposed to the cell-level performance highlighted in the model structure comparison. For this reason, ten replicates of each simulation were performed to provide replication at the landscape level. Calculations were made for each timestep of each replicate of each landscape model, and the plotted responses were examined to discern general and habitat-specific trends.

5.3 Results

5.3.1 Dispersal

The reparameterisation of the dispersal kernels to match the 30cm scale used in these simulations resulted in a different ranking of kernel fits compared to those found in Chapter 3. There were three kernels that provided very similar fits (according to their AIC scores), which were distinguishably better than the AIC scores of the other kernels. These kernels were the two-parameter Cauchy function, the two-parameter negative exponential function, and the one parameter lognormal function (Table 5.1). The negative exponential function reflected the best (lowest) AIC score in all habitats, except in the alpine creek habitat where the lognormal function returned a better score. However, the transformation of the lognormal function to produce a cumulative distribution function (required for randomly sampling of the kernel; see methods) requires a numerical integration procedure, rendering it too complex for implementation in the simulation. Instead, the two-parameter negative exponential function was selected for use in all habitats as it was found to provide a good fit to the data, is robust to changes in the measurement scale, and its implementation in the software is achievable. The negative exponential function was parameterised using pooled data from across all of the habitats for implementation in the scrub habitat (no dispersal data were collected in this habitat).

Kernel Form	Metric	Forest Creek	Forest	Forest Gap	Alpine Creek	Tussock
Cauchy	AIC	-169.4^{2}	-168.3^{2}	-165.8^{3}	-169.2^{3}	-176.5^{3}
	α	1.321	1.230	0.6049	0.6668	0.6341
	β	-0.655	-0.595	-0.1894	-0.4184	-0.2940
log-normal	AIC	-158.0^{3}	-166.9^{3}	-178.2^{2}	-196.2^{1}	-195.9^{2}
	α	41.53	39.32	26.21	34.85	30.16
negative exponential	AIC	-176.8^{1}	-188.1^{1}	-209.0^{1}	-173.4^{2}	-199.0^{1}
	α	5.364	4.943	2.1665	3.3182	2.6368
	C	1.521	1.426	0.7369	0.8515	0.7821



Figure 5.1: Trajectories of the density of adults in individual cells were obtained from simulating the *H. lepidulum* population over 100 time steps. The simulations were initiated with either 1, 10, or 50 adult individuals in each cell, and demographic models reflected either a closed model structure (in black) that did not incorporate dispersal between the cells, or a complete model structure (in red) that included interactions between cells driven by the dispersal of seed. Shaded areas represent a one standard deviation confidence interval around the mean response, calculated at each time step. Note variation in x-axis between habitats.

5.3.2 Model structure comparison

Differences between the aspatial closed model structure and the open and complete model structure varied between habitats. Both approaches reflected a high level of variability between the individual cells (Figure 5.1). With either approach, the density of adults in occupied cells in the forest creek and forest habitats appeared to grow in an almost linear fashion, and do not appear to have reached a maximum density by the end of the simulation. In contrast, the densities in the forest gap, alpine creek, scrub, and tussock habitats appeared to have reached a maximum density at lower levels than the forest or forest creek. The initial seeding density appears to have a slight influence on projections in the forest, forest creek, forest gap, and alpine creek habitats, while the densities in the scrub and tussock habitats appear to all converge at similar levels, regardless of their initial state. Overall, it appears that model structure (open or closed) does not have a significant influence on mean density after 100 years of population development, as trajectories from both structures are very similar, and comparisons of confidence interval reflecting one standard deviation above and below indicate a great deal of overlap between the two model structures (Figure 5.1). However, even though the standard deviations suggest this pattern was not significant, the closed system did consistently produce higher mean adult densities than the complete system.

The trajectories of total population size from the closed and complete model structures (measured as the total number of adults in the simulated landscape) appear to differentiate in some, but not all of the habitats examined (Figure 5.2). In those habitats where differences between the two model structures are evident, the complete system tends to result in larger populations compared to the closed model structure (forest creek, forest, and tussock habitats); population size in the remaining habitats appears to be nearly identical. The forest creek and forest habitats appear to be able to support the largest populations, followed by the alpine creek habitat. Populations in the tussock habitat, while relatively small, appear to be steady or increasing in size, in comparison to the forest gap or scrub habitats, which appear to exhibit negative growth throughout the simulation period, and appear to be headed for extinction. The initial conditions appear to have a strong influence over the population size after 100 years of simulated growth in most of the habitats, regardless of whether or not the population is stable by this time. In general, initial densities were positively correlated with population size at the end of the simulation run for most habitats (except scrub). However, the effect of the initial density on the general trajectory is less clear; populations in forest gap and scrub appear to be headed for extinction regardless of the initial condition. In other habitats (forest, forest creek, and alpine creek), higher initial densities result in apparently selfsustaining populations, while lower initial densities seem destined for extinction. This result is further confounded by the influence of the different model structures as well.

In general, the complete model almost always resulted in a higher occupancy rate at the



Figure 5.2: Projections of the population trajectories obtained from simulating the *H. lep-idulum* population over 100 time steps. The simulations were initiated with either 1, 10, or 50 adult individuals in each cell, and demographic models reflected either a closed model structure (in black) that did not incorporate dispersal between the cells, or a complete model structure (in red) that included interactions between cells driven by the dispersal of seed. As an aggregate measure of performance, there are no replicates at this level and therefore no measure of variability in these values.



Figure 5.3: Trajectories of the occupancy rates of cells by adults were obtained from simulating the *H. lepidulum* population over 100 time steps. The simulations were initiated with either 1, 10, or 50 adult individuals in each cell, and demographic models reflected either a closed model structure (in black) that did not incorporate dispersal between the cells, or a complete model structure (in red) that included interactions between cells driven by the dispersal of seed.

end of simulating 100 years of population growth (Figure 5.3). Differences in model performance were barely perceptible in the scrub habitat, but in the remaining habitats the complete model clearly had higher occupancy rates at the end of the simulation. Patterns in the change of occupancy rates over time also emerged. Cell occupancy tended to decline in nearly all of the simulations immediately following the initial 100% occupancy. Beyond this, however, a distinction can be made between those simulations where occupancy rates recovered, and began to increase after the initial drop, those simulations where occupancy rates levelled out, and those simulations that continued to decrease. The occupancy rates of simulations using the closed model structure typically continued to decrease over time. Only in the forest creek habitat do occupancy rates of the closed model appear to level off; none of the simulations with the closed model showed any increases in occupancy during the simulations. Patterns of occupancy from the simulations using the complete model structure are more indicative of a self-sustaining population; while simulations from this model appear to continue to decline throughout the simulation in some habitats (forest gap and scrub), they appear to level out (alpine creek) or even increase in others (forest creek, forest, and tussock; Figure 5.3). Also notable is the apparent influence of initial starting densities; simulations with higher initial densities were not only more resilient in terms of the initial drop in occupancy (compared to comparable simulations with lower initial densities), but they also appear to approach a higher sustainable occupancy level in some habitats (i.e. forest and alpine creek habitats).

5.3.3 Projected growth

Table 5.2: The projected mean population sizes, occupancy rates, and adult density of occupied cells in each habitat produced after running the complete model structure for 100 years, with an initial condition of 10 adult individuals in each of the centre four cells of the landscape. The standard deviation of the different measures is shown in parentheses.

Habitat	Mean population size (SD)	Occupancy (SD)	Density (SD)
Forest Creek	2085.7^A (786.2)	$379.5^A (107.7)$	$5.4^A (0.6)$
Forest	$140.3^C (168.5)$	19.7^C (22.1)	$4.9^A (2.9)$
Forest Gap	5.6^C (7.7)	$1.6^C (2.0)$	$1.7^B (2.0)$
Alpine Creek	$7.8^C \ (16.7)$	$1.0^C \ (2.1)$	1.6^B (3.3)
Scrub	$0.0^{C} ({ m n/a})$	$0^C (n/a)$	0^B (n/a)
Tussock	$1132.8^B (549.5)$	$192.6^B (78.9)$	$5.6^A (0.9)$

Simulations of the open and complete model structure to project population growth revealed that there was a significant difference in the size of the adult populations in different habitats after 100 years (one-way ANOVA; F(5,54)=45.3, p < 0.001). Tukey's range test

(Zar 1999) was used to compare population sizes in the different habitats at the end of each simulation, and showed that populations were largest in the forest creek habitat (p < 0.001), followed by the tussock habitat (p < 0.001). The remaining habitats (forest, forest gap, alpine creek, and scrub) were statistically indistinguishable in terms of landscape-level population size by the end of the simulation, although the forest habitat consistently had larger populations than the others (albeit highly variable; Table 5.2). Occupancy rates in the different habitats also differed significantly (one-way ANOVA; F(5,54)=76.991, p < 0.001; Tukey's range test indicated the occupancy rate in the forest creek habitat was again significantly higher than the others (p < 0.001), followed by the tussock habitat (p < 0.001). Again the remaining four habitats were statistically indistinguishable. Simulations in the different habitats also differed in terms of the density of adults in the occupied cells (one-way ANOVA; F(5.54)=11.516, p < 0.001), these differences were slightly different than compared to groupings based on population size or occupancy rate. A Tukey's range test divided the habitats into two statistically similar groups according to density; the forest creek, forest, and tussock habitats all have similar densities ranging from 4.92 to 5.63 individuals per cell, which were not significantly different from one another (p > 0.1). Simulation results in these habitats were significantly different than the remaining habitats (forest gap, alpine creek, and scrub; p < 0.001). Simulated densities in the forest gap, alpine creek, and scrub habitats ranged from 0.00 to 1.70, and were not significantly different to one another (p > 0.1).

5.4 Discussion

5.4.1 Comparison of model structure

The primary difference in utilising the complete model structure (which incorporates dispersal) as opposed to the closed structure (which does not incorporate dispersal) is that incorporating dispersal allows the local demographic processes (that occur within individual cells) to be influenced by populations in locations through the exchange of seed. This creates an interlinkage between the individual cell-level populations, and the landscape-level dynamics are more representative of a single spatially connected population as opposed to the aggregate behaviour of multiple independent replicates. At the same time, applying the demographic models at the local (individual cell) scale ensures an accurate representation of the density dependent processes, as this is the scale used when fitting the models which describe this phenomenon (Chapter 2). Comparing the results of simulations using the two approaches allows me to examine how well we can apply these models which reflect the local demographic processes to project population dynamics at a larger scale. While in the end, it appears that both approaches tended to produce very similar projections of overall population size (Figure 5.2), a close comparison of the occupancy and density of individual cells reveals that they arrive at these end



Figure 5.4: The projected performance of simulated populations in the different habitats (using the complete model structure), measured in terms of total population size, occupancy rate of cells by adults, and mean density of occupied cells. These simulations were all initiated with 40 adult individuals distributed among the centre four cells and run for 100 timesteps.

points via distinctly different paths. In general, omitting dispersal with the closed model simulations results in a strategy that utilises a relatively small number of cells occupied at high densities (Figure 5.1 and Figure 5.3). The relatively high rate of local extinction in the absence of dispersal creates a condition of highly localized populations (Kean & Barlow 2004). Conversely, incorporating dispersal (using the complete model structure) results in a greater proportion of cells containing H. lepidulum at lower densities, creating sparse population conditions (Kean & Barlow 2004). Depending on the tolerance of the existing community for H. lepidulum, these two different dynamics may result in significantly different outcomes; the sparse distribution is more likely to be successfully assimilated into the existing community, while the localized invasions are more likely to displace other species, at least at smaller scales.

The omission of dispersal in the closed model structure results in seeds remaining within their cell of origin, which produces a localised effect of propagule pressure compared to the open model structure, in which a portion of the seed would disseminate, and the propagule pressure originating from one cell would be dispersed among a number of neighbours. This localisation of propagule pressure effectively amplifies the trajectory achieved by the local population through stochastic variation in the simulation; if a local population starts out poorly, the result is compounded by a decrease in the number of reproductive individuals, which reduces replacement of dying individuals, creating a negative feedback loop. The converse is also true, where local populations which are successful early on produce more reproductive individuals, which produce more propagules, and so on creating a positive feedback. However, while increased seed supply does result in increased recruitment, the relationship is not linear, and the proportion of seed that result in a viable recruit decreases as the seed input to a cell increases (Duncan et al. 2009). Permitting the dispersal of seed between cells by using the complete model structure achieves two things; first, it disseminates the seed more broadly, helping to mitigate the effects of intra-specific competition, and effectively increases the per-seed recruitment rate (Howe & Smallwood 1982; Hil Res Lambers et al. 2002; Harms et al. 2000). Secondly, the dissemination of seed between cells reduces the impact of the feedback loops, which tend to reinforce the initial population trajectory. This dissemination of seed essentially works to 'spread the wealth' of a locally successful population, and allows the diminishing return of increasing propagule pressure in successful cells to be redispersed to locations with potentially lower competition from conspecifics, where they would have a higher probability of surviving. However, the use of absorbing boundaries probably also reduces the relative success of the complete model structure observed in figure refChapter05-closed-v-open-popSize; the use of reflective boundaries or a toroidal surface would likely result in higher differentiation between the two approaches. This interaction between cells (via dispersal) adds a measure of resiliency against local extinction through this addition of propagules, or can even provide an avenue for potential recolonisation after a local extinction occurs. This is analogous to the rescue effect in metapopulation dynamics (Brown & Kodric-Brown 1977),

but in a spatially continuous landscape. This effect of dispersal increasing occupancy at the landscape level is seen on all but one of the habitats (scrub) simulated. These results help to reveal exactly how incorporating dispersal into models of invasion can have a significant effect on the resiliency and extent of invasive populations, two attributes that can substantially influence the effectiveness of control efforts.

If utilised properly, demographic models such as this can serve as a useful tool when attempting to predict invasion success (Parker 2000; Caswell et al. 2003). However, this comparison highlights a few of the potential caveats that should be acknowledged when using projections from these types of models to decide on management actions. First, it is clear from this comparison that the overall assessment of invasion success may be influenced by the model structure. The incorporation of explicitly spatial processes (such as dispersal) with demographic models may be necessary to obtain accurate projections (Jongejans et al. 2008). Accounting for these spatial interactions provides a better understanding of the inherent resiliency in the population; this is exemplified in the dynamics of the occupancy rates when the population is initialised with low numbers, and both model structures start with a high rate of local extinction, but the simulations of the complete model structure are in most cases able to rebound and end up with positive growth by the end of the simulation period (Figure 5.3). The use of a non-spatial demographic projection may therefore lead to an underestimation of the resiliency of these populations, and in turn an underestimation of the level of intervention required to successfully combat the invasive population. Secondly, the effect of including a spatial component to these population projections can vary depending on the local environmental conditions and existing community structure (e.g. Brown et al. 2008; Harris et al. 2011). The differentiation between the two model structures is dependent on what habitat is simulated, particularly when examining the simulations that were initialised at lower densities (Figure 5.3). This is exemplified in the tussock habitat simulations, where the population represented using the complete model structure appears to be self-sufficient, while that of the closed model appears headed for extinction. This interaction between model structure and landscape heterogeneity can be an important aspect to consider when projecting population growth. When applied properly, demographic projections can be an invaluable tool to evaluate the potential effectiveness of control efforts (Davis et al. 2006; Brown et al. 2008; Jiao et al. 2009). However, these findings suggest that the effectiveness of removal efforts may be underestimated using a traditional closed model approach. However, this investigation does not directly investigate the minimum population size required for persistence; such information would presumably also be useful when evaluating the effectiveness of control efforts.

In this example, the results show that the choice of model structure had a substantial impact on not only the final predicted state of the invasion, but also the underlying mechanisms and dynamics by which the invasive population reached that state. It was therefore prudent in this application to utilise the additional complexity afforded by the open/complete model structure. However, this is not necessarily the case in all applications, and persons should strive for parsimony, and find the simplest model that addresses the question at hand. In addition, the costs in terms of additional data collection and analysis required for these types of analyses must be carefully weighed. The application described in this chapter is meant as an example to illustrate the potential for model structure to influence the outcomes, not to infer that additional complexity is always better.

5.4.2 Projections of *H. lepidulum* spread

The second set of simulations were performed to examine how a small introduction of H. lepidulum would spread into homogeneous landscapes (as above). The complete model structure was used for these projections. Again, the high level of between-habitat variability in invasion success projected by the simulations reinforces the importance of considering habitat when assessing invasibility (e.g. Luken & Mattimiro 1991; Shea et al. 2005). It is clear from these simulations that *H. lepidulum* is much more successful in the forest creek habitat when compared to the other low-elevation forest habitats (forest and forest gap; Figure 5.2). Deconstructing the total population size into occupancy and density of individual cells suggests (as in the model comparison section, above) that high occupancy rates are the primary mechanism driving this distinction, as there is very little differentiation between the habitats in terms of individual cell-level density (Figure 5.4). This differentiation in occupancy shows that *H. lepidulum* is better able to establish viable populations within previously unoccupied cells of the forest creek habitat. This increase in occupancy is at least in part due to increased susceptibility of the habitat to invasion, as reflected by the increased seed production and increased survival seen across multiple stages in this habitat compared to others (Chapter 2). The relative invasibility of these three habitats generally matches the pattern seen from the non-spatial application of the population model performed in Chapter 2. This result again reiterates the importance that the forest creek plays in the invasion, not only in terms of providing invasible habitat, but also providing that habitat in a strategic context of the landscape, forming a continuous corridor by which the invasion could potentially bypass the less invasible forest habitats to reach the alpine habitats.

In contrast to the patterns in the lower elevation forest habitats, the results in the higher alpine habitats appear to contradict the projections of invasion success from Chapter 2. The spatial projections performed in this chapter show that of the three high elevation habitats, the largest total population size is found in the tussock habitat (Figure 5.4). This contradicts those findings from Chapter 2, which projects that the greatest number of individuals at higher elevations would be found in the alpine creek habitat (Figure 2.5). Again, examining the combination of occupancy and individual-cell level density provides additional insight; occupied cells in the spatial simulations produce higher densities in

the alpine creek habitat compared to either the tussock or scrub habitats (Figure 5.4). This relatively higher density at the individual cell level is more in agreement with the results from Chapter 2. However, the occupancy rate in the alpine creek habitat is so low, that the total population size in this habitat is lower than in the tussock habitat. Instead, the population in the tussock habitat is able to net a greater total population size by occupying more cells, albeit at lower densities than in the alpine creek habitat. These findings suggest that *H. lepdiulum* is likely to have substantially different dynamics in these habitats; dynamics within the alpine creek habitat appear to be less stable, with higher variability in occupancy and density. We can therefore postulate that this habitat is likely to have fewer occupied sites, but these have a greater chance to support high densities of *H. lepidulum*. In contrast, individual sites within the tussock landscape are more likely to be occupied, but at a lower and more consistent density of individuals. Presumably, this difference is a function of the variability in environmental conditions, suggesting a higher degree of variability within the alpine creek habitat. The scrub habitat appears to be largely resistant to invasion, in contrast to the projections from Chapter 2. Increasing the initial densities (as in the model structure comparison) in this habitat appear to have a positive effect, and appear to be more likely to result in a self-sufficient population (Figure 5.3). This could potentially reflect that successful establishment in this habitat may require a higher critical mass of propagule input to successfully compete with the dense scrub vegetation.

The extremely high seed inputs explored in Chapter 2 along with the retention of all offspring from the closed model system may have provided enough propagules to sustain a population from those experiments; such conditions would be harder to achieve with the relatively small initial densities utilised in the projections from this chapter. In addition, the addition of dispersal results in the loss of some seed to other cells via dispersal. This essentially decreases the seed input when a successful subpopulation within a cell is surrounded by less successful subpopulation; this successful subpopulation acts as a source, and the surrounding cells as sinks. This reduction in self-seeding of a subpopulation as a result of dispersal could have a significant effect on the probability of extinction if it pushes the seed input below the critical threshold necessary to overcome a strong Allee effect that can occur as a function of stochasticity in the demographic model (Lande 1998). Lastly, while the size of *H. lepidulum* populations in the less invasible habitats (forest, forest gap, scrub, and alpine creek) is significantly smaller than in the forest creek or scrub habitats, the simulations suggest that pockets of *H. lepidulum* could persist in these less invasive habitats (although less likely in the scrub habitat). If control efforts were to only focus on the most invasive habitats, these pockets could serve as refugia for the invasion, and potentially supply propagules after eradication in the other habitats.

5.5 Conclusions

Overall these results suggests that even at the relatively small scales examined in this chapter, including dispersal between neighbouring individuals or groups did not substantially influence estimates of population size. This agreement between the approaches may be transient, however, and the fact that the underlying processes were substantially different between the model structures suggests that this agreement between the two approaches may be spurious. These results clearly show that very different paths produced a similar end state, and that the processes by which these results were reached differs substantially between the two different modelling approaches. This highlights the strong interdependent demographic relationships that can arise between locations, similar to those seen in metapopulation models (Hanski 1991), and the importance of acknowledging them to achieve accurate predictions as they tend to promote the overall success of the invasive population by decentralising successful population growth and redistributing this success to other locations. This approach makes it possible for existing individuals to either recolonize empty cells, or provide additional propagules to counteract the extinction of failing cells, spreading the wealth of productive locations. Other studies have also noted the spatial interdependence of groups of individuals, either through observing the spatial autocorrelation of organism densities (Watkinson et al. 2000), synchronising effects of migration processes (Gyllenberg et al. 1993), or the previously mentioned metapopulation-level rescue effects (Brown & Kodric-Brown 1977; Hanski 1991). However the implication here that these interactions serve to increase population performance across local subpopulations in a spatially continuous landscape has not previously been explored to the best of my knowledge. The important distinction in this examination is that these interdependencies and interactions influence population dynamics even in relatively continuous groupings of individuals, and are not specific to the context of discretised groupings of individuals in which they are often discussed. This phenomenon highlights the importance of using a bottom-up approach to investigate the underlying processes that shape the observed result, as opposed to modelling the higher level response directly.

Interestingly, the initial conditions of the simulation not only influenced the final outcome, but appear to dictate the dynamics of population growth. In the well stocked simulations, the forest and forest creek habitats appeared to support the largest populations; reducing the initial stocking to the relatively sparse conditions used to initiate the population projections resulted in the population in the tussock habitat exceeding that of the forest habitat. Again, deconstructing the population performance into measures of occupancy and density clearly show that increasing the proportion of the landscape occupied (as measured by the occupancy rate) is much more indicative of overall population success compared to the success of individual locations (as indicated by the population density). While this reiterates the conclusion (reached above) that occupancy is a primary driver of population success, it also highlights how improving the spatial extent of a population during the early stages of invasion can increase population level growth more rapidly than a population whose strategy focuses on increasing its local density. In effect, this dynamic suggests that increased dispersal ability of plants may confer an advantage to invasive success not only by allowing them to spatially disseminate to new locations, but also to increase their demographic success relative to less mobile species through the exploitation of new growing space and release from conspecific competition.

The inclusion of a spatial dynamic to the population projections by applying them in a complete model structure has a drastic enough effect to make it necessary to reassess the conclusions drawn from the non-spatial model in Chapter 2. The general dynamics in the lower elevation forest habitats remain largely unchanged; the forest creek habitat still threatens to provide a vector of suitable habitat which the invasion can potentially use to bypass the less hospitable forest matrix. The difference in this case is that the spatial projections suggest that the forest habitat is more invasible than indicated by the non-spatial projections, although it still represents less than ideal habitat compared to the forest creek, and may still act to slow an advancing front. In contrast, the projected susceptibility that was common to all alpine habitats no longer remains; instead, a finer classification of invasibility was obtained, where the tussock habitat appears the most likely to be invaded, while the alpine creek habitat appears slightly invasible, and the scrub completely inhospitable to *H. lepidulum*. These changes serve to highlight how the incorporation of spatial interactions and dissemination of individuals can have a dramatic influence on overall levels of abundance and reiterates the importance of either using appropriately scaled data collections on which to base projections of population growth, or, when this is not practical, attempting to accurately incorporate the appropriate mechanisms and interactions that influence population dynamics.

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Chapter 6

Scaling up: applying local spatial dynamics to make landscape-level predictions

6.1 Introduction

Spatially predictive models of spread can be invaluable tools when attempting to combat the effects of invasive species. While ideally invasive spread would be controlled by limiting propagule transport of potential invaders worldwide, identifying problematic species prior to their introduction is difficult (Pyšek & Richardson 2007; Diez et al. 2009) and invariably problematic species will occasionally slip through established safeguards. The ability to accurately predict the severity and extent (collectively the 'success') of the resultant populations can help us to better manage their impacts. Realistic assessments of the success of these populations can be used to more accurately target appropriate management actions to achieve the greatest result. In particular, this increased understanding can help by allowing us to target control efforts where the invasion is likely to occur, as opposed to apply efforts homogeneously across the landscape. This not only increases the economy of control efforts, but can also help to minimise non-target impacts that can lead to further degradation of the system (Suding et al. 2004; Smith et al. 2006).

Accurately predicting the success of a population requires that predictions be made in the context of the existing landscape. Early models of organism spread tended to neglect variation in landscape structure, and made the assumption that the landscape was homogeneous. More recent research has revealed how heterogeneity within the landscape can have a marked influence on population success. For example, simply quantifying the proportion of suitable habitat within a landscape can impart a substantial influence on estimates of overall population size (Andren 1994; With et al. 1997; Fahrig 2002). The spatial arrangement and functional connectivity of suitable habitat can also impact demographic success; as the amount of viable habitat is reduced, the spatial arrangement
of that habitat begins to affect how well dispersal mechanisms can maintain connectivity between groups. This connectivity has been shown to play an important role on the demographic success of the population (Gustafson & Gardner 1996; Flather & Bevers 2002; Fraterrigo et al. 2009; Kinezaki et al. 2010). Disrupting this connectivity has two primary repercussions; first, it can effectively slow or cut off a population from exploiting additional suitable habitat which is spatially isolated from the main population (Flather & Bevers 2002; Wiegand et al. 2005). Secondly, the exchange of propagules made possible by the connectivity can serve as a lifeline to a population, allowing the recolonisation of extinct patches (Brown & Kodric-Brown 1977; Fraterrigo et al. 2009) or even just reinforcing disjunct populations by providing additional propagule input until they become self-sufficient (Keitt et al. 2001). Reductions in the connectivity between locations makes it less likely that these interactions can occur.

The choice of how heterogeneity within the landscape is classified can also influence projections of population success. In the simplest form, heterogeneity can be represented as a binary classification, as either wholly suitable or unsuitable (Andren 1994; Wiens 1997; Matlack & Monde 2004). While this assumption can help to simplify the system and help to refine research questions, classifying suitability as a binary response is often an inappropriate over-simplification of landscape heterogeneity, except in cases such as oceanic islands, where the matrix of the landscape (water) is of a fundamentally different nature (Gustafson & Gardner 1996; Murphy & Lovett-Doust 2004). Instead, it is much more informative to acknowledge that the landscapes exists as a gradient of suitability. This approach is becoming more common, and suitability is more often described using an ordinal scale with multiple factor levels (With et al. 1997; Wiegand et al. 1999, 2005) or even treated as a continuously variable measure (Pearson & Dawson 2005; Kinezaki et al. 2010). Increasing the fidelity of this landscape attribute can have a significant effect on the invasion projections, as habitats which are not necessarily suitable for population establishment may still provide functionality in terms of connectivity or (pseudo) sink populations, and can significantly influence population success (Wiegand et al. 2005).

In the previous chapter, I investigated the relative success of *Hieracium lepidulum* in the range of habitats encountered during its invasion into montane catchments in the Southern Alps of New Zealand. Those results highlighted the importance that local spatial population dynamics have on demographic success at the overall population level. However, in order to obtain a better understanding of how the invasion is likely to progress in a real landscape, it is important to examine the dynamics at a larger scale. This allows me to examine if the dynamics observed at smaller scales are scale-dependent, or if they hold true over larger spatial extents. Applying the simulations at a larger scale also allows me to incorporate additional realism in the form of landscape heterogeneity, and examine how this influences spread dynamics. In general, the habitats within the landscape examined in this study can be divided into two primary groups based on their elevational position; at lower elevations, the landscape consists of a matrix of forest, interspersed with gaps and stream corridors, and at higher elevations the matrix is a mixture of tussock and scrub habitats, bisected by stream corridors (a more detailed description of the simulation landscapes can be found in Section 6.2.2). Insight provided from the simulations in the previous chapter allows me to hypothesise how the differential suitability of the habitats along with their spatial configuration will influence the invasion. I can then test these hypotheses by extending the approach used in Chapter 5 to apply the simulation of H. lepidulum spread in larger and more complex landscapes. This allows me to examine how changes in the scale, complexity, and spatial configuration of the landscape influence the success (in terms of severity and extent) of the invading population.

6.1.1 Effects of landscape on invasion

In order to examine the interaction of the landscape with the invasion of *H. lepdiulum*, I constructed a series of abstracted virtual landscapes designed to emulate the basic features of the montane catchments of the Craigieburn Valley, an area located in the Southern Alps of New Zealand which is currently under threat of invasion by *H. lepidulum*. These virtual landscapes range from homogeneous representations of the six different habitat types common to the area, to heterogeneous combinations containing up to three of these habitats. Habitats in the landscapes are differentiated by their effect on the demographic performance of *H. lepidulum* derived from Chapter 5; incorporating this variation is described in detail in Section 6.2.1. The spatial configurations of the habitats within the heterogeneous landscapes are intended to mimic the configuration of the habitat types within the actual catchments. The different configurations examined in the simulations can be categorised into three groups; heterogeneous mixtures of different habitats, homogeneous landscapes bisected by riparian corridors, or heterogeneous mixtures bisected by riparian corridors. Specific details of the habitats and the landscape configurations are described below. These abstractions, while designed to mimic the conditions of the study area, also cover a majority of the basic landscape configurations likely to be encountered by most invasions (Kinezaki et al. 2010). In addition, alternative configurations of each landscape group are utilised to reflect variability in a number of the landscape features (such as corridor width, patch size, and relative composition of different habitats) in order to examine how sensitive the invasion dynamics were to changes in the configurations. Using the habitat-specific measures of invasibility from Chapter 5, I made some general hypotheses regarding how the invasion would progress is these larger and more complex landscapes. These hypotheses are organised into three categories which focus on the effect of changing the scale of prediction on simulation results, the incorporation of landscape heterogeneity in the form of patches, and the addition of linear features.

Homogeneous landscapes at different scales

The most basic representation of a landscape is a homogeneous one, consisting of a single habitat type. These conditions are broad generalisations not likely to actually exist, but they are used to evaluate the effect of changing the extent and grain size of the simulation, and to establish a baseline measure of performance against which the more complex landscapes can be evaluated. In this chapter, the simulations are applied at an extent of 3x3km, which is a significantly (10,000x) larger area than the 30x30m extent examined in the previous chapter. Regardless, I expect that the relative performance of the invasion in large-scale implementation of homogeneous habitats will be the same as in the smaller scale simulations from Chapter 5. I expect that at this larger scale, the underlying mechanisms that influence the final population size (specifically population density and occupancy) will behave much as they did at the smaller scale observed in Chapter 5.

Incorporating heterogeneity

Heterogeneous mixtures of habitats are found throughout the invaded catchments; in the lower elevations, treefall gaps in the beech forests provide small isolated patches of habitat that are markedly different than the surrounding forest matrix, both in terms of the demographic performance of *H. lepidulum* (Chapters 2 and 5) and environmental conditions (Stewart et al. 1991; Lusk & Smith 1998). At higher elevations the landscape is comprised of a mixture of alpine scrub and tussock communities, which occupy approximately equal proportions (pers. observation). Here the difference in demographic performance of *H. lepidulum* in the tussock and scrub habitats is more pronounced than between the forest and forest gap habitats (Chapters 2 and 5). However, in reality neither combination contains greater than 50% habitat considered to be 'unsuitable' to invasion by *H. lepidulum* (see Section 6.2.2 for details).

Other studies have suggested that the spatial distribution of available habitat does not begin to affect the success of a species until the landscape is reduced to approximately 30 to 40% suitable habitat by area (Andren 1994; King & With 2002; Fraterrigo et al. 2009). Given that only a small portion of the lower elevation landscape is comprised of unsuitable habitat, I do not expect the configuration of the landscape to have a significant effect on invasive success. The alpine landscape is on average approximately 50% suitable, and while this is closer to the 30 to 40% cutoff, there should still be sufficient suitable habitat that the invasion is not significantly affected by the configuration patterns. In addition, the 'unsuitable' habitat in the alpine landscape (scrub) is not entirely uninvasible (Chapter 5); I would expect this partial suitability to further reduce any potential impact of the specific configurations. In the end, I expect that the performance of simulations in these landscapes will not be influenced by the spatial configuration of the component habitats, but will be a function of the proportional composition and comparative suitability of the different habitats.

Linear features

The incorporation of linear features in the landscape is functionally very distinct from heterogeneous mixtures that are dispersed across the landscape. The linear features (in this case, riparian stream corridors) by their nature exist in a contiguous and continuous configuration. If these features are inherently susceptible to invasion, their continuity produces an uninterrupted vector to invasion, which facilitates spread (Planty-Tabacchi et al. 1996; Stohlgren et al. 1998; Brown & Peet 2003). However, if the feature is inherently not susceptible to invasion (based on community composition, environmental variables, or other factors), it can have an inhibitory effect on spread, and represent a barrier to population movement (Hastings et al. 2005). The previous chapter indicates that the two riparian habitats found in these landscapes (forest creek and alpine creek) provide two distinctly different functional roles; the invasion appears to thrive in the forest creek habitat, while it is much less successful in the alpine creek habitat. Given the relative suitability of these habitats, I expect that the addition of either of these corridors to different landscapes will have contrasting effects; in the case of the forest creek habitat, I expect that it's inclusion into a landscape will act as a vector to facilitate spread and contribute disproportionately to invasion success, resulting in a more successful invasion (both in terms of the overall population size and the spatial extent) than what is projected based on the areal composition of the landscape. Conversely, given that the alpine creek habitat appears relatively unsuitable to *H. lepidulum*, I expect that it will have an opposite effect and disrupt spread, reducing invasion success from projections based on the areal composition.

To test these hypotheses, I simulated the spread of H. lepdiulum over all of the landscapes described. These simulations use a combination of a detailed dispersal kernel (Chapter 3) with demographic growth models to develop a stochastic simulation of plant spread. In the previous chapter, I used a fine-grained (30x30cm) simulation model to project the population growth of H. lepidulum across a 30x30m area in six different habitats. As experimental manipulation and observation are less logistically feasible at the larger grain used in these simulations (30x30m) (D'Antonio et al. 2004), I use the projections from the previous chapter to develop a series of descriptive models which summarise the population growth of H. lepidulum at the coarser resolution. I then apply these models at the coarser grain to simulate the spread of H. lepidulum over a larger (3x3km) spatial scale. While this summarisation process may result in some loss of detail, it ensures that applying the simulations over a larger spatial scale is computationally achievable. Additionally, the Bayesian modelling approach used to quantify the demographic processes helps to assure that these summary models accurately convey the variability and uncertainty present in the small-scale simulations. This approach allows me to simulate spread at a larger scale in order to test how different spatial configurations of the habitats affect spread using reasonably realistic estimates of habitat suitability and demographic stochasticity. This also permits me to assess the relative impact of specific features on spread success by contrasting landscapes with and without the specific features. I can then use this setup to examine how the realistic approximations of habitat suitability and their general spatial configurations affect the invasive spread of H. lepidulum, and attempt to draw conclusions to other situations.

6.2 Methods

6.2.1 Scaling up population dynamics

Landscape level simulations of the growth and spread of *H. lepidulum* are performed on a 3x3km landscape using a combination of the MDiG (Pitt et al. 2009) and PopMod (Chapter 4) software, similar to the approach used in Chapter 5. Simulating the population at this extent requires a simplified demographic model compared to those employed in Chapters 2 and 5, in order that the calculations remain computationally achievable. To this end I built a series of summary models that describe the aggregate population dynamics when the 30x30m landscape is simulated at the 30x30cm resolution using an open complete model structure (Chapter 5). As we saw in Chapter 5, the the total population growth over a 30x30m area is relatively robust to the modelling approach (open or closed). As this measure is relatively insensitive, I can be confident that using a nonspatial approach to project growth at the coarser 30x30m grain remains accurate. The approach used to create these projections is described in the following section; the first part describes the application of a matrix population approach to reduce the demographic models presented in the previous chapters to a minimal representation of the life-cycle which utilises only two stages; the seed stage (in which all of the movement occurs), and the adult stage (which represents the achievement of reproductive success). This model is of the form

$$\begin{bmatrix} 0 & Fec \\ Rec & S_A \end{bmatrix}$$
(6.1)

which describes the probability of an individual transitioning between the two lifestages, where Fec is the seed production of an individual adult, Rec is the probability of a seed becoming an adult, and S_A is the probability of adult survival. The calculation of each individual element within the matrix is described below.

Recruitment

In previous chapters, the transition from seed to adult was described by transitioning an individual though multiple juvenile stages before reaching reproductive maturity. In this chapter, the juvenile stages have been omitted in order to reduce the computational load of applying the model at a large spatial scale. Instead, the transition value is represented as a single value (Rec) which reflects the probability of a seed germinating and growing to reach an adult stage. At each timestep, an individual trial is performed for each seed by drawing a random number from a uniform distribution from zero to one; if the number is below the value of Rec, the individual becomes an adult; otherwise it dies.

This approach assimilates the intermediary juvenile stages represented in Chapter 5 into a single probability. In order to preserve the influence of the juvenile transitions, the estimates of the (Rec) parameter are modelled based on simulations of the recruitment of *H. lepidulum* from seed using the 30×30 cm resolution simulation in combination with the higher resolution demographic model which incorporates the juvenile stages, just as in Chapter 5. These simulations were performed in a landscape consisting of 10,000 30x30cm cells. In each iteration of the simulation, all the cells in the landscape are all assigned a single habitat value, and a single initial seed density. These trials are set up using the same methodology as in Chapter 5, except that dispersal, reproduction, and adult mortality processes were disabled in order to isolate the maturation process. Disabling dispersal allows each cell in the landscape to be treated as an individual trial without interference from surrounding cells. Removing reproduction and adult mortality from the simulation allows me to obtain an accurate count of the the number of adults, as the time to maturity is variable and can be confounded by individuals dying and being replaced by new individuals. These simulations were run in each of the six habitats using four levels of initial seed density, for a total of 24 density x habitat combinations. The resulting proportion of seed recruiting to the adult stage (Rec) is modelled as a function of the initial seed density (d_s) using a logistic model of the form

$$Rec = \frac{1}{1 + e^{b_{0,Rec} + b_{1,Rec} * d_s}}.$$
(6.2)

The b_0 and b_1 parameters were estimated using a Bayesian hierarchical modelling approach, in which the probability of a seed recruiting to an adult was modelled as a binomial response. The parameters b_0 and b_1 were assigned minimally informative priors, using a normal distribution centred around zero with the variance modelled as dgamma(0.001, 0.001) (Spiegelhalter et al. 2003). Parameter values were estimated independently for each habitat, and the resulting posterior distributions of each parameter are used to define the stochastic sample space when the recruitment function is implemented in the 3x3km landscape. Using this approach allows me to summarise the behaviour described by the more complex demographic model without incurring its computational load.

After parameterisation, the recruitment model required two additional modifications so that it could be rescaled to the 30x30m resolution of the landscape-scale simulations. First, the recruitment model had to be re-scaled so that it could be applied at the 30x30m cell size resolution. The simulations used to parameterise the recruitment model were performed at the 30x30cm cell scale, to match the scale of the original data collection. In order re-scale the model and apply it at the coarser resolution of the 30x30m cell size utilised in this chapter, the seed input in equation 6.2 (d_s) is divided by 10,000 (the number of 30x30cm cells that fit within a 30x30m cell). This approach assumes that there are 10,000 individual 'micro-cells' within the 30x30m cell, and that the incoming seed are distributed evenly amongst these micro-cells. The recruitment of a single 'micro-cell' is then calculated, and extrapolated to the entire 30x30m cell. While this approach is not perfect, it provides a simple and straightforward approach to re-scaling the recruitment process, and the relative linearity and minimal slope of the function produces a very small deviation between the functions at the lowest seed density levels (see results).

Secondly, as the rates of adult survival are not density-dependent (see below) it was necessary to modify the recruitment rate so that the population would not simply grow exponentially and unbounded, which is not only biologically unrealistic, but also becomes computationally unfeasible and causes the software to crash. This was achieved by modifying the recruitment function (equation 6.2) to include an additional term M. This term utilizes the ratio of the current adult population size within the cell N to the projected habitat-specific carrying capacity of an individual 30x30m cell K to proportionally reduce the probability of recruitment if the carrying capacity of the cell is exceeded. This term is calculated as

$$M = \begin{cases} 1 - \frac{N}{K} & \text{if } N \le K \\ 0 & \text{if } N > K \end{cases}$$
(6.3)

The carrying capacity (K) is calculated as the greatest population density observed in a single 30x30cm cell from the simulations in Chapter 5 multiplied by 10,000 (the number of 30x30cm cells within a 30x30m area). This effectively projects the highest density observed in each habitat at a 30x30cm scale to a 30x30m area.

Adult survival

The probability of adult survival (S_A) is the same as in Chapters 2 and 5; estimates of adult survival are derived from the field observations of tagged individual plants, and are modelled as a binomial process. Estimates of survival rates are calculated for each of the habitat types, again using a Bayesian hierarchical approach. No density- or age-specific relationships were obtainable from the dataset, so the model consisted of an intercept-only form, using a logit transformation to restrict the response to the interval [0,1]:

$$S_A = \frac{1}{1 + e^{b_0}}.\tag{6.4}$$

The parameter b_0 was provided a minimally informative prior (normal distribution with mean=0 and variance=1000), and was estimated independently for each habitat.

Seed production

Just as with adult survival, the number of seed produced annually per adult plant (Fec) is modelled using the same approach as in Chapters 2 and 5. The seed production is modelled in two parts. First, the number of flowers on each plant was modelled using the data obtained from the tagged individuals. By definition, all adult plants had at least one flower. I subtracted one from the observed number of flowers on each plant to model the number of flowers as a Poisson process:

$$Flowers_{hab} - 1 \sim DPoisson(\lambda_{flowers,hab}). \tag{6.5}$$

This represents a simpler approach than implementing a zero-truncated Poisson distribution in the confines of the OpenBugs model specification. An n + 1 transformation is then performed on the predicted values to construct the posterior distribution. Once the seed had set, a subsample of the seedheads was collected to model seed production at the individual flower level as a Poisson process:

$$Seed_{f,hab} \sim DPoisson(\lambda_{seed,hab}).$$
 (6.6)

Habitat specific estimates of seed production at the plant level (Fec) are then calculated by multiplying the number of flowers by estimates of seed production per flower:

$$Fec_{hab} = (Flowers_{hab} + 1) * Seed_{f,hab}.$$
(6.7)

6.2.2 Dispersal

Parameterisation of kernel

The initial analysis of dispersal in Chapter 3 found that a Cauchy function

$$f(d) = \frac{1}{\pi \alpha [1 + (\frac{x - \beta}{\alpha})^2]}$$
(6.8)

provided the best fit to H. lepidulum dispersal data. However, just as in Chapter 5, the dispersal kernels needed to be reparameterised to match the 30m resolution of the simulations. This re-scaling was performed by altering the measurement scale of the dispersal

data to reflect dispersal distances in terms of the number of 30x30m cells instead of SI units (metres). All of the candidate kernels described in Chapter 3 were re-parameterised with the 30m measurement scale using the nls algorithm in the R statistical software language (R Development Core Team 2009). The fit of the kernels was then evaluated by calculating the Akaike's information criterion (AIC) for each kernel, which provides a standardised technique to compare the deviation of fitted models from the actual data (Burnham & Anderson 2001).

Implementing dispersal

Although individual habitat-specific parameterisations of the dispersal kernel were produced in Chapter 3, in this chapter I employ a single kernel, fit using the dispersal data pooled across all of the habitats. This approach was utilised because implementing habitat-specific empirical dispersal kernels becomes overly complex at habitat intersections. Because of the sheer number of individuals simulated in this chapter, processing the dispersal of every seed individually as in Chapter 5 quickly became unwieldy, both in terms of processing time and available memory. To make the dispersal process more computationally achievable, the dispersal of seed is employed using a two-stage approach; the local dispersal (to directly adjacent cells) is calculated as a deterministic function, while those dispersal events traveling beyond the adjacent cells are implemented individually and stochastically.

Simulating the local dispersal is performed by taking a proportion of the seed produced within a cell (described below), and distributing them evenly amongst the four adjacent cells that share an edge with the parent cell. The distance and direction of the dispersal of these seed are assumed to be evenly distributed between the four adjacent cells in a deterministic manner as opposed to stochastically generating a distance and direction for each individual. This approach handles the majority of dispersal events, and drastically reduces processing time and memory usage compared to simulating each of these events individually.

The proportion of events dispersed beyond these cells are processed individually, using an approach almost identical to that employed in Chapter 5. The dispersal distance for each event is determined by randomly selecting a probability value between 0 and 1, and using the cdf of the dispersal kernel to calculate the corresponding distance (see Chapter 5, (Pitt 2008)). In order to only use this approach to model dispersal events beyond the adjacent cells, instead of selection a number between 0 and 1, a randomly generated value from a uniform distribution on the interval $[p_{min,d}, 1]$ is produced, where $p_{min,d}$ is the probability that an event will disperse the minimum distance required to move beyond the directly adjacent cells. A random value from a uniform distribution on the interval $[0, \frac{d_{1,s}}{2}]$ is added to the dispersal distance to approximate a random origin within the cell $(d_{1,s}$ is defined below).

Proportion dispersed by each method

The proportion of individuals dispersed by the deterministic and stochastic approaches are determined using the partial integral of the dispersal kernel

$$AUC_{d_1,d_2} = \int_{d_1}^{d_2} f(d) \tag{6.9}$$

which is used to calculate the amount of area under the curve of the dispersal function between the distances of d_1 and d_2 . To determine the proportion of events handled by each approach, I calculated the area under the kernel bounded by the range of distances that would result in an event travelling to either one of the adjacent cells ($[d_{1,d}, d_{2,d}]$ for the local deterministic approach), or moving beyond them ($[d_{1,s}, d_{2,s}]$ for the stochastic approach). This quantity is then used to calculate the proportion of dispersal events (P(e)) falling within the range $[d_{1,s}, d_{2,s}]$, determined by dividing AUC_{d_1,d_2} by the amount of area under the entire curve

$$P(e_{[d_1,d_2]}) = \frac{\int_{d_1}^{d_2} f(d)}{\int_0^{100000} f(d)}.$$
(6.10)

A distance of 1,000,000 cells was chosen for the endpoint of the integral describing the total area under the curve, as further distances provide no perceivable change in values of (P(e)) (primarily due to the computational limits of using double precision floating-point format numbers). While it is possible that dispersal events occur beyond this distance, they would be far beyond the spatial extent of the simulation anyway, and would not influence the final results.

As dispersal from the cell is assumed to be random in terms of direction, and the cells are represented as 30x30m squares, the dispersal distance required to reach one of the adjacent cells is variable. A dispersal event originating from the centre of the cell travelling in a direction directly perpendicular to the edge of the cell would have to travel 15 metres to reach the edge, while a dispersal event travelling towards a corner of the cell would have to travel 21.21 metres to reach the edge. As a compromise, I used the mean distance of 18.1 metres as the dispersal distance required to leave the parent cell $(d_{1,d})$. In addition, I included a constant u to this value; initially each dispersal event was to include a random value from the distribution $Dunif(0, d_{1,d})$ to account for the event originating at a random location between the centre of the cell and the edge. Instead, the constant (u) is calculated as the mean of that distribution $(\frac{d_{1,d}}{2})$. The second endpoint of the integral $((d_{1,d}-u)+30)$ approximates the furthest edge of adjacent cells, and dispersal events travelling further than this are implemented by the stochastic dispersal process (discussed below).



Figure 6.1: Satellite image of Examples of the Craigieburn basin, where the seed sowing trials were located. Forest habitats are located in the lower elevations (lower right in the picture), and as elevation increases to the upper left, the transition to the higher elevation alpine habitats is clearly visible. North is towards the top of the image (Google Earth 2010).

Landscape construction

The *H. lepidulum* simulations are executed in 24 different virtual landscapes, with ten replicates performed in each landscape (for a total of 240 simulation runs). These landscapes are designed to reflect simplified versions of the core landscape features the invasion is likely to encounter. This landscape (Figure 6.1) is decidedly more complex than the simplified versions used here, although the general configurations and relative composition are approximately accurate and are intended to more generally represent the types of landscape configurations likely to be encountered. A sample of the landscapes which contain the major features are displayed in Figure 6.2 and a brief description of the full range of landscapes is presented in Table 6.1. Homogeneous landscapes consisting of a single habitat represent the simplest type of landscapes used in the simulations. Even though the homogeneous landscapes do not reflect actual conditions the invasion would encounter, they are implemented in order to develop a baseline of the expected behaviour of the population for each habitat.

Next, a series of patch landscapes were developed to reflect some of the spatially hetero-

geneous landscapes the invasion is likely to encounter. The first of these patch landscapes was designed to emulate the distribution of treefall gaps within the intact forest. A portion of cells within the landscape were randomly chosen to represent treefall gaps, although the 30x30m cell size is slightly larger than the gaps typically created by individual treefalls in these forests (Harcombe et al. 1997; Stewart 1986). The remaining cells in these landscapes were classified as forest. The frequency of treefall gaps in these forests is not well documented; however, existing estimates suggests that these gaps constitute anywhere from <1 to 7% or more of the area (Stewart 1986; Runkle et al. 1995; Harcombe et al. 1997; Lusk & Smith 1998). Two different gap-density landscapes were therefore constructed, with either 5% (Forest Gap I) or 10% (Forest Gap II) of the landscape classified as gap habitat. These configurations along with the homogeneous forest landscape span the range of reported gap frequency in this type of forest. These landscapes were randomly generated before each replicate of the simulation to ensure that the results were not representative of only a single spatial configuration.

Patch landscapes representing the mixture of tussock and scrub habitat were also constructed; however unlike the forest-forest gap landscapes which are dominated by a forest matrix, the relative proportions of tussock and scrub habitats are more evenly distributed. These landscapes were generated using two different approaches; the first was constructed by randomly assigning each cell either habitat type, representing a completely random mix of the two (Tussock/Scrub I). The second approach constructed the landscape by spatially aggregating the habitat types in a more realistic manner (Tussock/Scrub II). To construct these landscapes, I randomly located 250 points within the landscape, and used them to construct a set of Thiessen polygons, which were then randomly assigned one of the two habitat types. This number of points was chosen because the resultant patterning and complexity of patches visually approximated that of the real landscape (Figure 6.2). As neighbouring polygons with the same habitat type are effectively merged, this procedure produces a patch landscape consisting of habitats with complex and random shapes while maintaining an approximately even proportion of the landscape in each habitat. Each of these landscape types was uniquely generated prior to each replicate of the simulation (just as with the forest-forest gap landscape), allowing me to attribute any trends in spread dynamics that arise from these simulations to the generic spatial structure as opposed to having to interpret them in the context of the individual configurations.

Finally, a range of corridor landscapes were constructed to examine the addition of two different sized (30m and 90m wide) riparian corridors to each of the previously described landscapes. These landscapes are constructed by overlaying the corridors comprised of the appropriate habitat (forest creek or alpine creek) onto a homogeneous forest (Forest Corridor I and Forest Corridor II), homogeneous tussock (Tussock Corridor I and Tussock Corridor II), or homogeneous scrub (Scrub Corridor I and Scrub Corridor II) habitat. Riparian corridors of both widths were also overlain onto the two heterogeneous mixtures of forest and forest gap habitats to produce the Forest/Gap Corridor I-IV landscapes,



Figure 6.2: Examples of some of the heterogeneous landscape patterns used in the modelling of *H. lepidulum*. Clockwise from top left, these landscapes represent a 5% randomly distributed mixture (Forest Gap I), a 30m corridor (Forest Corridor I), a 50% aggregated mixture that includes a 90m corridor (Tussock/Scrub Corridor IV), and a 50% randomly distributed mixture (Tussock/Scrub I). This subset of landscapes exemplifies the range of configurations used in the simulations. More specific details of all the landscapes are found in the text or Table 6.1.

and also overlain over the two mixtures of tussock and scrub habitats to produce the Tussock/Scrub Corridor I-IV landscapes. This approach permits me to contrast how the patch landscapes further modify the result of including a riparian corridor which bisects the homogeneous habitats. These landscapes also offer the most realistic depiction of the field conditions under which the data for this project were collected, and should correspondingly provide the most accurate depiction of how the invasion is likely to proceed in these catchments.

6.2.3 Running simulations

The simulations were run in a 100x100 cell landscape, where each cell represents a 30x30m area, creating a total landscape size of 3x3km. Simulations were run for 100 (annual) time steps, and replicated 10 times in each of the landscapes described above. Those landscapes containing patchily distributed habitats were uniquely generated prior to each iteration so that the results would be representative of the general landscape construction rules, as opposed to a particular configuration. All simulations contained an initial population located in a 4x4 cell configuration in the bottom centre of the landscape. Each of these cells contained the maximum number of adults allowed according to the estimated carrying capacity of each specific habitat (see results). The choice of clumping the initial population was selected as it better fit the biology of this species, being more representative of a nascent focus originating from a single accidental introduction point as opposed to a linear element, such as a plantation edge (i.e. Higgins & Richardson 1998). Initiating the population at carrying capacity in these cells helped to ensure that the observed spread dynamics were a function of plant growth and dispersal, and to isolate these dynamics from the influence of propagule availability.

Parameters in the simulation (recruitment, mortality, and fecundity) were implemented by randomly drawing values from the Bayesian posterior distributions that defined each parameter. For those models which required the estimation of multiple parameters, these values were drawn from concurrent positions in the vectors describing the posterior distributions. This assured that any covariance between parameters in the same model was accounted for without having explicitly specify their interdependency.

6.2.4 Analyses

The analysis of the simulated spread is based on a number of key metrics; total population size, population density, the occupancy rate of cells, and the location of the topmost occupied cell (extent). Density and total population size reflect the local and global success of the population, while occupancy and extent reflect the areal extent of the invasion (spatial spread). These metrics are calculated at each timestep in the simulation period, and are monitored over the entire simulation. The calculation of these metrics

Patch Landscapes		
Name	Generic Configuration	Description
Forest Gap I	Patch Landscape I	Forest matrix with 5% of landscape as gap
Forest Gap II	Patch Landscape II	Forest matrix with 10% of landscape as gap
Tussock/Scrub I	Patch Landscape I	Approximately 50% scrub and 50% tussock mixture, randomly distributed
Tussock/Scrub II	Patch Landscape II	Approximately 50% scrub and 50% tussock mixture, aggregate clumps
Corridor Landscapes		
Name	Generic Configuration	Description
Forest Corridor I	Corridor Landscape (30m)	30 metre forest creek corridor bisecting homogeneous forest matrix
Forest Corridor II	Corridor Landscape (90m)	90 metre forest creek corridor bisecting homogeneous forest matrix
Scrub Corridor II	Corridor Landscape (90m)	90 metre alpine creek corridor bisecting homogeneous scrub matrix
Tussock Corridor I	Corridor Landscape (30m)	30 metre alpine creek corridor bisecting homogeneous tussock matrix
Tussock Corridor II	Corridor Landscape (90m)	90 metre alpine creek corridor bisecting homogeneous tussock matrix
Patch-Corridor Landscapes		
Name	Generic Configuration	Description
Forest/Gap Corridor I	Patch (I) Corridor (30m) Landscape	30 metre forest creek corridor bisecting Forest Gap I landscape
Forest/Gap Corridor II J Forest/Gap Corridor III J	Patch (I) Corridor (90m) Landscape Patch (II) Corridor (30m) Landscape	90 metre forest creek corridor bisecting Forest Gap I landscape 30 metre forest creek corridor bisecting Forest Gap II landscape
Forest/Gap Corridor IV	Patch (II) Corridor (90m) Landscape	90 metre forest creek corridor bisecting Forest Gap II landscape
Tussock/Scrub Corridor II	Patch (I) Corridor (90m) Landscape	90 metre alpine creek corridor bisecting Tusseck/Scrub I landscape
Tussock/Scrub Corridor III]	Patch (II) Corridor (30m) Landscape	30 metre alpine creek corridor bisecting Tussock/Scrub II landscape 90 metre alpine creek corridor bisecting Tussock/Scrub II landscape
TUPPOUN DU UN COLLINCE T V		A distribution of the second structure to the second of th

omits the 4x4 cell area containing the initial populations. This approach allows me to focus on the development of the invasion in previously unoccupied areas, while assuring that propagule supply is not a limiting factor. This in turn permits me to focus on the processes and dynamics of an expanding invasion, and not be concerned about dynamics that occur as a result of a limited propagule supply, such as Allee effects and/or limited propagule pressure.

In order to compare the effect of different landscape configurations on population success, I calculated the relative amount of change in the total population size as landscape complexity increases. To do this, I utilised the simulated population size in the homogeneous landscapes as a baseline measure of expected population performance. For this analysis, the forest, scrub, and tussock habitats are denoted as primary habitats, as they are the most abundant habitat types in these communities, and comprise the majority of the landscape matrix (pers. observation). The remaining (secondary) habitats are relatively small components of the landscape, and therefore primarily only serve to modify the primary habitats. This perspective has no quantitative effect on the outcomes; it simply allows me to better focus the analysis on combinations of landscapes that are actually likely to exist, and allows me to ignore unrealistic configurations, such as a landscape consisting entirely of forest gaps.

The relative change in population performance was calculated in two ways; first, I calculated the projected population size of each of the heterogeneous landscapes as a function of the observed population performance in homogeneous landscapes of the component habitats, multiplied by their relative composition within the heterogeneous configuration. These projections can be formalised as

$$N_{proj} = \sum_{h=1}^{n} = p_h N_{h,homo} \tag{6.11}$$

where N_{proj} is the projected population size of the heterogeneous landscape, n is the number of habitats that make up the heterogeneous landscape, p_h is the proportion of the heterogeneous landscape comprised of habitat h, and $N_{h,homo}$ is the mean population size of the homogeneous landscape h after 100 years. This projection is based entirely on the proportional composition of the landscape, and ignores any potential influence of spatial configuration. This projected size is then compared to the results of simulating the population in the heterogeneous landscape (N_{sim}) by calculating the proportional change between the two approaches as

$$\Delta N_{sim,proj} = \frac{N_{sim} - N_{proj}}{N_{proj}}.$$
(6.12)

A perfect match between the projected and simulated population sizes would produce a value of zero, and positive or negative values would describe the direction and relative magnitude of difference between the projected and simulated results. This comparison allows me to identify the contribution that the spatial configuration of the habitats within the landscape have on the final size of the population. Projected and simulated population sizes were duplicated in the case of the heterogeneous mixtures that contained both tussock and scrub habitats, as both habitats represent equal components of these heterogeneous mixtures. The exact same procedure was used to compare projections of occupancy between heterogeneous landscapes and their homogeneous counterparts.

The second approach used to quantify the effects of landscape configuration on population success was to compare the population size from the simulations in the heterogeneous landscapes to simulations in homogeneous landscapes of the corresponding primary habitat. This approach allows me to assess how the addition of landscape complexity changes the projected outcome compared to a homogeneous landscape consisting entirely of the dominant habitat type (the landscape matrix). The proportional change in population size between the homogeneous landscapes of primary habitat and simulated population sizes in heterogeneous habitat was calculated in a similar fashion as

$$\Delta N_{sim,homo} = \frac{N_{sim} - N_{homo}}{N_{homo}} \tag{6.13}$$

where N_{sim} is the simulated population size after 100 years in the heterogeneous landscape, and N_{homo} is the simulated population size after 100 years in the homogeneous landscape of the primary habitat. Again, a perfect match results in a value of zero, with other values representing the magnitude and direction of the deviation from the population estimates from the homogeneous landscape.

The effect of landscape attributes on invasion success was evaluated by simulating *H. lep-idulum* spread for 100 years with replicated 10 times in each landscape, and using the population state at the end of the simulation period to evaluate the influence of the landscape configuration and composition on spread. Although populations will continue to develop beyond the 100 year simulation period, this temporal extent provided enough time for the differentiation of populations in some of the landscapes, and provides a useful time frame for planning management strategies. Performance of the population was assessed using the four metrics described above (population size, population density, occupancy rate, and extent). Landscapes were divided into two groups based on their elevational positioning, and metrics from the simulations were compared within each group using analyses of variance to detect differences. Pair-wise comparisons were subsequently performed to identify those differences which were statistically significant using a Tukey's range test (Zar 1999) with a cutoff of p < 0.001.

Results 6.3





Probability of seed reaching adulthood

10000

Figure 6.3: Recruitment curves describing the probability of a seed maturing to a sexually reproductive adult in the different habitats. These functions reflect the rates obtained from simulating the development of seed using the full demographic model described in Chapter 2. Dashed lines represent the 95% confidence interval around the parameter estimates. See text for details.

The validity of the parameter estimates for the recruitment function were assessed by examining the convergence of three independent vectors of parameter estimates produced by the Gibbs sampling algorithm; consistency between the three vectors (or chains) means that each approximation of the parameter value arrived at the same location independently, suggesting the parameter estimation is robust and does not reflect a localised maxima. The convergence of these vectors was assessed using a potential scale reduction factor (PSRF); values of 1.2 or less suggest convergence of the chains (Gelman et al. 1995). The PSRF values for the different parameter and habitat combinations of the recruitment function ranged from 1.00 to 1.11, suggesting suitable convergence for all parameter estimations. Overall, rescaling this function from the 30x30cm scale to the 30x30m scale had a minimal impact on the probability of recruitment. The function is presumably most sensitive to the rescaling process at the lower end of the scale, as this is where the per-seed areal change in density is the greatest (one seed per 30x30cm cell vs. one seed per 30x30m cell). In the end, solving the recruitment function at the minimum density of one seed per cell at either the 30x30cm or 30x30m scale results in a change in the (*Rec*) parameter on the order of 10^{-8} to 10^{-10} percent (depending on habitat). This level of variation is relatively insignificant compared to the amount of variation obtained from the uncertainty in the parameter estimation, which can vary by five to nearly 60 percent at this minimum seed density (again, depending on the specific habitat). This variability due to uncertainty is the primary source of the total variation observed in recruitment, which ranged from approximately 0.00001 to 0.001 at the lowest seed density (1 seed per 30x30m cell), depending on the specific habitat (Figure 6.3). In general, the probability of recruitment decreased with increasing seed density across all habitats, although the rate of decrease differed between habitats.

Table 6.2: Ranking of the different dispersal kernels after fitting them using the 30m 'units'. This base unit was necessary to describe the dispersal distance in terms of the number of cells (30x30m) for compatibility with the landscape-level simulations.

Kernel Form	No. of Parameters	α	β	AIC value
Cauchy	2	0.001313	-0.032689	-882.6974
Clark generic (s= 0.5)	2	0.765	0.00911	-877.7905
negative exponential	2	0.2921	30.128	-855.9323
Gaussian	2	-0.213	0.008	-846.5925
log-normal	2	36.52	71.8	-842.5184
power	2	0.00316	0.945	-842.4014
Clark generic $(s=3)$	2	6.034	0.0462	-767.6124
Cauchy	1	10.49	N/A	-517.5419
Student's t	1	0.01207	N/A	-571.6194
Clark generic (s= 0.5)	1	13.95	N/A	-522.9708
power	1	0.0305	N/A	-522.0847
Guassian	1	173.2	N/A	-517.5210
negative exponential	1	32.63	N/A	-517.8896
Clark generic $(s=3)$	1	36.95	N/A	-517.5113
log-normal	1	0.269	N/A	-465.6617

6.3.2 Dispersal

Because of the interactions of some of the parameters in the various potential dispersal kernels, these functions required complete re-parameterisation in order to apply them at a scale that describes dispersal distance in terms of the number of 30x30m cells traveled as opposed to the SI units (metres) used in Chapter 3. This re-parameterisation altered

the fit of a few of the kernel forms, but the overall order of kernel options ranked by AIC values was the same as in Chapter 3. The two-parameter Cauchy function remained the top-ranked model (Table 6.3), and was therefore chosen for incorporation into the simulation.

6.3.3 Effects of landscape on invasion

Comparing the result of the simulations in different landscapes reveal that significant differences exist in comparisons of each metric for each landscape group (Table 6.3). Pair-wise comparisons (using a Tukey's range test) reveal which of the differences which were statistically significant (Table 6.4).

Table 6.3: Results of the analysis of variance comparing metrics of landscape spread. Landscapes were grouped by their elevational positioning, with forest dominated landscapes occurring at lower elevations, and alpine landscapes occurring at the higher elevations. Four metrics were calculated at the end of each simulation period; this table contains the result of comparing these metrics within the elevational groups.

Elevational Group	Metric	df between	df within	F-value	p-value
Forest	Population Size	10	99	58523	< 0.001
Forest	Density	10	99	5280	< 0.001
Forest	Occupancy	10	99	4626	< 0.001
Forest	Extent	10	99	9.977	< 0.001
Alpine	Population Size	12	117	225.6	< 0.001
Alpine	Density	12	117	70.6	< 0.001
Alpine	Occupancy	12	117	902.9	< 0.001
Alpine	Extent	12	117	33.28	< 0.001

Homogeneous landscapes

Comparisons of the simulations in homogeneous landscapes of the lower elevation habitats using pairwise comparisons revealed significant differences in nearly every metric of spread. Each metric indicated that the invasion was most successful in the homogeneous forest creek landscape, followed by the forest landscape, and lastly the forest gap landscape. Differences between the metrics for each of these landscapes was significant except in the case of extent, where the forest creek and forest landscapes were similar (Table 6.4). The extent of the invasion in the homogeneous landscape consisting wholly of forest gap habitat was significantly less than in the other two.



Figure 6.4: A comparison of the four measures of population success in each of the simulated landscapes from 10 replications simulated for 100 years each. Landscapes pertaining to the lower elevations of the catchment which is primarily a forested matrix are presented on the left, while the landscapes of the upper elevation alpine areas are on the right. The complexity of the landscapes generally increases from left to right within each panel, ranging from homogeneous landscapes, to homogeneous landscapes with corridors, to heterogeneous landscapes, to heterogeneous landscapes with corridors. The full range of each metric is represented by horizontal bars for each point; in many instances the range of response is small enough that it is not discernible in the figure. Specific details of each landscape are described in Table 6.1.



Figure 6.5: Visualisation of a time-lapse of simulated spread in two different landscapes; a homogenous landscape consisting entirely of forest creek landscape (left) and a mixture of scrub and tussock habitats in a landscape where the two habitats are spatially aggregated. The density of adult plants in each image is represented by the colour, which ranges from high (red) to low (green). The progression of the invasion is shown at the onset, represented by a small high-density introduction (t=0), at the midway point of the simulations (t=50), and at the final time step (t=100).

Many of the metrics of spread were significantly different in the homogeneous landscapes of the alpine habitats as well (Table 6.4). In general, the simulated spread was most successful in the homogeneous tussock landscape, followed by the alpine creek, and then the scrub habitats. Again, the differences between the different landscapes were significant for all metrics of invasion success, save for the measure of extent. In terms of extent, the tussock habitat produced a value which was significantly greater than either the alpine creek or scrub habitats. The extent of the invasion in the alpine creek and scrub habitats were statistically indistinguishable.

Patch landscapes

Simulations of *H. lepidulum* spread in the patch landscapes represents an increase in both the complexity and realism of landscape representation. At lower elevation, this is represented in a landscape consisting of a primarily forested matrix, interspersed with a relatively small proportion of forest gaps. Results in the two variants of this mixture were statistically indistinguishable using the reported metrics (Table 6.4). However the inclusion of the patches of forest gap habitat significantly reduced invasion success in these landscapes compared to the homogeneous forest landscape, except in terms of the extent of the spread (which was statistically indistinguishable). Conversely, invasion in the patch landscapes was significantly more successful compared to in the homogeneous forest gap landscape, except in terms of the density of occupied cells. The success of simulated invasion into the patch landscapes outperformed the projected metrics of both total population size (Figure 6.6) and occupancy (Figure 6.7) which were calculated based on their areal composition.

Simulations of spread in patch landscapes of the alpine landscapes reflected how spread would progress in a landscape consisting of even parts of scrub and tussock habitats, represented using two different levels of aggregation. Just as in the lower elevation landscapes, the two variants of the patch landscape (Scrub/Tussock I II) were indistinguishable from one another based on the metrics used to describe spread success (Table 6.4). The relationship to their homogeneous counterparts is more complicated. Simulations in either alpine patch landscape significantly exceeds the success of simulations in the homogeneous scrub habitat by all metrics examined. Compared to the simulations in the homogeneous tussock landscape, the invasion in the randomly distributed mixture of tussock and scrub habitat (Scrub/Tussock I) was significantly less successful across all metrics. Simulations of *H. lepidulum* in the landscape where the spatial distribution of tussock and scrub habitats are clumped into groups (Scrub/Tussock II) were mostly less successful as well; however, the measure of the density of occupied cells overlapped between these two landscapes. Just as with the lower elevation landscapes, the simulated invasion into the alpine patch landscapes produced smaller overall population sizes (Figure 6.6) and occupancy rates (Figure 6.7) than what was projected based on their proportional composition.

Landscape	Population Size	Density of Occupied Cells	Occupancy Rates	Furthest Extent
Low-elevation forest matrix landscap)es			
Forest Creek	24889372.4^{a}	21385.5^{a}	1164.1^{a}	2799^{a}
Forest	4460939.0^{b}	9652.6^{b}	462.2^{c}	2211^{ab}
Forest Corridor II	3761736.6°	7524.6^{c}	$500.3^{ m b}$	2271^{ab}
Forest/Gap Corridor III	$3637505.3^{ m cd}$	7503.0°	484.9^{b}	$2076^{ m b}$
Forest/Gap Corridor IV	$3551316.6^{\rm d}$	7613.6^{c}	466.7^{c}	$2052^{ m b}$
Forest Corridor I	2214577.6^{e}	$5153.1^{ m d}$	429.9^{d}	1914^{b}
Forest/Gap Corridor II	2211004.6^{e}	5152.4^{d}	$429.2^{ m d}$	2139^{ab}
Forest/Gap Corridor I	1487911.3^{f}	3893.5^{e}	382.3^{e}	1878^{b}
Forest/Gap I	1339872.2^{g}	3640.1^{e}	368.3^{ef}	2133^{ab}
Forest/Gap II	1295764.8^{g}	$3615.0^{\rm e}$	358.5^{f}	2184^{ab}
Forest Gap	481171.6^{h}	3769.3^{e}	127.9^{g}	876°
TE-4 donation claims lond				
$n_{1gn-elevation}$ at pine tanascapes				
Tussock	11004271.5^{a}	$11955.3^{ m b}$	920.6^{a}	2691^{a}
Tussock Corridor I	$7140991.8^{ m b}$	$9362.6^{ m cd}$	$762.9^{ m b}$	2391^{ab}
Tussock Corridor II	6081316.3°	8781.8 ^{cd}	692.7^{c}	2292^{ab}
Scrub/Tussock II	3474650.6^{d}	10399.6^{bc}	319.8^{d}	1941^{b}
Tussock/Scrub Corridor III	$3309736.7^{ m de}$	$10442.0^{ m bc}$	311.3^{d}	1875^{b}
Tussock/Scrub Corridor IV	3011563.4^{de}	$9248.4^{ m cd}$	$319.7^{ m d}$	1878^{b}
Scrub/Tussock I	3009269.2^{de}	$8643.0^{ m cd}$	348.3^{d}	1803^{b}
Tussock/Scrub Corridor I	2817110.9^{de}	8489.3^{cd}	331.6^{d}	1848^{b}
Tussock/Scrub Corridor II	$2463801.1^{ m e}$	7660.0^{de}	$320.7^{ m d}$	1794^{b}
Alpine Creek	1217632.5^{f}	15996.1^{a}	76.5^{e}	$720^{\rm c}$
Scrub	125454.7^{g}	5620.5^{e}	22.5^{f}	297^{c}
Scrub Corridor II	1944.4^{g}	56.5^{f}	34.5^{ef}	$480^{\rm c}$
Scrub Corridor I	677.2^{g}	36.5^{f}	19.2^{f}	237^{c}



Figure 6.6: The difference between projected and simulated population size in heterogeneous landscapes. Bars represent the proportional magnitude with which the simulated populations deviate from the projected population size for the different landscape variants. These variants are represented by the habitat that occupies the majority of that landscape, representing the landscape matrix (Forest, Tussock, or Scrub). Specific details of individual landscape configurations can be found in Table 6.1, but in general the patch landscapes represent the heterogeneous mixtures of two habitats, corridor landscapes are the addition of a riparian corridor to an otherwise homogeneous matrix, and the patch corridors represent the addition of a corridor to the different levels of the heterogeneous mixtures. Projections of expected population size were based on population sizes in homogenous landscapes, and calculated using equation 6.11. The patch landscapes of the tussock and scrub matrices are duplicates, as these two habitats occupy equal proportions of each of corresponding patch landscape (i.e. Patch Landscape I of the tussock matrix is the same landscape as patch landscape I of the scrub matrix). These comparisons were made using the mean values from all simulations performed in a specific landscape configuration; a more conservative comparison using appropriate maximum and minimum values resulted in the same relationships (see text).

Corridor landscapes

The addition of corridors of riparian habitat (forest creek) to the homogenous forest habitat reduced the total population size and density of *H. lepidulum* in occupied cells compared to simulations in homogeneous landscapes of either forest creek or forest habitat (Table 6.4). The wider (90m) corridor resulted in more successful invasion measured by all metrics than the more narrow (30m) corridor, save for the extent, which was identical between the two. The occupancy rate within the 90m corridor landscape was less than in a homogeneous forest creek landscape, but higher than in the homogeneous forest habitat. Occupancy in the 30m corridor landscape was lower than in either the 90m corridor landscape or either of the homogeneous landscapes (forest or forest creek). These four different landscapes were largely indistinguishable in terms of the extent, save for the 30m corridor being of a slightly lower extent than in the homogeneous forest creek landscape. Just as before, simulations of invasion in these landscapes underperformed the projected population size (Figure 6.6) and occupancy rates (Figure 6.7).

Including corridors into the alpine habitats of scrub or tussock reduced the invasion success compared to the homogeneous tussock landscape. Simulations in the homogeneous tussock landscape resulted in the greatest population size and density, followed by those in the tussock habitat with a 30m corridor, and finally the tussock habitat with a 90m corridor. Occupancy rates of the two corridor landscapes were also lower than in the homogeneous tussock landscape, with a higher occupancy in the 90m corridor compared to the 30m corridor. The extent of the invasion was the same between the three landscapes. In scrub-dominated landscapes, the addition of riparian corridors reduced invasion success in most instances, but the effect was only significant in terms of the density of occupied cells. The simulations from the two different corridor widths were indistinguishable from each other in terms of the four invasion metrics.

Patch-corridor landscapes

In the final and most complex set of landscapes, the riparian corridors are combined with the patch landscapes to create landscapes consisting of three different habitats. In the lower elevation forest matrix, this is represented with a forest creek corridor bisecting the two variations of forest/forest gap mixtures. Simulated populations of *H. lepidulum* in these landscapes were slightly less successful than in the forest corridor landscapes without any forest gap habitat (Table 6.4). The metrics of spread success from simulations in the forest/forest gap mixtures with a 30m wide corridor (Forest/Gap Corridor I and Forest/Gap Corridor II) were just below that of the homogeneous forest landscape with a 30m wide corridor; however the only significant differences were between the Forest/Gap Corridor I landscape (with 5% of area in forest gap habitat) and the Forest Creek I landscape which differed in population size, density, and occupancy. The remaining metrics of spread were statistically indistinguishable between the three landscapes. Compared



Figure 6.7: The difference between projected and simulated occupancy rates in heterogeneous landscapes. Landscape descriptions and calculation methods are the same as in Figure 6.6. The projected occupancy rates are based on mean values from simulations performed in the homogeneous landscapes of the component habitats; to test the consistency of these differences, a comparison using the maximum and minimum occupancy values from homogeneous landscape simulations was performed to provide a conservative test examining if any of the the simulations overlapped with the projections; those comparisons in which the differences proved to be consistent across all observed outcomes are marked with an asterisk. The other comparisons revealed that some overlap between projections and simulations did exist at the extremes, suggesting a less significant relationship (see text).

to the forest/forest gap mixtures without corridors, the addition of corridors increased the invasion success of H. *lepidulum*; the addition of a 30m corridor resulted in a modest increase in success, significant only in terms of the population size, and the occupancy rate for one of the comparisons.

The effect of adding a 90m corridor to either forest/forest gap mixture elicited a very similar response to the homogeneous forest landscape with a 90m wide riparian corridor. The only significant distinction between these three was the increase in the population size and occupancy rates of the Forest Corridor II landscape compared to the Forest/Gap Corridor IV. The remaining metrics were all statistically similar to one another. Compared to the forest/forest gap mixtures without a corridor, the addition of a 90m corridor increased the invasion success of *H. lepidulum* across all metrics save for the extent. Overall, the projections of invasion performance (based on the proportional habitat composition) in these lower elevation landscapes consistently over predicted the results of the simulations, both in terms of overall populations size (Figure 6.6) and the number of cells occupied (Figure 6.7).

The addition of a riparian corridor to mixtures of tussock and scrub appeared to consistently reduce the performance of *H. lepidulum* compared to the mixtures of tussock and scrub without the corridors, however significance tests showed that the effect of the corridors (of either width) was not significant (Table 6.4). From a different perspective, the addition of scrub habitat to a tussock landscape with a riparian corridor served to reduce invasibility; this reduction was more pronounced when the tussock and scrub were randomly mixed (Tussock/Scrub Corridor I and II) compared to aggregated (Tussock/Scrub Corridor III and IV). Comparing the four different Tussock/Scrub Corridor variants reveals that they differ very little from each other, with the only significant difference arising when comparing the occupancy of the 30m corridor bisecting the aggregated tussock/scrub landscape compared to the 90m corridor bisecting the randomly distributed tussock/scrub landscape.

The simulations performed in the alpine Patch I landscape (random assignment of scrub or tussock habitat to each cell) with a corridor width of either 30 or 90 metres underperformed projections based on the habitat-specific areal composition (Figure 6.6). However, the simulations of *H. lepidulum* in the alpine Patch II landscapes (aggregation of scrub and tussock habitats) outperformed both their projected population size (Figure 6.6) and projected occupancy (Figure 6.7).

6.3.4 Population size of heterogeneous vs. homogeneous landscapes

Compared to simulations in the homogeneous landscapes, increasing landscape complexity through the inclusion of multiple habitats within the landscape resulted in simulations



Figure 6.8: Relative change in population size between homogeneous and heterogeneous landscapes. Change is calculated relative to the population size from simulations in a homogeneous habitat indicated in the legend (primary habitat). Landscape complexity generally increases from left to right, including heterogeneous mixtures (Patch Landscapes), the addition of different size riparian corridors to the primary habitat (30m Corridor and 90m Corridor), and the combination of patch landscapes with different size riparian corridors. Relative mixtures of the primary and secondary habitat vary depending on the specific primary habitat; these proportions are designed to represent observed levels of landscape variability, and are detailed in Table 6.1. Values in the graph represent the mean population size from simulations; a more conservative comparison using appropriate maximum and minimum values resulted in the same relationships (see text).

where population size in the forest and tussock habitats decreased, and population size in the scrub habitat increased (Figure 6.8). Only the addition of riparian corridors to the scrub habitat contradicted these trends, resulting in a reduced population size compared to a homogeneous scrub landscape. Incorporating the tussock and scrub habitats into a single landscape produced the greatest magnitude change (relative to the homogeneous tussock landscape). Just as with the comparison of projected and simulated population size, I performed another comparison to see if there was any overlap between the minimum or maximum population sizes from any replicate of the simulations after 100 years in each configuration (i.e. comparing the minimum population size from the tussock scrub combination to the maximum population size from a homogeneous scrub habitat). While the magnitude of differences was reduced, there was still no overlap between the population size in heterogeneous and homogeneous landscapes.

6.4 Discussion

6.4.1 Scaling up population dynamics

The results of simulating the spread of *H. lepidulum* across the different homogeneous landscapes using a 30x30m cell were generally very similar to that seen using the 30x30cm cell in Chapter 5; invasion into the forest creek habitat produces the largest population, followed by tussock, forest, alpine creek, forest gap, and scrub. While this relative ranking of the invasibility of different habitats remained the same, applying the simulations at a larger scale did result in a higher level of differentiation between the habitat-specific results. The consistency of these habitat-specific differences reiterates the importance of examining invasion success in the context of the existing vegetative community (described here by the different habitat classifications). This context can have a substantial influence on the mechanisms which drive population growth, and help to explain (and predict) spatially explicit patterns of the extent and severity of an invasion. While the idea that some habitats are more invasible than others is nothing new (Huenneke et al. 1990; Meekins & McCarthy 2002; Chytry et al. 2008), these simulations reinforce the findings from Chapter 5 that the mechanisms which determine invasive success (measured as overall population size) are context-specific, and that the existing environment has a significant influence on invasion success.

Just as in Chapter 5, the overall population size in any landscape can also be decomposed into two contributing mechanisms; the effect of local success (density), and the ability of the population to spread into new areas (occupancy). The furthest extent of spread was also recorded, but had less meaningful interpretation. Decomposing these mechanisms revealed dynamics which were very similar to those observed in the finer-scale simulations in Chapter 5. The two metrics of extent (occupancy) and severity (local density) are generally correlated; large population sizes are typically achieved when the invasion displays a combination high-density/high-occupancy pattern, while less successful invasions typically display a low-density/low-occupancy pattern. This correlation can be seen in the consistency with which the different metrics are ranked (Table 6.4). However, the results in the alpine creek habitat reveal this was not always the case; there H. lepidulum produced relatively high densities in occupied cells compared to the other habitats, yet the relatively low occupancy rate meant that this local success did not translate into a large overall population. This high-density/low-occupancy pattern can also be seen (to a lesser extent) in the homogeneous scrub habitat, where the limited spatial distribution of the population resulted in the locally high densities not translating into a large landscape-level population size. While the high-density/high-occupancy pattern is clearly an effective invasion strategy, the high-density/low-occupancy response appears to be less successful at the scale of the entire landscape. This suggests that a few localised highdensity establishments may not constitute an immediate priority for control if there is

reason to believe the occupancy is not likely to increase.

The opposite situation (low-density/high-occupancy) was not observed in these simulations. This is surprising, as this has been predicted to occur in other simulations of spread (Kean & Barlow 2004). However in these simulations, local populations show a strong reliance on metapopulation dynamics, where the success of populations in each cell is highly dependent on interaction (i.e. additional seed input) with populations in other cells. While dispersal does deliver seed to a relatively large area (Figure 6.5) populations in these cells have a relatively low probability of persisting because of the relatively low rate of seed input. This is analogous to the dynamics of the closed systems examined in Chapter 5; the relative isolation of these outlying populations means that seed input from external sources is lower, making it less likely that the local population will reach the threshold density necessary for persistence, reducing it's chance of success. This difficulty is compounded by the fact that even an adult is able to establish and begin to produce seed, the seed input to the local population will be reduced below the input seen in the closed system from Chapter 5 as a result of dispersal. However, as these simulations are stochastic it is possible that this pattern could arise, and I would postulate that such a response could be troublesome for control efforts in practice, as the invasion would be widespread and possibly difficult to detect.

6.4.2 Effect of landscape configuration on invasion success

Heterogeneous mixtures

Previous investigations have shown that the amount of suitable habitat present in the landscape can have a disproportionate effect on population size (Schumaker et al. 2004). Research suggests that decreasing suitable habitat will result in the landscape-level population decreasing proportionally down to a threshold value. A diverse range of studies using different approaches all result in similar approximations that this threshold value is typically found when 30 to 40% (Andren 1994 and references therein, King & With 2002; Fraterrigo et al. 2009). Below this threshold, the reduction in the contiguity of suitable habitat becomes an impediment to population growth, and the falloff in population success deviates from being directly proportional, and instead begins to outpace the rate of habitat loss. The various patch landscape configurations used in these simulations represent heterogeneous mixtures of two different habitats, and (based on the performance in the corresponding homogeneous landscapes) were comprised of between 50 to 95% of habitat which appears susceptible to invasion. Given that the proportion of suitable habitat in these landscapes exceeded the 30 to 40% cutoff found in other studies, I hypothesised that the reduction in population size of simulations of *H. lepidulum* in these landscapes would be proportional to the reduction in the amount of suitable habitat (Equation 6.11). However, simulations in these patch landscapes substantially underperformed their projections (Figure 6.6). This was particularly surprising as the

habitats in these landscapes are not differentiated as suitable or unsuitable, but reflect a more subtle variation, which I hypothesised would lessen the negative effects of landscape configuration on population success. Instead, I thought using this continuous gradient of variability used to differentiate habitats in these simulations would mean that the amount of 'suitable' habitat would have to be reduced below the 30 to 40% threshold described above before a disproportionate effect of habitat abundance would be seen on the final population size; instead, a disproportionate effect was observed even though these landscape reflect a higher proportion of suitable habitat.

Just as the amount of suitable habitat can influence population success, so can the spatial distribution of that habitat. In general, the size and spread of a population of organisms tend to benefit from the aggregation of suitable habitat (King & With 2002; Pearson & Dawson 2005). The effect of the spatial distribution of suitable habitat is manifested in two primary mechanisms; first, the distribution of suitable habitat within the landscape affects the ability of the organism to reach and colonise new habitat. In the simulations of *H. lepidulum*, I tested the effect of aggregating habitat by constructing using two landscapes which either reflected a random distribution of suitable habitat (Scrub/Tussock I) or an aggregated distribution (Scrub/Tussock II). These two landscapes were otherwise identical in terms of the proportion and suitability of the different habitats. Simulations of *H. lepidulum* in these landscapes revealed that the spatial configuration of these habitats does not significantly affect either the proportion of the landscape invaded, or the furthest extent of that invasion (Table 6.1, Figure 6.4). However, both of these landscapes contain relatively high amounts of suitable habitat (50%) compared to the 30 to 40% cutoff described above. With such a high proportion of the landscape classified as suitable, randomly distributing the suitable locations means that they are not likely to be completely isolated from other suitable cells. This, combined with the relatively high dispersal ability of the organism (relative to the grain or resolution of the landscape) means that the organism is likely to be able to reach the majority of locations with at least a small number of disseminated seed.

The second mechanism by which the spatial distribution of habitat influences the success of a population is by having an affect on the functional connectivity of different locations. This connectivity dictates the ability of locations to exchange individuals. Results from the previous chapter demonstrated that an effective network of sub-populations connected via the dispersal of individuals (a complete system) is more successful than if the subpopulations were not connected (a closed system). Therefore, while a single dispersal event may establish a viable population in an isolated location, the lack of continued propagule exchange can effectively stunt the growth of that new populations. In the simulations of *H. lepidulum*, we can see that even though population size tends to fall short of the projected estimates, the simulations come quite close to the projected occupancy rate of cells (Figure 6.7). This suggests that even though the dispersal abilities of *H. lepidulum* allow it to occupy a large proportion of the landscape, the discontinuity of the landscape that result from heterogeneous representation of the landscape effectively inhibits the regular exchange of individuals between sub-populations to the extent that population growth is negatively effected. While the range of the dispersal process means that exchange of propagules is still possible between non-adjacent locations, the probability of these exchanges (based on the dispersal kernel) is so low that it can result in the functional isolation of a sub-population. This functional isolation has a similar negative effect on population growth as observed in cases of absolute isolation (Gustafson & Gardner 1996; Flather & Bevers 2002; Pearson & Dawson 2005; Fraterrigo et al. 2009; Kinezaki et al. 2010).

Linear features

The inclusion of riparian corridors in the landscape produced mixed responses from the simulated invasions. Simulations outperformed projected population sizes only in the landscapes with the wider 90m strip of alpine creek habitat, suggesting this was the only landscape in which the invasion benefited from the presence of a corridor (Figure 6.6). This benefit seemed to be largely derived from increased occupancy in the corridor (Figure 6.7); however the relatively low occupancy level in the homogeneous alpine creek habitat simulations (Figure 6.4, Table 6.4) means that the expected contribution from this habitat was quite low, and therefore relatively easy to exceed. The increased total amount of area in the 90m (vs. 30m) alpine creek corridor compounded this effect. In the simulations in these landscapes, the occupancy rates within the alpine creek habitat was between two and three times higher than the simulations in the homogeneous alpine creek landscape (data not shown). This increased level of occupancy is most likely a result of populations within the more suitable tussock habitat providing additional propagule supply to the alpine creek habitat. This additional propagule input allows the population within the alpine creek habitat to either maintain a sink population (Pulliam & Danielson 1991) or overcome Allee effects that may be hindering establishment (Keitt et al. 2001; Taylor & Hastings 2005).

While the inclusion of a corridor of forest creek habitat increased population sizes beyond that of the corresponding corridor-less landscapes, these populations did not exceed their projected levels, and in fact tended to under-perform them. Looking more closely, the occupancy rates in these landscapes were close to the projected levels (Figure 6.7), but the density of individuals within those cells was lower than expected. Given that the initial introduction of H. lepidulum offered equal access to all habitat types and these simulations did not incorporate habitat-specific variability in dispersal, the only plausible explanation for this reduced performance is to consider that the variability between the demographic processes of the different habitats results in a desynchronisation of populations between the different habitats, resulting in the two habitats becoming effectively isolated from one another. Variation in environmental conditions experienced in different habitats has been observed to affect the importance of different transition stages within the lifecycle, and potentially result in asynchronous population dynamics within a species (Oliver et al. 2010; Harris et al. 2011). In addition, the sensitivity analyses in Chapter 2 do suggest that populations in at least some of the habitats are largely shaped by the success of different life stages. What is unclear is if this difference is substantial enough to permanently reduce the landscape level capacity of *H. lepidulum*, or if the under-prediction is more indicative of the landscape heterogeneity producing a lag in population growth, as noted in other investigations (Schreiber & Lloyd-Smith 2009). While these simulations did not directly monitor the interactions or synchronicity of populations between different habitats, this represents the most plausible explanation for the phenomenon observed here.

6.4.3 Overall effect of landscape configuration on invasion

The results of these simulations help to confirm that the spatial configuration of habitats within a landscape can have a significant on invasion success. In general, it appears that increasing landscape complexity can affect the dynamics of spread in a number of ways. First, including a finer classification of habitat-specific suitability into the landscape has the obvious effect of reducing the potential extent and size of the invasion. Identifying and quantifying this variation in invasive success, and incorporating it into landscape classifications can significantly improve the accuracy of spread predictions. Secondly, the spatial distribution and juxtapositioning of these habitats also has an important effect on the success of the population. These aspects can influence the continuity of the landscape by providing barriers and/or corridors for movement. In addition, habitats with different demographic dynamics can also produce a range of interactions, which can include source-sink dynamics, rescue effects, and Allee effects; all of which is greatly influenced by the spatial configuration of the interacting habitats, and can have an substantial influence on the functional isolation of adjacent populations.

These results also highlight a number of important considerations when investigating landscape level population performance. First, it is important to distinguish between the spatial extent of the population (occupancy in this analysis) and the overall population size. This distinction is not always clear, and the two are often handled interchangeably. Secondly, it is important to distinguish between the absolute spatial isolation of locations (which precludes it being reached by dissemination of propagules), and the functional isolation of locations (which severely limit the exchange of individuals, and the interdependencies which provide a demographic boost in complete population structures). Thirdly, when evaluating isolation, it is important to do so in the context of the scale of the dispersal mechanism. While any given location in a rasterised landscape may be surrounded by unsuitable habitat, the resolution of the landscape may be such that this perceived isolation may be effectively nil when the dissemination abilities of the organism are taken into account (i.e. Wiegand et al. 2005).

Throughout this investigation, I have attempted to be as thorough as possible; however, there are three elements of spread dynamics in this system that were not addressed. First, any habitat-specific variation in seed dispersal has been omitted due to logistical constraints. This phenomena could potentially also have significant impacts on spread patterns. Part of the contention with corridor features is whether they enhance the physical movement of individuals, as opposed to just providing additional suitable habitat (Christen & Matlack 2006; Hoyle 2007; Andrew & Ustin 2010). The results of this investigation suggest that the influence of demography alone does not appear to increase invasion success, although different results would be obtained with corridors providing the only suitable habitat in an otherwise unsuitable matrix (Kinezaki et al. 2010). Dispersal has been observed to vary according to different habitats within a landscape (King & With 2002, Chapter 3), and that influence in heterogeneous landscapes would be the next logical step for investigation. Secondly, the presence of scree slopes which occur in this landscape was not included in the modelled landscapes. The reason for this is largely pragmatic; the seed sowing trials were not performed in these habitats, and while the invasion would most likely not take hold in these areas, I have no data to support that conclusion. As the investigations within this thesis have already dispelled some of the preconceptions held about the invasibility of different habitats in these landscapes, I would have a hard time assuming suitability of other habitats. In addition, the conclusions would not likely be significantly different than in the landscapes explored with the relatively uninvasible scrub habitat. Third, an assumption was made that the boundary conditions were to be absorbing, meaning that any seed dispersed beyond the extent of the landscape was assumed to be lost. This assumption fits with the nature of the landscape being investigated, as the lower elevation to the south (bottom in Figure 6.5) consists of an anthropogenically modified habitat and the other directions lead to (presumably) uninhabitable ridge tops typified by exposed rock; seed dispersed to any of these locations is presumably lost. However, other assumptions about the boundary conditions (reflective or toroidal) would increase seed input to the system, and serve to increase the success of the invasion.

6.4.4 Management implications

This study has produced a number of broader implications that can be applied to the planning of management activities. First, it is important to make a distinction between the extent and severity of invasion. These are often handled interchangeably in the literature, but represent fundamentally different mechanisms. The results of this study show that the extent of spread predominately corresponds with other patterns reported in the literature, but the severity (in terms of population size) tends to lag. The severity may catch up to extent in temporal extents beyond those examined here, but this may be an important distinction when optimising the use of limited resources. This means that continued monitoring may be necessary to identify any potential future flare-ups that may occur.

Secondly, while nascent foci and satellite patches have been identified as significant contributors to spread (Moody & Mack 1988; Andrew & Ustin 2010), it is important to realise that in certain conditions, these spatially disjunct introductions may suffer from isolation effects, and will not necessarily expand at the same rate as a spreading front of a well-established population. At the same time, these cannot be completely overlooked, as individuals with high survival (as many invasive species do) may endure for long periods under harsh conditions (Fraterrigo et al. 2009), patiently waiting for their opportunity to spread. This can be particularly relevant if managers assume that successful control requires targeting only the easily invaded habitats (i.e. forest creeks). If left unchecked, it is possible for small local populations to persist in some of the less suitable habitat, from which they could recolonise locations where control efforts had been applied. Given the relatively fast falloff of dispersal probability away from the source, I would predict that constructing a buffer area that extends 50 metres around those invasible habitats where control efforts were applied would be extremely effective at preventing any recolonisation from local sources. However, extreme long distance dispersal events (potentially from a variety of vectors, including humans) could reintroduce seed to these areas; as such, these areas must be diligently monitored in order to ensure total success.
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Chapter 7

Conclusion

7.1 Introduction

This objective of this dissertation was to develop and apply simulation tools in order to examine how heterogeneity in the landscape influences the invasion of *Hieracium lepidu*lum (Stenstroem) Omang (Asteraceae) into montane valleys of the Craigieburn Range in Canterbury, New Zealand. Previous work in this system has suggested that the progression of the invasion is significantly impacted by the habitat-specific variation in invasibility within the landscape. Analysis of these data from field surveys and initial results from a seed sowing trial indicated that the riparian stream corridors were potentially acting as vectors for the invasion, transporting *H. lepidulum* through an otherwise inhospitable barrier of mature forest, and allowing the invasion to reach the alpine habitats found at higher elevations (Miller 2006). Following this initial analysis, the seed sowing plots continued to be assessed annually over the following four years. The continued data collection expanded the initial data set to reflect a more complete picture of the full lifecycle of *H. lepidulum*. With these new data, this current project was initiated in order to evaluate if the development of a more sophisticated model of plant spread reflecting the entire life cycle (now possible with the expanded dataset) would produce qualitatively different predictions to the previous analysis.

To address this question, I used an incremental approach to develop a spatial-demographic model of *H. lepidulum*. To this end I focused on the development of sub models to represent the processes of dispersal and demography, two of the primary drivers of invasion dynamics (Neubert & Caswell 2000; Jongejans, Skarpaas, & Shea 2008; Coutts et al. 2010). Using this incremental approach allowed me to develop and analyse models representing these two major components independently, and evaluate the potential influence that each process would have on spread dynamics. A large portion of this dissertation is devoted to the development and analysis of quantitative models for both of these processes, developed using empirical data collected from field studies. The two models were then combined using a customised software package in order to provide a detailed spatial-demographic

simulation of invasion spread, which I then used to analyse and predict the expected dynamics of spread during an invasion of H. lepidulum. While the objective of this was to provide insight and understanding of the dynamics of the current invasion, a number of more abstracted theoretical questions regarding invasive spread were posed at the onset of the study that this model was used to address as well. These questions are as follows;

- 1. How does the inclusion of spatial interactions alter demographic dynamics within the population?
- 2. How does spatial heterogeneity in landscape structure influence demographic performance?
- 3. How does spatial heterogeneity in landscape structure influence invasive spread?

In this chapter I begin by discussing what the results of this study imply specifically for the spread of *H. lepidulum* into the catchments of the Craigieburn range in New Zealand, and how this approach is fundamentally different to other predictions of spread dynamics in this system. Following on, I will examine how this model of *H. lepidulum* spread addresses the three more generalised questions regarding general spread processes, and examine how the findings fit within the context of other similar studies. In addition, during the course of addressing these specific questions, this investigation produced a number of general theoretical implications and observations regarding the modelling of populations. These theoretical implications are discussed in more detail following the discussion of the three primary objectives.

7.2 Projecting *H. lepidulum* invasion

Combining the model describing the dispersal of H. lepidulum (Chapter 3) with the demographic model representing the entire life cycle (Chapter 2) to examine the invasive spread of H. lepidulum revealed that the dynamics of the invasion are more complicated than were suggested by analysis of either just the recruitment data (Miller 2006) or by examining the individual components of dispersal and growth on their own. The initial hypothesis regarding the spread progression in these landscapes was derived predominately from analysis of recruitment rates in the different habitats obtained from the seed sowing trials (Miller 2006). With the availability of additional data, my first step was to extend this initial analysis to produce a matrix-based demographic model which reflected the entire life cycle of H. lepidulum (Chapter 2). Separate parameterisations of this model were developed for each habitat within the landscape; using these models I projected the growth of populations in each of these habitats. These projections were then used to compare the relative invasibility of the different habitats to H. lepidulum based on the long term sustainable population size in each one. The results of these projections were largely the same as the those produced using just recruitment data and field surveys. This result was not entirely surprising, as the sensitivity analysis of the matrix model indicated that recruitment was an important component in determining population size; this step in the lifecycle has been observed to strongly influence the long-term viability of other plant species as well (Sletvold et al. 2010; Cipriotti et al. 2012). In the end, I found the predictions obtained from projections of the matrix demographic model largely reaffirmed the original hypothesis that the invasion is reliant on the forest creek corridors to gain access to the alpine habitats.

The agreement between the recruitment assessment and the matrix model projections led me to believe that the same patterns of invasibility would be observed even after expanding the matrix model to include dispersal. Dispersal is often considered to be the primary determinant of the overall speed of invasion (Coutts et al. 2010; Harris et al. 2011). As such, the development and inclusion of the dispersal functionality was primarily intended to provide a way to compare the speed of spread in different habitats. While the addition of dispersal did allow me to evaluate the spread of the invasion, it also had the unintended effect of creating a significant impact on population dynamics as well. This effect was largely driven by the newfound ability of local populations (individual cells in these simulations) to exchange propagules between other local populations, creating an interlinkage between them (Hixon et al. 2002; Cowen & Sponaugle 2009). This added an additional dimension to the demographic processes, and allowed the simulation to incorporate a new suite of dynamics that utilised these interlinkages, much like those found in metapopulation dynamics. The end result was that projections of population growth no longer suggested that any of the habitats were entirely resilient to invasion; instead the projections show the landscape is best described by a gradient of invasibility ranging from 'minimally invasible' to 'heavily invasible'. One of the most substantial changes came in the forest habitat, which was previously considered to pose an impermeable barrier to invasion, but the simulations suggest this habitat is in fact capable of supporting sustained populations of *H. lepidulum*. The results from combining the dispersal and demographic models highlight just how important spatial processes and relationships are to demographic processes, and how the local populations can be heavily dependent on interactions with other local populations. The addition of these dynamics substantially altered the findings of the two previous models of invasion, which both suggested that the forest creek corridors offered the only access to the alpine areas.

While this more subtle delineation of the invasibility of different habitat provides a more refined approximation of how we can expect H. lepidulum to perform, it also complicates the implications for management. The previous analyses suggested that the only way H. lepidulum could access the higher elevation habitats was via the forest creek habitat. This fit with the behaviour of other systems, where linear strips of riparian habitat are often more invasible than the surrounding matrix, and have been shown to act as transport corridors for invasions (Planty-Tabacchi et al. 1996; Hood & Naiman 2000; Es-

chtruth & Battles 2011). This type of situation is relatively ideal for management, as the restricted extent of this habitat forms a natural bottleneck, creating an well defined target for the effective application of control efforts. In that situation, it was clear that control efforts targeting this habitat could be quite effective at preventing H. lepidulum from reaching the higher elevation habitats. However, the spatial-demographic model reveals that the invasion is not constrained to these riparian areas, and that patches of H. lepidulum are capable of establishing self-sustaining populations in the surrounding matrix of forest habitat. The forest creek habitat remains the highest priority, as it is still projected to be the most invasible habitat, able to support a substantial number of individuals as well as potentially acting as a vector of spread (Christen & Matlack 2009; Andrew & Ustin 2010). Now, however, the long-term effectiveness of targeting only this habitat with control efforts is reduced, as populations of *H. lepidulum* that persist in the forest habitat could continue to supply propagules and re-establish the invasion following removal efforts in the forest creek corridors. To further complicate the dynamics, the establishment of populations in the forest habitat is relatively rare and sporadic, making it nearly impossible to predict where within the forest habitat the populations are likely to establish, further compounding the difficulty of control efforts. However, the analysis of dispersal in Chapter 3 suggests that the vast majority of dispersal events do not travel more than 10 metres, suggesting that extending the control efforts at least 10 metres into the surrounding forest would include a large percentage of the seed rain that occurs outside the riparian area, helping to reduce the amount of area that would need to be targeted for control efforts. While this would not address the low probability long-distance events that establish patches of *H. lepidulum* further into the forest interior, it may sufficiently reduce the invasion to levels which can effectively managed through continued periodic treatment (Simberloff 2009). Such an approach which which focuses more on controlling the impacts and less on complete eradication may prove more economically viable (Rejmánek & Pitcairn 2002; Epanchin-Niell & Hastings 2010).

7.3 Questions from the introduction

7.3.1 How does the inclusion of spatial interactions alter demographic dynamics within the population?

One of the initial objectives of this dissertation was to explore if the incorporation of spatial processes has a significant influence on demographic projections of *H lepidulum*. It is has been generally identified that the local demography can influence landscape-level spread dynamics (Skellam 1951; Okubo 1980; Kareiva 1983). We also know from investigations of metapopulation dynamics that the local demographic processes of spatially distinct sub-populations can influence each other through the flow and exchange of individuals (Hanski 1991; Wells & Richmond 1995; Wiens 1997; Freckleton & Watkinson

2002). However, it is often presumed that population dynamics within a homogeneous and contiguous area are simply an extrapolation of local processes applied at a larger scale (Freckleton & Watkinson 2002), and there is relatively little work that examine how these local populations interact via dispersal in continuous space, how these interactions within the continuous space can influence the local demographic dynamics, and whether these dynamics are relevant in influencing the overall extent and severity of the invasion.

More recently, the inclusion of detailed components or sub-models describing both demography and dispersal in invasion models has become more prevalent (Jongejans, Shea, et al. 2008; Miller & Tenhumberg 2010; Harris et al. 2011; Caplat et al. 2012). While this approach in and of itself is not inherently novel, the more closely these approaches are utilised and scruitinised, the more clear it becomes that dynamics of an invasion typically do not result from just the additive effects of these two mechanisms, but emerge as a result of their interactions. The importance of incorporating these interactions are highlighted in Chapter 5, which emphasises the strength of the influence that dispersal processes have on local population dynamics. The results from that chapter illustrate how dispersal facilitates a transition from high density localised invasions to become more sparse and widespread. This effect has been largely examined from the perspective of the individual, particularly how dispersal allows propagules to escape local density-dependent effects (Howe & Smallwood 1982; Nathan & Muller-Landau 2000), and even how species respond in an evolutionary manner by emphasising dispersal characteristics (Travis et al. 2009; Phillips et al. 2010). While these individual-level processes are relatively well studied, the simulations from Chapter 5 illustrate how the interaction of dispersal and demography can affect the local population. Levels of population success (i.e. density) are important at local levels, as the density in a location is often correlated with the level of the impact of the invasion (Yokomizo et al. 2009; Epanchin-Niell & Hastings 2010). In this analysis these dynamics arose as an emergent property of the system as a result of the interaction of the dispersal and demographic mechanisms, although such mechanisms could be approximated user simpler models, as long as the expected behaviour is clearly defined.

As previously noted, a close analogue to the dynamics of the interacting local populations can be found in metapopulation dynamics, where the exchange of individual between spatially distinct groups has been found to have a significant impact on the local dynamics (Brown & Kodric-Brown 1977; Hanski 1991; Eriksson 1996). However, by using the approach described here, and removing the requirement that the local populations exist as spatially distinct entities (Wells & Richmond 1995; Freckleton & Watkinson 2002), we can apply these dynamics at a finer grain across a more continuous landscape. The benefit of this approach is that it permits the grain of the model to reflect the the scale of local processes that affect demography (i.e. density dependence), while dispersal (operating at a different scale) can be superimposed on top, allowing the local populations to exist in a continuous interconnected network. The importance of incorporating both scaledependent mechanisms are clearly demonstrated in Chapter 5, and the results comparing the open and closed model structures highlight just how significantly incorporating both mechanisms influences the predicted outcomes.

7.3.2 How does spatial heterogeneity in landscape structure influence demographic performance and spread?

While initially the influence of spatial heterogeneity on the demographic performance and spread of the invasion was posed as two separate questions in the introduction, the interactions between the two render them so interlinked (as described in the previous section) that I found it more sensible to address these influences together. As discussed above, the spatial dynamics of a population can be extremely influential even in homogeneous settings; these dynamics are further complicated by applying them in heterogeneous landscapes where both the suitability and spatial distribution of different habitats is variable. This landscape-level heterogeneity results from a combination of the underlying mechanistic processes that determine the distribution of habitats within the landscape, and the differential suitability of those habitats from the perspective of the specific organism. The interaction of these processes result in different patterns of fragmentation as perceived by the organism in question. This fragmentation can affect the population dynamics of a species via three primary mechanism; either by reducing the total amount of suitable habitat available to a species through conversion to a different habitat type (Andren 1994; Fahrig 2002; Herrera & García 2010), reducing the connectivity of suitable habitat (Tallmon et al. 2004; Noel et al. 2006; Dornier & Cheptou 2012), or by creating edge effects, where the proximity to the edge of a habitat results in altered environmental conditions within a habitat (Murcia 1995; Aguilar et al. 2006; Watling & Orrock 2010). Currently there is no evidence to suggest if or how the performance of *H. lepidulum* varies in relation to distance to the habitat edge; I therefore made the simplifying assumption that abiotic conditions are equivalent throughout the entirety of the habitats. Instead, my analyses focused on comparing how the availability and connectivity of suitable habitat influences the dynamics of *H. lepidulum* populations.

I simulated the invasion of *H. lepdiulum* in homogeneous landscapes of each habitat in the study area, along with a range of different heterogeneous mixtures and configurations designed to represent the defining characteristics of the existing landscape. I utilised four different metrics of spread to assess the dynamics of these simulations; population size, occupancy rates, local densities, and spatial extent. In order to assess how these metrics were influenced by the specific landscape configurations, I developed a baseline of projections which estimated the metrics assuming that the spatial configuration of the landscape had no effect. I accomplished this by assuming the invasion in a specific habitat would perform the same as in a homogeneous landscape, simply scaled down based on the proportion of landscape in each habitat (see Chapter 6 for specific details). Similar research examining spread in heterogeneous landscapes has concluded that when a minimum of 30 to 40% of the landscape is considered suitable to a species, population performance is likely to scale with the amount of available habitat, and not suffer losses in performance due to connectivity constraints (Andren 1994; King & With 2002; Fraterrigo et al. 2009). Below this threshold, the lack of connectivity compounds the lack of available growing space, and the decrease in performance accelerates. The heterogeneous landscapes used in the simulations (designed to reflect the primary features of the real landscape) were all comprised of more than 40% suitable habitat (based on suitability estimations from Chapter 5), leading me to hypothesise that connectivity would not limit population performance, and that the projections based on the compositional makeup of the landscape would provide a good approximation of the simulated performance. However, the agreement between the projections and the simulations was mixed; the spatial extent of the population (in terms of either the occupancy or extent) was well predicted by the projections, and was generally in agreement with the simulations, suggesting that the spread of the invasion was not compromised by the connectivity of the heterogeneous landscape configurations examined here. In comparison, the measures of population size at both the landscape (total population size) and local (mean density) scales were significantly lower in the simulations compared to the projections, revealing that the landscape configurations examined here had a much greater impact on the severity of the invasion compared to the invasion extent.

These results exemplify how the connectivity of the landscape can have a differential effect on the underlying mechanisms which determine the extent and severity of an invasion. Previous work has illustrated that connectivity is able to affect the ability of invasions to reach and establish at a location (Jules et al. 2002; Florance et al. 2011). However, the variable nature of seed dispersal means that connectivity (in terms of the continued exchange of propagules) does not exist as an absolute yes or no attribute, but instead is better reflected as the potential level of exchange between locations. Even between areas with very little connectivity, there is usually a small chance that a single dispersal event could occur between the locations. Such a singular event is all that is needed for successful establishment, and subsequent increase in the absolute spatial extent of the population (i.e. spread) (Moody & Mack 1988; Clark et al. 1998). This is particularly applicable in the case of apomictic species such as *H. lepidulum*, which have the potential to establish a viable population from a single nascent individual. However, while a minimal level of connectivity between locations can allow for establishment events, the frequency of propagule exchange between the locations may be low enough to the point where the exchange is functionally non-existent (Ferreras 2001; Kadoya 2009). As evidenced by the results of Chapter 5, this exchange between populations can have a significant effect on the viability and size of the local population, directly influencing the severity of the invasion at a given location. While extent and severity have already been recognised as being largely shaped by separate mechanisms (Coutts et al. 2010; Harris et al. 2011), this example illustrates how the structure of the landscapes and its associated connectivity can differentially affect those mechanisms, and independently affect the extent and severity of an invasion.

The only caveat is that it is possible that this underperformance in population growth may represent only a transient lag in population performance as opposed to a more enduring resistance of the landscape (Crooks et al. 1999; Frappier et al. 2003; Catford et al. 2009). The dynamics observed here could be indicative of a secondary lag, where long distance dispersal events from the initial introduction provide a rapid increase in extent, while local growth is delayed until the populations reach a reproductive state in which they can supply an increased the local density requires a more local and substantial seed input (Wangen & Webster 2006). It appears that the spatial expansion of the population of *H. lepidulum* is achieved by a relatively small number of long distance dispersal. This period of rapid expansion of invasion extent would then potentially be followed by a more gradual 'filling in' of occupied area as the local populations continue to grow and approach their full reproductive capacity.

Additionally, refinement of the dispersal component of the simulation could significantly affect on the rate at which the invasion achieves the observed levels of extent. While variations between the dispersal kernels of different habitats appeared minimal, their differences were statistically significant. The propagation of these differences across an entire landscape could result in substantial differences in spread, and could affect the influence of specific landscape configurations (i.e. increasing dispersal distances in suitable habitats may increase the importance of that habitat to landscape level spread; Hoyle 2007; Andrew & Ustin 2010. In addition, this examination assumes that the seed are dispersed only via their standard means (wind); incorporating any additional dispersal vectors such as animals or humans that may be transporting seed could have a significant impact on the overall invasion dynamics (Higgins et al. 2003; Crespo-Pérez et al. 2011).

7.3.3 Additional implications

In total, the invasibility of the different habitats in this landscape has been compared using three different approaches; first, by comparing the initial recruitment levels (Miller 2006), then by evaluating non-spatial demographic models which incorporate the entire lifecycle (Chapter 2), and finally by evaluating those same demographic models in a spatial context by pairing them with dispersal models (Chapters 5 and 6). In each case, the approaches were based on largely the same data set, and in each case projections of these models produced different conclusions. This serves as an excellent example of how the choice of the specific method used to analyse and interpret a phenomenon can significantly impact the outcome, and highlights the importance of choosing a method which accurately reflects the suite of mechanisms responsible for the observed process. In order to alleviate some of this risk, I used a bottom-up approach to develop the simulations, similar to the application pattern-oriented modelling (Grimm et al. 2005; Railsback & Johnson 2011), where I first identified those mechanisms which appeared to be primarily driving the dynamics of the system (in this case demography and dispersal), and then constructed and validated submodels of those processes before combining them in the final application. In an effort to minimise the effect of my own bias and allow for the influence of different mechanisms to be present (or not) in the the demography sub-model, I began by constructing a minimal model framework that included those mechanisms without explicitly defining their strength or interdependencies a priori. Instead, these aspects of the mechanisms were modelled as latent variables, which allowed the strength and direction of the mechanisms to be dictated by data collected from the field. For example, I developed a generic model framework to describe the survival of juveniles amongst the different ages of *H. lepidulum* which contained parameters to describe the strength and direction of density dependence. These parameters and their uncertainty were estimated for each unique combination of age and habitat, producing individualised measures of density dependence for each life stage in each habitat. This allowed the response to be flexible and predominately driven by the data, and the result was that the strength, direction, and variability of the density dependence was unique for each transition. This type of approach can be extremely useful in cases such as this where a variety of mechanisms may or may not be having an effect on the final outcome, but omitting them from the model (and removing the potential for their influence) is not desirable. This is especially useful for applications such as this, where I wanted to apply the same model form to produce different transition probabilities between ages and habitats, and the effect of a particular mechanism might only be relevant in a subset of these situations. In addition, properly capturing and incorporating the range of responses provides a much more robust and realistic approach than would otherwise be possible.

The approach of defining the strength and direction of these mechanisms as latent variables and estimating their values and associated uncertainty using data collected from the seed sowing trials was made more accessible through the use of a hierarchical Bayesian approach to parameterise these models (Clark 2005; Latimer et al. 2009). This approach increases the fidelity of parameter estimation by not constraining it to a standard distribution which is determined *a priori*, but instead produces an empirical distribution, the characteristics of which (i.e. magnitude, frequency, and direction of deviation from the mean) are determined by the iterative fitting of the model to the data during the parameterisation process (Clark 2003). Incorporating this type of parameter estimation into the simulations helps to remove some of the opportunity for researchers to inject bias into their models (i.e. constraining a parameter to adhere to a predetermined distribution); bias which on the surface may seem small, but propagated throughout the simulation can have a significant effect (Finley et al. 2011; Halstead et al. 2012). The hierarchical Bayesian approach to modelling has proven quite useful in this (and many other) applications, and while it is not the best answer for every situation, this dissertation serves as a good example that ecological researchers should at least be aware that a range of approaches exists for activities from model construction to parameterisation, and highlights the importance of selecting an appropriate method for their analysis. The more clearly we are able to formulate and quantify models of ecological processes, the more useful they will tend to be.

As previously mentioned, the models used to project spread dynamics in Chapters 5 and 6 are the result of a bottom-up construction approach to model building. In such applications, the top-level phenomenon of interest (in this case, spread dynamics) are described by synthesising a suite of sub-models that describe lower-level processes. My intention with this approach was to begin by construct the sub-models which represent relatively straight forward mechanistic processes, and their collective behaviour and interaction when combined should then reflect the top-level phenomenon. In this dissertation, the spread of *H. lepidulum* was deconstructed into multiple sub-levels; the overall spread model was the result of a combination of demographic and dispersal processes, while the demographic processes were further deconstructed into models reflecting transitions between life stages. In some cases these transitions were deconstructed even further, as in where total plant level seed production was deconstructed into independent models representing the number of flowers per plant, and the number of seed per flower. One important aspect of this approach is that the combination of these mechanistic sub-processes may not be a simply additive process, and interactions between the sub-processes may result in unexpected responses. This was certainly the case in Chapter 5, where the combination of the demographic and spatial components resulted in unanticipated spatial population dynamics.

The bottom-up approach is in contrast to the more common phenomenological (or topdown) approaches to modelling specific phenomenon, where mathematical functions are used to describe the patterns of the observed phenomenon, without regard to the underlying processes. Phenomenological approaches are generally simpler and faster to construct, however the bottom-up approach will generally lead to more robust solutions that can be applied outside the conditions for which they were developed, as long as the appropriate underlying mechanisms are incorporated (Grimm et al. 2005). This can be critical for simulation applications, such as in this dissertation. In this case I have not used a completely mechanistic approach, but have used a hybrid approach, developing phenomenological models for some of the sub-models. In fact this is often the case (especially in ecology) where reducing the problem to their most basic first principles is not usually a feasible option. Even so, these this type of bottom-up approach still helps to provide a deeper understanding of the complex phenomena by requiring the deconstruction and identification of the underlying processes that shape them. Just as with the hierarchical Bayesian approach to modelling, the approach of bottom-up modelling is not intended to be a 'one-size-fits-all' type of solution that can be applied in all situations. Again, however, it is important to stress the importance that it be identified as a potential option in the tool set available to the ecologist, as it can certainly be a useful approach if applied in the right settings.

Lastly, an important outcome from this analysis is the recognition that the classification of landscape heterogeneity into finer scales than the binary classification of suitable or unsuitable produces a much more complex dynamic, that is often necessary for understanding of invasion dynamics. Reducing the landscape to this binary classification may be the only option where data is limited, but the result is a very coarse approximation of the actual dynamics of the system. It is clear from this and other studies that the suitability of different habitats within a landscape is most appropriately measured along a gradient, and that simplifying the landscape to a binary response fundamentally changes not only the representation of the environment, but also the interactions of population processes that interact with that environment (Meekins & McCarthy 2002; Melbourne et al. 2007; Chytry et al. 2008). For example, improving the fidelity of this classification has been show to have implications on population stability (Hector et al. 2010; Oliver et al. 2010), life history (Harris et al. 2011), and metapopulation dynamics (Holle & Simberloff 2005; Warren et al. 2011). While refined classification of habitat suitability is becoming more common (Pitt et al. 2009; Fitzpatrick et al. 2012), it is still important and relevant to reiterate how improving the fidelity of this classification can translate to improved understanding of the dynamics under study. Just as with the hierarchical Bayesian and bottom-up approaches described earlier, it is important to make sure these choices and their implications are taken into consideration when planning data collection or analyses.

7.4 Future applications

While I have attempted to be as thorough as possible during this examination of the spread of *H. lepidulum*, the time investment dedicated to the development of the models and the software means that there remain a number of remaining aspects of spread dynamics that would be interesting to examine, that I simply did not have the time to include. While I am satisfied with the construction of the model representing the growth and spread of *H. lepidulum*, it could certainly benefit from a more extensive application. For example, it could be quite informative to investigate a wider range of landscapes, and extend the representations used here to more hypothetical configurations in order to examine how the invasion progression would behave in novel systems, and if there are some more generic conclusions that can be drawn relating the amount and configuration of suitable habitat to invasion success. This approach would also benefit by adjusting some of the demographic parameters, in order to ascertain how other species with different life history traits might respond to the same set of conditions. In addition, I think it would be useful to track the dispersal of individual seed in order to get a better idea of the magnitude of propagule exchange between locations, and how this exchange is influenced by the distance and connectivity constraints imposed by specific landscape configurations.

Lastly, while this model does a good job representing the mechanisms and functionality of the specific organism, this work completely disregards the role of humans in invasive spread. Humans can impact spread dynamics in a variety of ways, from influencing the spatial arrangement and distribution of the landscape (Ficetola et al. 2010; Vila & Ibáñez 2011) to acting as vectors of spread by transporting seed (Crespo-Pérez et al. 2011; Wichmann et al. 2009). With some additional work, both of these aspects could be incorporated into the simulations, and could potentially produce a richer and more informative story.

7.5 Conclusions

This dissertation makes use of a number of approaches which are under-utilised in ecological research, including bottom-up model building approaches, hierarchical Bayesian approaches to parameterising models, and detailed measures of habitat-specific suitability to simulate the spread of *H. lepidulum*. This combination of approaches produces a complex yet highly tractable simulation of invasive spread, which I have used to investigate a number of interesting aspects of invasion dynamics, including spatial population dynamics, and the effects of connectivity on the extent and severity of invasions. These findings can easily be applied elsewhere, both to investigate other invasive species, and can potentially be applied to examine population dynamics of non-invasive species as well. My hope is that the work done here helps to lay out some of the initial groundwork for future applications of simulations to investigate ecological processes. While this dissertation only begins to scratch the surface of what is possible using these approaches, my hope is that enlighten others to how they can provide a unique and enlightening window into complex systems and their associated dynamics.

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Appendices

Appendix A

Defining stochastic parameters in PopMod

This list describes the suite of predefined distributions which PopMod can utilise (via the SciPy library of mathematical tools for the Python programming language) to define stochastic parameter behaviour. The function call column lists the name by which that particular distribution is called. Arguments for the function are listed as well; those within brackets are optional. This list is modified from http://docs.scipy.org/doc/numpy/reference/routines.random.html where additional details regarding the different distributions and their arguments can be found.

Function Call	Arguments	Description
beta	(a, b[, size])	The Beta distribution over $[0, 1]$.
binomial	(n, p[, size])	Draw samples from a binomial distri-
		bution.
chisquare	(df[, size])	Draw samples from a chi-square distri-
		bution.
mtrand.dirichlet	(alpha[, size])	Draw samples from the Dirichlet distri-
		bution.
exponential	([scale, size])	Draw samples from the Exponential
		distribution.
f	(dfnum, dfden[, size])	Draw samples from a F distribution.
gamma	(shape[, scale, size])	Draw samples from a Gamma distribu-
		tion.
geometric	(p[, size])	Draw samples from the geometric dis-
		tribution.
gumbel	([loc, scale, size])	Draw samples from a Gumbel distribu-
		tion.
hypergeometric	(ngood, nbad, nsample[, size])	Draw samples from a Hypergeometric
		distribution.

Function Call	Arguments	Description
laplace	([loc, scale, size])	Draw samples from the Laplace or dou- ble exponential distribution with spec- ified location (or mean) and scale (de- cay).
logistic	([loc, scale, size])	Draw samples from a Logistic distribu- tion.
lognormal	([mean, sigma, size])	Return samples drawn from a log- normal distribution.
logseries	(p[, size])	Draw samples from a Logarithmic Se- ries distribution.
multinomial	(n, pvals[, size])	Draw samples from a multinomial dis- tribution.
multivariate normal	(mean)	Draw random samples from a multi- variate normal distribution.
negative binomial	(n, p[, size])	Draw samples from a negative binomial distribution.
noncentral_chisquare	(df, nonc[, size])	Draw samples from a noncentral chi- square distribution.
noncentral_f	(dfnum, dfden, nonc[, size])	Draw samples from the noncentral F distribution.
normal	([loc, scale, size])	Draw random samples from a normal (Gaussian) distribution.
pareto	(a[, size])	Draw samples from a Pareto distribu- tion with specified shape.
poisson	([lam, size])	Draw samples from a Poisson distribu- tion.
power	(a[, size])	Draws samples in [0, 1] from a power distribution with positive exponent a - 1.
rayleigh	([scale, size])	Draw samples from a Rayleigh distribution.
standard_cauchy	([size])	Standard Cauchy distribution with $mode = 0.$
standard_exponential	([size])	Draw samples from the standard expo- nential distribution.
standard_gamma	(shape[, size])	Draw samples from a Standard Gamma distribution.
standard_normal	([size])	Returns samples from a Standard Nor- mal distribution (mean=0, stdev=1).

Arguments	Description
(df[, size])	Standard Students t distribution with
	df degrees of freedom.
(left, mode, right[, size])	Draw samples from the triangular dis-
	tribution.
([low, high, size])	Draw samples from a uniform distribu-
	tion.
([mu, kappa, size])	Draw samples from a von Mises distri-
	bution.
(mean, scale[, size])	Draw samples from a Wald, or Inverse
	Gaussian, distribution.
(a[, size])	Weibull distribution.
(a[, size])	Draw samples from a Zipf distribution.
	Arguments(df[, size])(left, mode, right[, size])([low, high, size])([mu, kappa, size])(mean, scale[, size])(a[, size])(a[, size])(a[, size])