

**Legacies of *Pinus contorta* invasions drive ecosystem change
in short tussock grasslands**

Elise Aimee Arnst

A thesis submitted to
Auckland University of Technology
in fulfilment of the requirements for the degree of
Doctor of Philosophy (PhD)

2026

Department of Environmental Science
School of Science

Supervisors:
Professor Bradley Case
Professor Hannah Buckley
Dr Duane Peltzer

Thesis Abstract

Biological invasions are expanding worldwide, causing negative ecological impacts and economic costs. Plant invasions can alter ecosystem properties as well as biotic interactions, these effects may persist long after the invasive species has been removed, influencing ecosystem recovery. While the impacts of biological invasions and short-term outcomes following their management are widely understood, few studies have considered the long-term outcomes for plant communities. This thesis investigates how short tussock grassland communities in Te Manahuna / the Mackenzie Basin, New Zealand change following extensive invasion and management of the non-native tree species *Pinus contorta*. By combining space-for-time field observations with statistical modelling I show that soil and plant community legacies persist for at least 16 years following management. Native plant communities are influenced both directly by past invasion and indirectly through altered soil biogeochemistry and competition from non-native grasses. Trajectories are strongly shaped by the original invasion stage, with late-stage invasions resulting in simplified communities dominated by non-native species. By integrating plot-scale data with four decades of aerial imagery to assess invasion and legacy patterns across landscapes, I demonstrate that early management is critical for preserving native biodiversity, that invasion dynamics reflect propagule pressure, and that management outcomes vary with property-level management decisions. These findings provide useful insights for conservation management, informing decisions about the timing of invader removal and the need for additional management to achieve specific conservation goals.

Keywords: Invasion impacts, non-native species, exotic, conifer, wilding pine, *Pinus contorta*, legacy effects, retrospective analysis, weed control, management, succession, trajectories, plant communities, grasslands, dryland ecosystems, biodiversity, spatial ecology, aerial imagery, image classification, landscape scale

Table of Contents

Thesis Abstract	ii
List of Tables.....	v
List of Figures	vii
Attestation of Authorship	xi
Artificial Intelligence Declaration	xii
Co-Authored Works	xiii
Acknowledgements	xv
Chapter 1 General Introduction	16
1.1 Theoretical background.....	16
1.1.1 Plant invasion	16
1.1.2 Invasion across scales.....	20
1.2 Study system	21
1.2.1 Non-native pines.....	21
1.2.2 Tussock grasslands.....	22
1.2.3 Te Manahuna / Mackenzie Basin	24
1.3 Thesis outline	28
Chapter 2 Legacies of <i>Pinus contorta</i> Invasion Persist For At Least 16 Years Following Management.....	29
2.1 Introduction	29
2.2 Methods.....	30
2.2.1 Study area	30
2.2.2 Data collection.....	31
2.2.3 Data analysis.....	32
2.3 Results	34
2.3.1 Pine legacy effects on environmental conditions	34
2.3.2 Impact of historical pine invasion and management on plant communities.....	38
2.3.3 Reinvansion.....	45
2.4 Discussion	45
Chapter 3 Invasion Legacies of <i>Pinus Contorta</i> Drive Successional Trajectories of Short-Tussock Grassland Plant Communities.....	49
3.1 Introduction	49
3.2 Methods.....	50
3.2.1 Study area	50
3.2.2 Drivers of plant community change	51
3.2.3 Plant community plots.....	53
3.2.4 Long distance dispersal	55
3.2.5 Structural equation modelling	59
3.3 Results	60
3.4 Discussion	66
Chapter 4 Timing of Invasion Management Shapes Land Cover Trajectories Over Four Decades	70

4.1	Introduction	70
4.2	Methods	71
4.2.1	Study area	71
4.2.2	Image pre-processing and classification.....	73
4.2.3	Plant community data	75
4.2.4	Data analysis.....	76
4.3	Results	77
4.4	Discussion	83
Chapter 5 General discussion.....		86
5.1	Synthesis and novel contributions.....	86
5.1.1	Invasion legacies and drivers of plant community trajectories	86
5.1.2	Timing of invasion management.....	88
5.1.3	The importance of scale	89
5.1.4	Management implications post invader removal.....	90
5.2	Future directions.....	91
5.3	Conclusions	92
References		93
Appendix A Additional information for Chapter 2.....		107
A.1	Supporting Information	107
A.2	Supplementary Tables	108
A.3	Supplementary Figures.....	115
Appendix B Additional information for Chapter 3		119
B.1	Supplementary Figures.....	119
Appendix C Additional information for Chapter 4.....		123
C.1	Supplementary Tables	123
C.2	Supplementary Figures.....	130

List of Tables

Table 1.1 Summary information for five study sites within Te Manahuna / the Mackenzie Basin	26
Table 2.1 Generalised linear model comparisons showing differences in species richness and percent cover between native and non-native species at different historical pine invasion stages. Stars show significance * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$	39
Table 3.1 Hypotheses and predictions of the drivers of native plant communities used in structural equation modelling, and the potential pathways through which these mechanisms act.	52
Table 3.2 Parameters used in the WALD dispersal model to estimate relative propagule pressure for each plant community plot.	55
Table 3.3 Structural Equation Model (SEM) results for the model with native species community composition (NMDS 1) as the primary response variable	62
Table 3.4 <i>Post-hoc</i> pairwise comparisons of Structural Equation Model (SEM) results to show the significance of the different historical pine invasion stage in relationships that were significant in the overall SEM for both native plant community composition and species richness.....	63
Table 3.5 Structural Equation Model (SEM) results for the model with native species richness as the primary response variable.	65
Table 4.1 Modified land cover categories used to assess land cover change. For the image classification a larger set of classes based on the LCDB classification were used (Dymond et al., 2017). Classes were subsequently merged into categories of interest for data analysis.	74
Table 4.2 Aggregated confusion matrix showing accuracy assessment scores for the pixel-based image classification across all Areas of Interest (AOIs) and years	80
Table S2.1 Distribution of plots across historical pine invasion stages, and the length of time between when control was undertaken and plant community plots were measured.	108
Table S2.2 Results of a Principal Components Analysis (PCA) conducted to explain the relationships among key environmental variables. These statistics relate to Figure 2.3.....	109
Table S2.3 Plant species frequency (proportion of plots present) and mean cover when present (%) for species that are not rare (i.e. occur in >10% of plots, or have at least one occurrence with >1% cover). Species are sorted in descending order of frequency.....	110
Table S2.4 Results of pairwise comparisons between non-native and native species cover and richness between historical pine invasion stages. Stars show significance * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$	112
Table S2.5 Hierarchical Modelling of Species Communities (HMSC) model statistics for the native and non-native plant species models.	113
Table S2.6 Generalised linear model comparisons showing differences in proportional cover between historical pine invasion stages for different plant growth forms. Comparisons were calculated separately for non-native and native plant species.	114
Table S4.1 Details of aerial imagery used for the land cover classification.....	123
Table S4.2 Assignment of species to merged land cover classes; based on growth form, bio status, and habitat preference	124

Table S4.3 Overall image classification accuracy for each Area of Interest (AOI) and year of
aerial imagery 125

Table S4.4 Transition tables showing the pixels level change in land cover type (as a percentage
of the total number of pixels) between each time step of aerial photography for each of
the five Areas of Interest (AOIs)..... 126

List of Figures

Figure 1.1 Conceptual representation of invasion stages across spatial and temporal scales, with examples of scale-dependant filters that may influence any stage of the invasion process. The curved trajectory illustrates how invasion processes expand from local, early-stage events toward broader landscape through time. Impacts are displayed outside the trajectory because they can occur at multiple scales and stages. Based on Theoharides and Dukes (2007).	17
Figure 1.2 An example of <i>Pinus contorta</i> invading a short tussock grassland at Pūkaki Flat Conservation Area in the Mackenzie Basin, New Zealand.	23
Figure 1.3 Mackenzie Ecological Region, showing dominant land cover types based on LCDB v6 (Manaaki Whenua - Landcare Research, 2025a). Study sites are denoted by purple squares.	25
Figure 1.4 Photos of study locations show (top to bottom): an early stage invasion at Pūkaki; an intermediate stage invasion at Quailburn; a late stage, dense invasion at Irishman Creek.	27
Figure 2.1 General linear models for each of the key environmental characteristics, showing the relationship with historical pine invasion stage. Points differ in colour by historical pine invasion stage (green = early, yellow = intermediate, orange = late). The larger central point is the model estimated mean, error bars show 95% Confidence Intervals. Horizontal brackets are pairwise comparisons between historical pine invasion stage. Stars show significance * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$	35
Figure 2.2 General linear models for each of the key environmental characteristics, showing the relationship with time since management. For significant relationships ($p < 0.05$), the black line shows the predicted relationship, and the grey shading is the 95% Confidence Interval. Points differ in colour by historical pine invasion stage.	36
Figure 2.3 Principal Components Analysis (PCA) biplots showing how sampling plots (points) varied in their environmental characteristics (arrows). Plots are coloured by historical pine invasion stage, and their size is proportional to time in years since pine management was undertaken. All relationships shown are statistically significant ($p < 0.01$), and the length of the arrows is proportional to the strength of the relationship. The variance explained by each principal component (PC) is given as a percentage on the relevant axis. Plot a) compares the relationship between PC 1 and PC 2; b) the relationship between PC 1 and PC 3; and c) the relationship between PC 2 and PC 3.	37
Figure 2.4 Non-metric Multidimensional scaling (NMDS) ordinations for three dimensions, showing the distribution of species recorded in plant community plots. Plot a) shows axes 1 and 3; b) axes 1 and 3; and c) axes 2 and 3. Non-native species are pink and native species are turquoise. Point size is proportional to mean species cover when present. The names of the five most abundant species are displayed. Pine species were excluded from the analysis.	38
Figure 2.5 Distribution of (a) percent cover and (b) species richness across plots, categorised by the invasion stage of <i>Pinus contorta</i> at time of management. The horizontal line inside each box represents the median, the box spans the interquartile range (25th–75th percentile), and the whiskers extend to the smallest and largest values within $1.5 \times$ the interquartile range. Points beyond the whiskers are plotted individually as outliers. Horizontal brackets are pairwise comparisons between historical pine invasion stage for	

native species only. Stars show significance * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. There were no significant differences between historical pine invasion stages for non-native species. 40

Figure 2.6 Hierarchical modelling of species communities (HMSC) comparing the relationship between predicted native species richness and plot principal component scores (black line) with 90% confidence interval (grey shading). The measured plot values are shown as points are coloured based on historical *Pinus contorta* invasion stage. Plot a) shows the relationship with Principal Component 1 (positively associated with historical pine invasion stage, soil moisture and Olsen phosphorus; negatively associated with time since management, canopy openness and pH); b) Principal Component 2 (positively associated with available nitrogen and total carbon; negatively associated with Olsen phosphorus); and c) Principal Component 3 (positively associated with pH and Olsen phosphorous; negatively associated with time since management and total carbon)..... 42

Figure 2.7 Proportion of total plant cover for non-native and native species, by growth form in plots that varied in their historical pine invasion stage. 43

Figure 2.8 Hierarchical modelling of species communities (HMSC) results comparing the relationship between predicted species richness by growth form correlated with each of three principal components (solid lines), with 90% confidence interval (shading). Plots a-c) show predictions for native species for each of the principal components; and plots d-f) show predictions for non-native species for each of the principal components. 44

Figure 3.1 Structural Equation Model with potential pathways based on *a priori* hypotheses. Colours indicate causal mechanisms. Orange = direct pine effects, tan = soil legacies, dark green = reinvasion, olive = secondary invasion, pale blue = native plant community composition. 51

Figure 3.2 Principal Components Analysis (PCA) biplots showing variation among sampling plots (points) in relation to soil properties (arrows). Plots are coloured by historical pine invasion stage and their size is proportional to time in years since pine management was undertaken. All relationships shown are statistically significant ($P < 0.01$), and the length of the arrows is proportional to the strength of the relationship. The variance explained by each principal component (PC) is given as a percentage on the relevant axis. Plot a) compares the relationship between PC 1 and PC 2; b) PC 1 and PC 3; and c) PC 2 and PC 3. 54

Figure 3.3 Workflow for creating point locations of pine trees from aerial imagery. Training polygons were created in ArcGIS Pro, all subsequent steps were undertaken in R using the ‘terra’ package. 57

Figure 3.4 Structural Equation Model (SEM) diagram showing a) significant paths for the native Plant community composition (native NMDS) model; b) significant paths for the native species richness model. Stars show significance * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Arrow widths are proportional to the strength of the standard coefficient. The exception is invasion stage which has no standard coefficient, so linewidth is set at 1. Blue arrows indicate positive relationships, and red arrows indicate negative relationships. Model explanatory power for endogenous variables: Soil legacies ($R^2 = 0.43$), Non-native grass cover ($R^2 = 0.13$), Survivors ($R^2 = 0.27$), Native plant community ($R^2 = 0.80$), Native species richness ($R^2 = 0.56$). 61

Figure 4.1 Location map showing the Areas of Interest (AOIs), the plant community plots measured and within the Mackenzie Basin. Public conservation land is that owned by the Crown and managed for conservation purposes; the decade protected indicates when either the ownership or the reserve purpose changed.....	73
Figure 4.2 Pixel-based image classification within each of five Areas of interest (AOIs) at four timesteps. Land cover classification is based on merged LCDB types (Table 4.1).	78
Figure 4.3 Change in the abundance of land cover types through time, shown as the percentage of the pixels classified for each Area of Interest (AOI) at each time step based on the pixel-based image classification.....	78
Figure 4.4 Change in the percentage of the pixels classified as a) live pine and b) dead pine within the five Areas of interest (AOIs).	79
Figure 4.5 Comparison of image-derived and plot-derived land cover classifications for plant community plots measured in a) 1984 and b) 2022-23. The colour in filled circles is the plot-derived class, the colour of the border is the image-derived class.....	82
Figure S2.1 Location of study sites within the Mackenzie Ecological Region. Basemap sourced from ESRI/LINZ.	115
Figure S2.2 Total cover of non-native species in each plot compared to canopy openness (a measure of light availability). Lower light levels indicate standing dead trees or survival/reinvasion of live trees. Point colours show the historical pine invasion stage.....	115
Figure S2.3 Hierarchical modelling of plant species communities (HMSC) comparing the relationship between predicted non-native species richness and plot principal component scores (black line) with 90% Confidence Interval (grey shading). The measured plot values are shown as points colour coded based on historical pine invasion stage. Plot a) shows the relationship with PC 1; b) PC 2; and c) PC 3.	116
Figure S2.4 Hierarchical modelling of species communities (HMSC) variance partitioning showing the proportion of variation in plant species occurrence explained by each principal component and by the site-level random effect for a) native species; and b) non-native species.	117
Figure S2.5 Plant species responses to principal components, modelled using Hierarchical modelling of species communities (HMSC). Plot of beta parameters showing how species responded to environmental covariates represented by principal components for a) native species; and b) non-native species. Only coefficients where 95% of posterior samples were either > 0 or < 0 are considered supported. The heat map shows the magnitude (mean effect sizes) and direction (positive or negative) of each species' responses. The phylogeny indicates the relationship of plant species to family level.	118
Figure S3. 1 Non-metric Multidimensional scaling (NMDS) of native plant communities. Points are proportional to cover when present. The six most frequent and six most abundant species are labelled (<i>Festuca novae zelandiae</i> is the only species in the top six of both groups). This plot compares the relationship between NMDS axes 1 and 2.....	119
Figure S3.2 Example of point locations identified as pine trees derived from pixel-based image classification. Basemap sourced from ESRI/LINZ.	120
Figure S3.3 Comparison of percent cover of pine derived from supervised pixel-based classification with the propagule pressure metric calculated using a WALD dispersal	

kernel. Both metrics were derived using a 1 km radius buffer around the centre of the plant community plots.....	120
Figure S3.4 Pairwise relationships between variables included in the Structural Equation Modelling (SEM). The blue line shows the relationship predicted by the general linear model, and the grey shading shows the 95% Confidence Interval.....	121
Figure S3.5 Pairwise correlations among plant community metrics, including cover and richness, and bare ground. Points are the observed values, the blue line shows the fitted linear relationship, and grey shading shows the 95% Confidence Interval.....	122
Figure S4.1 Binary depiction of whether there was a change in classification of individual pixels between each time step of aerial imagery for each of the five Areas of Interest (AOIs).	130

Attestation of Authorship

I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person (except where explicitly defined in the acknowledgements), nor used artificial intelligence tools or generative artificial intelligence tools (unless it is clearly stated, and referenced, along with the purpose of use), nor material which to a substantial extent has been submitted for the award of any other degree or diploma of a university or other institution of higher learning.

Signed:

17 April 2026

Artificial Intelligence Declaration

<i>Specify the chapter number(s) in your research proposal/research component where AI was used.</i>		
Chapter number(s):	1, 2, 3, 4, 5	
<i>Briefly explain why the AI tool was used (e.g., idea generation, summarization, data analysis, image creation, etc.).</i>		
Purpose of AI Use:	AI tools were used for minor technical purposes only. Specifically, for editing of selected written sections to refine sentence structure or improve flow, and for debugging R code.	
<i>Clearly state the AI tools used.</i>		
AI Tool(s) Used:	Copilot for writing and ChatGPT for R code	
<i>Prompts or queries entered into the AI tool (only the instructive portion of the prompt is required). Include all relevant variations.</i>		
Prompts Used:	Please tidy this sentence/section of text. Why does this code not work?	
<i>A summary or description of the AI-generated output.</i>		
Output Received:	Specific revisions to the input were generated. For writing, this included improvements to grammar, word choice and sentence structure. For R code output consisted of revised code, sometimes using alternative packages.	
<i>Describe how the AI output was used, edited, or transformed.</i>		
Post-AI Processing Methods:	All AI output was critically assessed to ensure it was correct. Written suggestions were reviewed to ensure that they did offer improvements to the text without changing the meaning or style of my writing. Output from R code was checked to ensure that it produced the expected results.	
STUDENT DECLARATION		
<i>By signing you are confirming that the AI use stated in the table(s) above are accurate and follow AUT's recommended guidelines detailed in the AI Hub and Postgraduate Handbook.</i>		
Student Name:	Elise Arnst	Signature:  Date: 17/04/2026

Co-Authored Works

STUDENT AND SUPERVISOR APPROVALS

By signing you are confirming that the co-author contributions stated in the table(s) below are accurate.

Student Name	Elise Arnst	Signature		Date	16 th April 2026
Supervisor Name	Bradley Case	Signature		Date	16 th April 2026
Supervisor Name	Hannah Buckley	Signature		Date	16 th April 2026

Chapter Number:	Two (2)
Manuscript Title:	Legacies of <i>Pinus contorta</i> invasion persist for at least 16 years following management
Publication Status:	Submitted for Publication
AUTHOR: (order as per manuscript)	CONTRIBUTION
Arnst	Conceptualisation, design, data collection, analysis, writing, revising
Case	Conceptualisation, contribution of knowledge, critically revising
Peltzer	Conceptualisation, contribution of knowledge, critically revising
Buckley	Conceptualisation, contribution of knowledge, critical contribution

Chapter Number:	Three (3)
Manuscript Title:	Invasion legacies of <i>Pinus contorta</i> drive successional trajectories of short-tussock grassland plant communities
Publication Status:	Unpublished/Ready for submission for Publication
AUTHOR: (order as per manuscript)	CONTRIBUTION
Arnst	Conceptualisation, design, data collection, analysis, writing, revising
Buckley	Conceptualisation, advice on analysis, contribution of knowledge, critically revising
Peltzer	Conceptualisation, contribution of knowledge, critically revising
Case	Conceptualisation, advice on analysis, contribution of knowledge, critically revising

Chapter Number:	Four (4)
Manuscript Title:	Timing of invasion management shapes land cover trajectories over four decades
Publication Status:	Unpublished/Ready for submission for Publication
AUTHOR: (order as per manuscript)	CONTRIBUTION
Arnst	Conceptualisation, design, data collection, analysis, writing, revising
Buckley	Conceptualisation, contribution of knowledge, critically revising
Peltzer	Contribution of knowledge, critically revising
Case	Conceptualisation, advice on analysis, contribution of knowledge, critically revising

Acknowledgements

Thank you to my supervisors Bradley Case, Hannah Buckley and Duane Peltzer, you made a great team. I appreciate your knowledge and willingness to share expertise, as well as your enthusiasm and patience. Brad and Hannah – thank you for (almost) turning me into a morning person; your positivity meant that I always left our meetings with a smile and has been a big part of actually enjoying the journey.

I am grateful for the funding provided by an AUT Vice-Chancellors Doctoral Scholarship and Manaaki Whenua - Landcare Research which enabled me to undertake this research.

There were many people who contributed knowledge and advice in numerous ways. Firstly, a huge thank you to Pedro Willemse for being so willing to share knowledge and suggestions for study sites, such in-depth local knowledge gained over many years of work in conservation was invaluable. Thank you to Rowan Buxton, Hamish Maule, Jennifer Bufford and Liadan Dickie for the field assistance, your company and contributions were invaluable. Thank you for the thought-provoking conversations and unique perspectives – Sarah Richardson, Jennifer Bufford, Sarah Sapsford, Matt Scott, Tom Etherington, Rowan Sprague, Nicola Day, James McCarthy, Warwick Allen, Sarah Wyse. Thank you to Gary Houliston for being a great mentor, pushing me to strive for more and supporting me to do so.

To my family and friends, thank you for being understanding while I have been missing in action. Simon, thank you for believing in me, listening to me get excited about progress, and for reminding me to take a break. Your patience and support have enabled me to both start and complete this thesis.

Chapter 1

General Introduction

1.1 Theoretical background

Human-induced change of the natural environment is compounding, driving complex changes in ecosystems (Franklin et al., 2016; Tylianakis et al., 2008; Walker & Steffen, 1997). Biological invasions, land use change and climate change are three of the key drivers of global change and have profound impacts on biodiversity (Sala et al., 2000; Tylianakis et al., 2008). Invasions are particularly problematic because they cause many negative ecological impacts and economic costs, and global assessments show that biological invasions continue to increase in extent and impact worldwide (IPBES, 2023). Despite this knowledge, and the substantive funding and effort that goes into managing invaders, the long-term outcomes for invaded ecosystems are poorly understood (Allen et al., 2022; Kettenring & Adams, 2011). The overall focus of this thesis is on quantifying and understanding ecosystems and their trajectories following the management of a landscape invader, using pine invasion of New Zealand's short tussock grasslands as a study system.

1.1.1 Plant invasion

Biological invasions occur in a staged manner (see Figure 1.1; Blackburn et al., 2011; Sakai et al., 2001). Non-native species, also commonly referred to as exotic or alien species, are those that have been introduced to new areas outside of their natural geographic range (Roy et al., 2024; Theoharides & Dukes, 2007). Pathways of introduction are commonly related to trade and human movement (Hulme, 2021). Non-native species that establish self-sustaining populations are regarded as naturalised (Blackburn et al., 2011; Theoharides & Dukes, 2007). A species is considered to be invasive when it has negative effects on native species or ecosystems, and where its resident populations are self-replacing, producing reproductive offspring at large distances from the original source population (IPBES, 2023; Richardson & Pyšek, 2006; Richardson et al., 2000; Theoharides & Dukes, 2007). Following a species introduction there is often a significant delay, known as a lag phase, between arrival and subsequent population expansion (Pyšek & Hulme, 2005; Theoharides & Dukes, 2007). Invasion ecology seeks to understand which species become invasive, which habitats are most susceptible to invasion, the effects of invasions, and how they can be effectively managed (Rejmanek et al., 2005; Richardson & Pyšek, 2006).

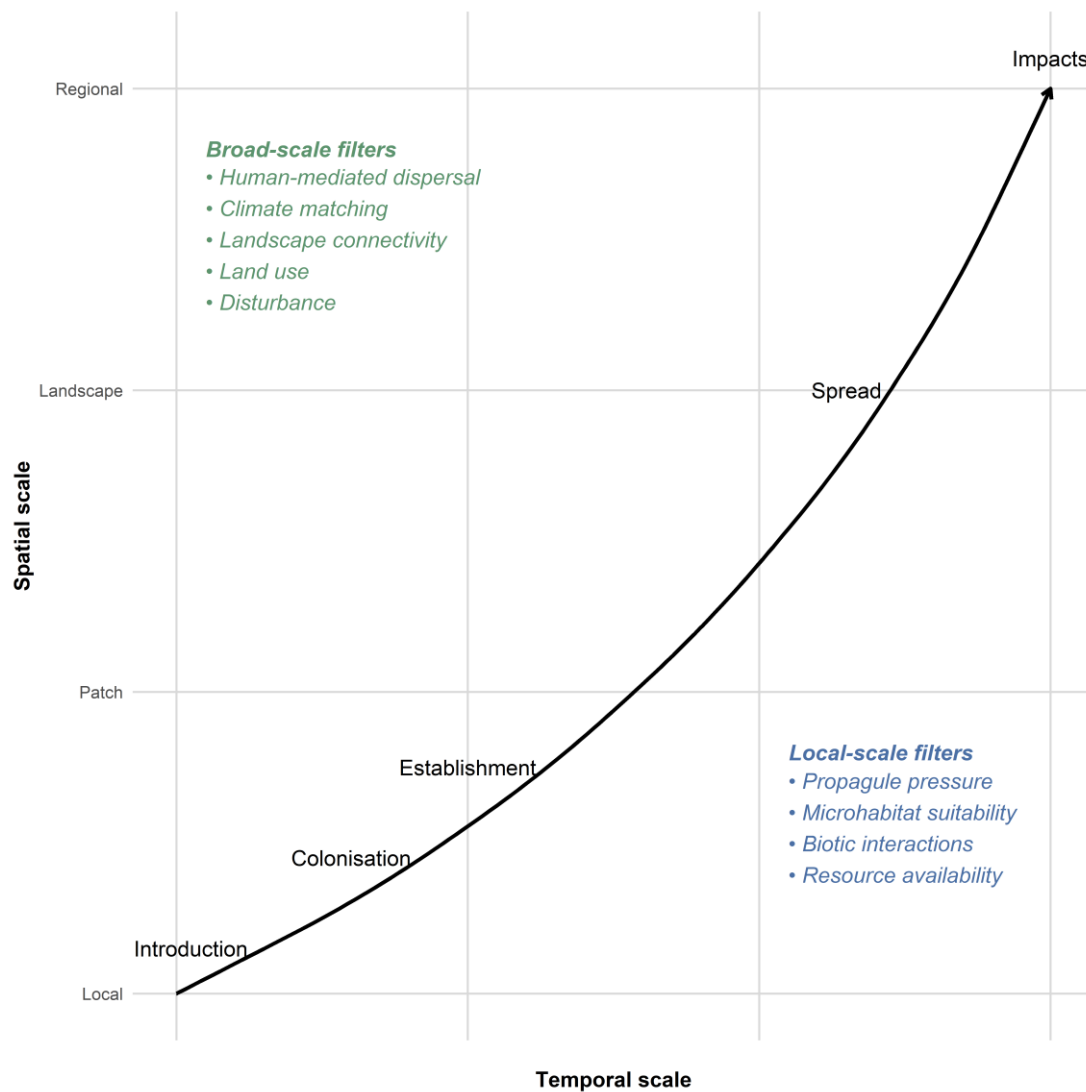


Figure 1.1 Conceptual representation of invasion stages across spatial and temporal scales, with examples of scale-dependant filters that may influence any stage of the invasion process. The curved trajectory illustrates how invasion processes expand from local, early-stage events toward broader landscape through time. Impacts are displayed outside the trajectory because they can occur at multiple scales and stages. Based on Theoharides and Dukes (2007).

Recent efforts to integrate invasion theory have identified five broad factors that explain why some species become invasive and why some ecosystems are vulnerable to invasion, namely: resource availability, biotic interactions, introduction events, species traits and phylogenetic similarity (Enders et al., 2020). Specifically, key determinants of invasion success include the traits of the non-native species, propagule pressure, the invasibility of the recipient ecosystem, and interactions among these factors (Catford et al., 2009; Davis et al., 2000; Novoa et al., 2020; Rejmanek, 2011; Simberloff, 2009). Traits of invasive plant species are highly variable, although they are more likely to have high seed production, an early reproduction age, be easily dispersed, and have broad environmental tolerance (Pyšek & Richardson, 2007; Rejmanek & Richardson, 1996). Ecosystems that are highly disturbed or have greater resource availability are thought to

be more easily invaded (Davis et al., 2000; Mack et al., 2000). Ecosystem vulnerability to invasion is also influenced by climate, ecosystem type and land use history (Rejmanek et al., 2005; Vilà & Ibáñez, 2011).

1.1.1.1 Impacts of plant invasion

Plant invasions are a major driver of ecological change, influencing species interactions, community structure, and ecosystem processes (Dukes & Mooney, 2004; Vitousek et al., 1997). Invasive plants can displace native species through mechanisms such as resource competition or by co-invading alongside mutualists or pathogens, ultimately reshaping plant community composition (Hejda et al., 2009; Wardle & Peltzer, 2017).

Invasive species have the potential to alter ecosystem level properties in the systems they invade, and these effects are widespread (Ehrenfeld, 2003, 2010). Abiotic changes to ecosystem level properties such as water availability, fire regimes, nutrient cycling, or soil properties are well documented (D'Antonio & Vitousek, 1992; Richardson et al., 2000; Weidlich et al., 2020). These impacts are widely evident, especially for invasive woody species which can dramatically alter soil nutrient dynamics and accelerate ecosystem transformation (Jo et al., 2017; Vilà et al., 2011; Vitousek & Walker, 1989). Some invaders act as ecosystem engineers by modifying the abiotic environment in ways that reinforce their own success (Crooks, 2002; Romero et al., 2015). When a single invader modifies abiotic and biotic conditions in a manner that facilitates multiple non-native species, it can function as a 'keystone invader' (Ricciardi & Simberloff, 2025). Invasions can also cause biotic homogenisation; this has been observed across multiple spatial scales within grassland ecosystems (Stotz et al., 2019). Where there have been widespread invasions by similar species, the resulting convergence in species composition can drive the homogenisation of ecosystems worldwide (Olden et al., 2004). As a result of these changes, invasive non-native species can fundamentally change both ecological processes and ecosystems (Ehrenfeld, 2010; Jeschke et al., 2014).

Invasions by woody species are receiving increasing global attention due to their widespread distribution and substantial ecological impacts (Richardson & Rejmánek, 2011). Tree invasions, in particular, can fundamentally alter ecosystem structure and function, posing significant challenges when they encroach into non-woody systems (Martin et al., 2009; Rundel et al., 2014). Such encroachment not only threatens native biodiversity but can also constrain future land-use options, amplifying the long-term consequences of invasion (Peltzer, 2018; Richardson & Rejmánek, 2011).

1.1.1.2 Legacies of plant invasions

Legacies are the long-lasting ecological impacts that persist after an invasive species has been removed, arising from biotic and abiotic changes initiated during the invasion process (Cuddington, 2011; Vilà et al., 2011). For example, legacies may include changes to soil abiotic properties and microbial communities (Crooks, 2002; Ehrenfeld, 2010; Vitousek et al., 1997). Fundamental changes to ecosystems through altering soil nutrient cycling, water use, soil microbial communities and fire regimes, have been well documented for widespread invasive genera such as *Acacia* Mill. (Hellmann et al., 2011; Marchante et al., 2015; Yelenik et

al., 2004); and many species in the Pinaceae family (Craine & Orians, 2004; Dickie et al., 2014; Nuñez et al., 2021; Sapsford et al., 2022). These persistent effects can either directly or indirectly influence long-term successional trajectories and complicate restoration efforts, ultimately shaping the structure and composition of recovering plant communities (Corbin & D'Antonio, 2012; Nuñez & Dickie, 2014; Pyšek & Richardson, 2010). Despite the recognition of their importance, there is little evidence showing how long these legacies persist and how the effect changes over time (Hulme, 2020).

Persistent legacy effects can influence native plant community recovery (Cuddington, 2011; Wardle & Peltzer, 2017), redirecting successional pathways away from native dominance and toward novel or degraded communities (Flory & Clay, 2010). Depending on the nature and magnitude of these legacies, multiple outcomes are possible including re-invasion by the same species, secondary invasion by other non-native species, or recovery of native species (O'Loughlin & Green, 2017; Pearson et al., 2016; Pyšek & Richardson, 2010; Zavaleta et al., 2001). Understanding these trajectories and the underlying drivers is essential for predicting plant community outcomes and, therefore, for designing effective management strategies.

1.1.1.3 Managing invasions

Once an invasive species has established in an area, management efforts are commonly focused on its removal (Myers et al., 2000). Removing a non-native species at early stages of invasion is the most cost-effective management option and minimises the impacts on native communities (Ahmed et al., 2022; Hulme, 2006). However, in many cases, by the time a management problem is identified, the invasive species has already spread and is well-established; alternative methods are therefore needed to manage these widespread invaders to limit further ecological changes (Norton, 2009; Simberloff, 2003).

The removal of invasive plants is often the primary focus of management and usually assumes that removing the invader will allow the ecosystem to recover (Hobbs & Humphries, 1995). However, previously invaded sites rarely revert to pre-invasion conditions; instead recovery is often slow, incomplete, or redirected toward some alternative state (Corbin & D'Antonio, 2012; Grove et al., 2015; Ogden & Rejmánek, 2005; Stephens et al., 2009). Post-management successional trajectories can vary depending on the ecosystem type, the stage of the invasion at the time of management (which influences density and propagule pressure), and the type or frequency of management (Case et al., 2016; Rohal et al., 2019). Together, these dynamics highlight that both the presence of invasive species and their removal can generate long-lasting ecological consequences that shape the future ecosystem trajectories. However, most research has focused on the impacts of invasion or the short-term outcomes following management, and few studies have quantified long term changes.

1.1.2 Invasion across scales

The importance of spatial and temporal scale in shaping ecological processes is well recognised in the ecological literature (Dale, 2000; Leibold et al., 2004; Levin, 1992). Biological invasions are scale-dependent, with different controlling processes and factors operating across different spatial and temporal scales (see Figure 1.1; Pauchard & Shea, 2006; Theoharides & Dukes, 2007), making it essential to take a multi-scale research approach to disentangling their influences (Hulme, 2017; Strayer et al., 2006). Spatial patterns arise from the influences of abiotic factors, such as climate and soil type, and biotic factors, such as species traits or plant-plant interactions, operating as ecological filters across multiple scales, resulting in patchiness or gradients (Hulme, 2017; Musseau et al., 2024; Pauchard & Shea, 2006).

At finer, local scales, propagule pressure, habitat suitability, and biotic interactions play a significant role in determining both the success of invaders and the extent of their spread (Levine et al., 2004; Simberloff, 2009). These local processes also interact with broad scale factors (Melbourne et al., 2007; With, 2002). At larger spatial scales, invasions are shaped by heterogeneity in landscape-level features and processes (González-Moreno et al., 2013; Theoharides & Dukes, 2007). Landscape heterogeneity comprises spatial and temporal variation in the configuration of the environment, including topography, and the spatial arrangement of land cover types, and its composition, i.e. the number and proportion of cover types (Fahrig et al., 2011; Kotowska et al., 2022). Landscape heterogeneity affects patterns of invasion and habitat invasibility; more heterogeneous landscapes often experience greater levels of invasion because the wider range of habitat conditions and greater resource availability may favour invaders, and because the variation in landscape structure can facilitate their spread (Kotowska et al., 2022; Melbourne et al., 2007; With, 2002). Disturbance events such as land use changes, management activities, and climate events can increase landscape complexity by altering resource availability or habitat structure (Pickett et al., 1985); these changes can influence both the likelihood of invader colonisation, and the speed and extent of subsequent spread (Hobbs & Huenneke, 1992; Vilà & Ibáñez, 2011).

Temporal scale is also an important consideration when understanding biological invasions because different processes that drive invasions work across multiple timescales (Strayer et al., 2006; Theoharides & Dukes, 2007). Short-term dynamics such as seasonal fluctuations and disturbance events can influence establishment success (Britton-Simmons & Abbott, 2008; Wainwright et al., 2012). Over longer timescales, lag phases are often determined by introduction pathway, species traits, and the characteristics of the invaded habitat (Aikio et al., 2010; Larkin, 2012); in addition, changes in land use or climate trajectories can alter invasion pathways (Hobbs & Huenneke, 1992; Sharma et al., 2023). Non-native species may maintain low densities for extended periods of time before rapid expansion occurs, often triggered by shifts in disturbance regimes or environmental conditions (Aikio et al., 2010; Crooks, 2005).

Global change is a major driver of biodiversity decline worldwide, with biological invasions and land use change both contributing to this trend (IPBES, 2019). Land use change is also a strong predictor of invasion, with highly-modified or disturbed habitats particularly susceptible to colonisation of invasive

species (Vilà & Ibáñez, 2011). Despite the importance of these drivers, their combined influence on long-term ecosystem trajectories remains poorly understood, particularly at landscape scales (Didham et al., 2007). Understanding these interactions is essential for explaining how invasion outcomes vary across space and time.

The interactions between factors operating at different scales mean that invasion outcomes are inherently context dependent, requiring multi-scale assessment and the consideration of interactions among drivers (Catford et al., 2022). Addressing this gap requires data that capture broad spatial patterns and address long-term dynamics. Remotely sensed data are available at large spatial and temporal scales, and are particularly beneficial for providing standardised data across space and time to enable analyses that would not otherwise be possible (del Río-Mena et al., 2020; Morgan et al., 2010; Rogan & Chen, 2004). Remotely sensed data are commonly used to assess land cover and land use and provide spatio-temporal information and so can be used as a tool for tracking change (Francis et al., 2024; Müllerová et al., 2023). For example, imagery can be utilised for purposes such as monitoring tree invasions into grasslands (Mast et al., 1997; Sprague et al., 2019). These data are particularly useful when ground-based information is not available, for providing information about remote areas, and helping to fill information gaps, including enabling the reconstruction of historical changes.

1.2 Study system

1.2.1 Non-native pines

Non-native invasive Pinaceae (also known in New Zealand as ‘wilding pines’) are a significant economic and biodiversity threat across the Southern Hemisphere (Nuñez et al., 2017; Richardson et al., 1994). Pines are also problematic in the Northern Hemisphere, both outside of their native range (Engelmark et al., 2001; Nandasena et al., 2023; Wasowicz et al., 2025) and in non-forest ecosystems within their native range (Steers et al., 2013; Taylor et al., 2016a). Due to their globally well-documented invasions, non-native Pinaceae are considered an ideal model study taxon for understanding invasion dynamics and management (Gundale et al., 2014). Globally, there is a growing body of evidence that pine invasions alter ecosystem properties, including nutrient cycling and fire regimes (Craine & Orians, 2004; Ferraina et al., 2021; Franzese et al., 2017; Nuñez et al., 2021; Sapsford et al., 2022), and both above and below ground biotic communities (Cox & Dickie, 2026; Franzese et al., 2017; Sapsford et al., 2022). New Zealand has advanced pine invasions and a relatively long history of trying to control them (Froude, 2011), including globally uncommon practices such as aerial broadcast application of herbicides for dense late-stage invasions (Peck et al., 2022). However, other regions such as Argentina, Chile and Iceland are experiencing rapid expansion from plantations and these invasions are also being managed, or likely will need to be in the near future. Little is known about the efficacy of removing pines as a strategy to restore native ecosystems (Nuñez et al., 2017), this means the New Zealand experience of managing pine invasions can be utilised to provide globally relevant insights.

Planting of non-native pines for shelter belts, land stabilisation and small forestry blocks occurred in New Zealand from the 1920s onwards, and most extensively between the 1950s and 1970s (Ledgard & Belton, 1985; Young, 2016). Pines are climate matched to New Zealand because of their deliberate introduction for forestry and soil conservation (McGregor et al., 2012); they also possess several traits that make them more likely to be invasive, specifically a short juvenile period and seed characteristics that enhance dispersal, such as small seed mass and seed wing morphology (McGregor et al., 2012; Wyse & Hulme, 2021b). For example, in New Zealand *Pinus contorta* Loudon grows faster and also spreads more rapidly than in its native range, because it begins reproducing as early as three years old and produces a larger number of cones and seeds per tree (Carlin et al., 2025b; Ledgard, 2001; Taylor et al., 2016b). These characteristics also mean that *P. contorta* invasions can rapidly progress from sparse to dense, self-sustaining stands, in New Zealand this commonly occurs in less than 20 years (Ledgard, 2001; NZPCN, 2026).

These deliberately planted pines have subsequently spread, creating widespread landscape scale invasions (Ministry for Primary Industries, 2014). *Pinus contorta* is one of the most invasive and widespread pine species in New Zealand (Lloyd et al., 2016); it is shade intolerant and frequently invades open grassland (Richardson & Bond, 1991). The spread of pines is recognised as an issue for biodiversity, productive land use and water availability (Froude, 2011). Coordinated management efforts began in the 1960s, and a national control programme was established in 2016, with substantial funding and effort spent on controlling or eradicating invasive pines in recent decades (Edwards et al., 2020; Ministry for Primary Industries, 2014). Management is predominantly undertaken using herbicides, either ground based or aerial application, and mechanical or manual control are also commonly utilised (National Wilding Conifer Control Programme & Environment Canterbury, 2020).

1.2.2 Tussock grasslands

Grassland ecosystems contain relatively high levels of biodiversity, support essential ecosystem services, and are essential for agricultural production (Bai & Cotrufo, 2022; Hopkins & Holz, 2006; Newbold et al., 2016). Grasslands are recognised as being ecologically and economically important, but are facing multiple threats from biological invasions, land use change and climate change (Boulant et al., 2009; Leidinger et al., 2017; Prangel et al., 2023; Stevens et al., 2017; Straffelini et al., 2024).

New Zealand's grasslands are predominantly tussock forming and largely occur within montane to low alpine zones (Mark & McLennan, 2005). Short tussock grasslands occur below 800 m, which is below the natural treeline, and are generally less than 50 cm tall, with widespread *Festuca novae-zelandiae* (Hack.) Cockayne and *Poa cita* Edgar (see Figure 1.2; Day et al., 2023; Mark et al., 2013; Mark & McLennan, 2005). The current short tussock grassland plant communities are predominantly modified tussock grassland and shrubland, with some remnant pockets of beech (Nothofagaceae) (Meurk et al., 2002). These ecosystems have been highly-modified, and long been managed as semi-productive landscapes for pastoral grazing (Day et al., 2023). Pre-human settlement, the slopes supported forested ecosystems, and the flats were

predominantly shrublands (McGlone & Moar, 1998), but fire and grazing have reduced the extent of these vegetation types so that by the late 1800s there were predominantly only shrublands and tussock grasslands remaining (Connor & Vucetich, 1964; Duncan et al., 2001; O'Connor, 1981; Treskonova, 1991). There have been multiple waves of invasive species, with pines being the most recent and having the biggest impact (Mark et al., 2013). Much of the grassland has been grazed by sheep (*Ovis aries*), by the widespread populations of introduced rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*), and more recently introduced wallabies (*Notamacropus rufogriseus*); which all impact the plant communities (Allen et al., 1995; Latham et al., 2020; Rose & Frampton, 2007). Despite the extensive changes, these landscapes have high ecological value, supporting many threatened native plant, lizard and invertebrate species (Day & Buckley, 2013; Mark et al., 2013).



Figure 1.2 An example of *Pinus contorta* invading a short tussock grassland at Pūkaki Flat Conservation Area in the Mackenzie Basin, New Zealand.

Much of the South Island high-country covers areas of tussock grassland that were farmed under long-term crown pastoral leases, many of which underwent a tenure review process between 1998 and 2017, splitting the ownership into freehold agricultural land and public conservation areas (Brower & Page, 2017). While many higher elevation areas with high biodiversity values have been designated as conservation areas, the lower elevation areas which are dominated by short tussock grasslands are under-represented and have predominantly become freehold land (Mark et al., 2013; Parliamentary Commissioner for the Environment, 2009). In more recent decades, irrigation and the conversion of some of these freehold areas to high

producing grassland using sown mixtures of non-native pasture species has substantially altered these dryland ecosystems (Brower et al., 2018; Peart & Woodhouse, 2020).

There is currently no consensus on the goals or desired conservation outcomes for these systems; several potential management goals are possible (Dickie et al., 2022). The most rudimentary goal would be to focus solely on controlling the invasion, aiming to either eradicate or retain only a low level of pines but not considering the broader ecosystem. This may mean that the landscape is a productive one, rather than specifically managed for conservation purposes. Alternatively, the focus could be on protecting native species or native species abundance, but usually with no specified community sought. Or a more ambitious outcome, that requires more planning may be aiming to restore the ecosystem to a pre-determined state (Dickie et al., 2022). However, there are also differing viewpoints on whether or not the restored state should be tussock grassland (Mark et al., 2013), shrubland (Walker et al., 2003), or some other outcome. To be able to set achievable management goals, more understanding of the persistence of ecosystem level impacts following invader removal is required.

1.2.3 Te Manahuna / Mackenzie Basin

Te Manahuna / the Mackenzie Basin is a glacial intermontane basin in the central South Island of Aotearoa / New Zealand (Figure 1.3). The basin covers 269,000 ha and ranges in elevation between 375 – 800 m a.s.l (Peart & Woodhouse, 2020). The basin is an alluvial plain formed by glaciation, and relief is predominantly fan, moraines and outwash terraces (Barrell et al., 2011; Espie et al., 1984). The climate is semi-arid with mean annual rainfall 500 mm, mean annual temperature 9.1°C, and mean winter minimum temperature -3.1°C (Espie et al., 1984; Leathwick et al., 2002).

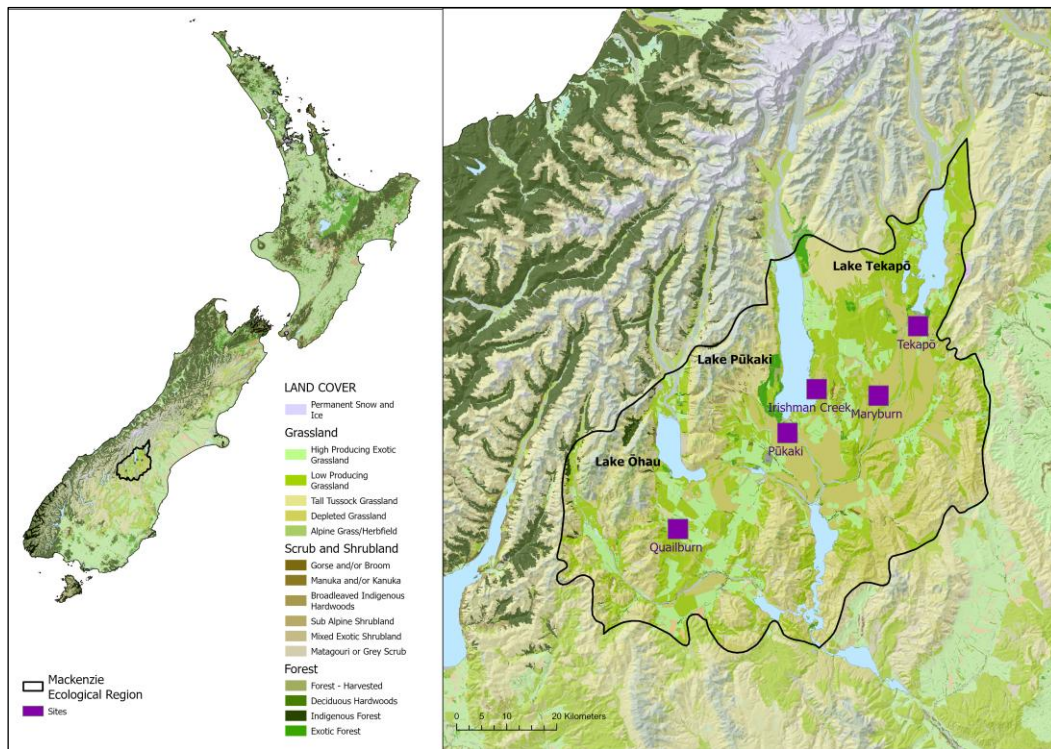


Figure 1.3 Mackenzie Ecological Region, showing dominant land cover types based on LCDB v6 (Manaaki Whenua - Landcare Research, 2025a). Study sites are denoted by purple squares.

These semi-arid intermontane basins are unusual in that they are one of the few areas in the South Island high country that did historically support tussock grassland ecosystems, in addition to the more widespread shrubland ecosystems (McGlone & Moar, 1998; McGlone, 2001; Wardle, 1991). However, they exemplify the change seen across tussock grasslands, with land use change and widespread invasions putting native biodiversity under immense pressure.

1.2.3.1 Study location

Within Te Manahuna / the Mackenzie Basin I identified areas with known pine invasion and management histories based on local expert knowledge (pers. comm. Pedro Willemse, Te Papa Atawhai-Department of Conservation and individual landowners), published information (Peart & Woodhouse, 2020; Young, 2016) and the New Zealand Wilding Conifer database (LINZ, 2021). Subsequent to site selection additional information was also collated to describe the study sites (LINZ, 2026; Sapsford & Dickie, 2023; Young, 2023). Within these areas I established five study sites with varying stages of invasion at the time of management and with management occurring between two and 16 years prior (Table 1.1; Figure 1.4). Sites were selected to cover both a broad range of time since management, and the range of invasion stages from early invasion with small, scattered individuals through to late stage invasions with large trees forming a dense closed canopy. Based on the combination of invasion stage and time since management, I aimed to achieve an approximately balanced sample within the constraints of utilising the existing landscape-scale invasion and management.

Table 1.1 Summary information for five study sites within Te Manahuna / the Mackenzie Basin

<i>Site</i>	<i>Land tenure</i>	<i>Land use</i>	<i>Invasion history</i>	<i>Management history</i>
<i>Tekapō</i>	The study site is within Tekapō Scientific Reserve. Tekapō township is to the north. Sawdon Station is to the south and east, this is Crown owned leasehold land.	Conservation land within a matrix of low-intensity sheep farming and adjacent to non-native forestry and an urban area.	Sparse invasion, seed source from pines present in shelterbelts and plantations adjacent to the conservation area.	Management has been undertaken at early stages of invasion, so pines never became widespread.
<i>Irishman Creek</i>	Previously leasehold farmland across The Wolds and Irishman Creek Stations that became a conservation area in 2017 as part of tenure review.	Conservation land within an agricultural matrix and adjacent to a hydro-generation area.	Pines managed by leasee, this lapsed while undergoing tenure review. Invasion was widespread by the time the land transferred to Crown ownership.	Recent but intensive aerial spraying of intermediate and late stage invasions. Area now dominated by standing dead pines.
<i>Maryburn</i>	Previously leasehold farmland that became a conservation area in 2015 as part of tenure review.	Conservation land within an agricultural matrix, including some high-intensity irrigated land.	Pines present in distant shelterbelts, low propagule pressure.	Management has been undertaken at early stages of invasion, so pines never widespread.
<i>Pūkaki</i>	Publicly owned land in the northern part of the site, managed primarily for electricity generation. The southern area is a conservation reserve that became publicly owned in 2008 as part of tenure review.	Conservation land adjacent to an airstrip and a hydro-generation area.	Seed source from Pūkaki Downs to the north. Pines well established in the northern part of this site. Invasion progressively less developed moving south.	Northern part of the site has had minimal management, and it is not consistent across the area. Invasions managed on conservation area in the south.
<i>Quailburn</i>	Primarily freehold land with multiple landowners. Some areas were freehold prior to tenure review. Parts of Ben Dhu, Ribbonwood and Quailburn Stations became freehold as part of tenure review.	Predominantly agricultural area, with a mix of low and high intensity production. Two conservation areas exist to protect specific ecosystems: a shrubland and a wetland complex.	Pines present in shelterbelts and plantations. One of the earlier areas in the Mackenzie Basin to have late-stage invasion.	Management was undertaken earlier than many other locations, although the invasion was well advanced. Complete removal of some forestry blocks has reduced the local seed sources.

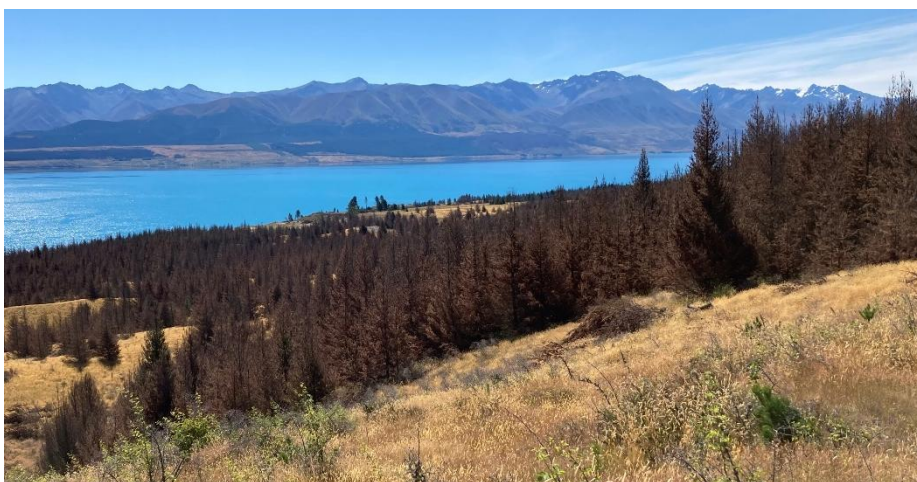


Figure 1.4 Photos of study locations show (top to bottom): an early stage invasion at Pūkaki; an intermediate stage invasion at Quailburn; a late stage, dense invasion at Irishman Creek.

1.3 Thesis outline

The overall aim of this thesis was to develop a better understanding of the legacy effects of a dominant landscape invader on plant communities and ecosystem processes following its management. The objective was to provide a quantitative assessment of the magnitude and persistence of legacies to provide a foundation for future conservation management decisions.

To achieve this objective, I asked the following research questions:

1. Do non-native pines continue to influence native plant communities following management, i.e., do legacies persist?
2. What are the drivers shaping successional trajectories of native plant communities, and are these trajectories more strongly driven by direct mechanisms related to pine invasion, or indirect mechanisms such as competition from secondary invaders or reinvasion by pines?
3. What are the landscape scale patterns of invasion and subsequent management on a multi-decadal scale?

To address the stated research questions, this thesis covers the following:

In **Chapter 2** I investigated if legacies of *Pinus contorta* invasion persist. I used an observational study that takes advantage of a space-for-time substitution approach to use a natural landscape level study as a proxy for an experiment, utilising a chronosequence of management over 16 years in a tussock grassland ecosystem. This provided a quantitative assessment of the ecosystem level impacts of the legacy effects of a dominant landscape invader. I also used hierarchical modelling of species communities to test if the environment (i.e. abiotic legacies) were the key drivers of plant community structure.

In **Chapter 3** I evaluated the mechanisms by which historical pine invasion and subsequent management have influenced native plant communities in terms of structure and species richness. This built on the abiotic and biotic legacy effects quantified in the previous chapter with the aim of understanding underlying drivers. Specifically, I used structural equation modelling to determine whether invasion history directly influences either native species richness or native plant community structure; or whether soil legacies, secondary invasion by non-native grasses or reinvasion by pines influence trajectories, and therefore the outcomes following management.

In **Chapter 4** I investigated the landscape scale effects of both the invasion and its management, specifically quantifying changes in land cover over four decades. Here I utilised a novel analysis approach by integrating field-based plot data measured at a local scale with remotely sensed landscape scale data to provide a multi-disciplinary assessment of invasion legacies and how they interact with land use change.

Finally, in **Chapter 5** I provide a synthesis of the results and formulate general conclusions, including discussing implications for conservation management and proposing directions for future research.

Chapter 2

Legacies of *Pinus contorta* Invasion Persist For At Least 16 Years Following Management

2.1 Introduction

Plant invaders cause numerous ecological, environmental and economic impacts (Dukes & Mooney, 2004; IPBES, 2023; Vitousek et al., 1997), and can fundamentally change the ecosystems they invade (Ehrenfeld, 2010; Vilà et al., 2011). Consequently, landscape-scale weed invasions are often managed to avoid or reverse these negative impacts, creating *de facto* experimental removal treatments that can be used to investigate community outcomes of biotic interactions. However, removal of a widespread invader does not necessarily benefit native species (Ogden & Rejmánek, 2005; Stephens et al., 2009), and may not prevent persistent long-term changes or legacy effects in ecosystems (Corbin & D'Antonio, 2012; Cuddington, 2011).

Long-lasting ecological impacts that persist after invasive species removal can continue to influence the community and successional trajectories; for example, by altering soil nutrient processing or fire regimes (Crooks, 2002; Cuddington, 2011), and can influence the structure of the plant community (Wardle & Peltzer, 2017). Surprisingly few studies assess the impact of removing weeds on the remaining plant community at landscape-scales, at different stages of the invasion process or over multiple growing seasons (Kettenring & Adams, 2011; Peralta et al., 2020), despite suggestions that these factors should influence the strength and duration of legacy effects and downstream impacts on plant communities (Hulme, 2020; Sapsford et al., 2020).

Non-native Pinaceae (hereafter, termed ‘wilding pines’) are a widespread problem causing major economic and biodiversity impacts across the Southern Hemisphere (Nuñez et al., 2017; Richardson et al., 1994), and in the Northern Hemisphere both outside their native range (Engelmark et al., 2001; Wasowicz et al., 2025), and in their native range where they encroach into non-forest ecosystems (Steers et al., 2013; Taylor et al., 2016a). Pines cause fundamental changes to ecosystems by altering soil nutrient cycling, water use, soil microbial communities and fire regimes (Craine & Orians, 2004; Dickie et al., 2014; Nuñez et al., 2021; Sapsford et al., 2022). A single invader, such as pine, that alters biotic or abiotic conditions in a manner that facilitates multiple non-native species can be a ‘keystone invader’ (Ricciardi & Simberloff, 2025; Simberloff & Von Holle, 1999).

Wilding pines have invaded vast areas, for example at least 2 M ha of New Zealand (Froude, 2011); including areas of high conservation value. Major management efforts to contain or eradicate wilding pines at landscape-scales have been undertaken over recent decades (McConnachie et al., 2015; Ministry for Primary Industries, 2014), but the outcomes for biodiversity, ecosystem properties or secondary invasions are rarely evaluated as a part of this management process (Peltzer, 2018; Prior et al., 2018). New Zealand is

regarded as being at the forefront of wilding pine management, having implemented a nationally coordinated programme operating at landscape scales (Sprague et al., 2022). Although other countries such as South Africa, Chile and Argentina are also increasingly undertaking management, this tends to be more recent or at smaller scales (Nuñez et al., 2017). Globally, there are few studies evaluating post-management outcomes, and those that do are also at a small scale and cover relatively short timeframes (e.g. Fuentes-Lillo et al., 2026). Little is known about the efficacy of removing pines as a strategy to restore native ecosystems (Nuñez et al., 2017), this means that the New Zealand experience of managing pine invasions can be utilised to provide globally relevant insights.

We take advantage of repeated, large-scale management of wilding pines as a landscape-scale removal experiment to understand the outcomes of managing a dominant invasive species over time. To determine the drivers of plant community composition and species richness along a post-invasion gradient, we quantified the environmental changes resulting from invasion and subsequent wilding pine management in a modified short tussock grassland ecosystem. Specifically, we determined the impacts of pine invasion and management on abiotic soil properties and native plant communities, to understand whether persistent legacies following management are related to the combination of density and size as a proxy for the stage of invasion. We also evaluated whether pine removal has positive, negative or neutral impacts on either native or co-occurring non-native species. Finally, we assessed whether pine reinvasion or secondary invasion of other non-native species increased with historical pine invasion stage.

2.2 Methods

2.2.1 Study area

We evaluated the impacts and legacies of pine invasions and removal in Te Manahuna / the Mackenzie Basin, a large glacial intermontane basin within the South Island of Aotearoa-New Zealand, (WGS84 -44.22 S, 170.13 E; see also Figure S2.1). The climate is semi-arid with mean annual rainfall 500 mm, mean annual temperature 9.1 °C and winter minimum temperature -3.1 °C and elevation of 500 m a.s.l. (Espie et al., 1984; Leathwick et al., 2002). Since human settlement, most indigenous ecosystems have been highly modified from the original native forests on slopes, and shrublands or tussock grasslands on flats (Meurk et al., 2002). Fire and grazing reduced the extent of native vegetation such that, by the late 1800s, shrublands and tussock grasslands largely dominated the landscape (McGlone & Moar, 1998; Wardle, 1991). Current vegetation is largely tussock grassland and shrubland (Duncan et al., 2001; Meurk et al., 2002), with multiple non-native species, including more recent invasions from pines, which are continuing to alter the community (Mark et al., 2013). Despite this, many sites have high ecological value, supporting threatened native plant, lizard and invertebrate species (Mark et al., 2013).

2.2.2 Data collection

We first located areas with known *Pinus contorta* invasion and management history. Sites were selected from across the Mackenzie Basin that had similar rainfall (300 – 700 mm/year), elevation (400 – 750 m a.s.l.), flat to moderate slope gradients (0 – 15°), predominately south-west facing aspects (150 – 272°), and soil types composed of greywacke gravels, loess, colluvium and till on moraine or outwash surfaces (Barrell et al., 2011). Plant community and soil properties were characterised within replicate plots (10 × 10 m), established at randomly generated points within each site, with the number of plots scaling with size of the site, i.e., the smallest site was 19 ha and contained two plots and the largest site was 244 ha and contained 18 plots. Sites varied in their time since management from two to 16 years. The age and density of pines is directly related to the stage of invasion (Peña et al., 2008). Due to the progressive nature of invasion, sites that had been invaded the longest had the highest pine densities and largest individuals. The invasion stage of pines at the time of management had not been measured quantitatively, so we categorised sites into three levels based on a combination of density and the size of individuals, following commonly adopted definitions: ‘Late’ stage invasion, where trees had formed a closed canopy, with greater than 400 stems per ha (sites = 3; plots = 18); ‘intermediate’ stage invasion, where many saplings and small trees were present, but the canopy had not yet closed, with 20 – 400 stems per ha (sites = 3; plots = 19); and ‘early’ stage invasion, with scattered seedlings and saplings, and less than 20 stems per ha (sites = 4; plots = 17). We utilised a natural invasion with *ad hoc* management, meaning the distribution of historical invasion stage and time since management was unbalanced, with late invasion sites predominantly managed in the last ten years (Table S2.1). All sites were managed with herbicide applications as the primary means of removal, predominantly either aerial broadcast spray for dense infestations, or ground-based herbicide application for sparse infestations (Rolando et al., 2025). We did not encounter any completely uninvaded sites in the site selection process; however, other studies have considered locations similar to our ‘early invasion’ sites with scattered pine seedlings as ‘uninvaded’ (Dickie et al., 2014; Peralta et al., 2020).

We measured plant communities in 54 plots which we permanently marked. Within each 10 × 10 m plot, we visually estimated the percent cover of each vascular plant species present across the whole plot area. Within each plot we counted live pine individuals, categorised by life stage; seedlings (< 135 cm tall), saplings (> 135 cm tall but < 2.5 cm diameter at 135 cm height) and trees (> 2.5 cm at 135 cm height), following Hurst and Allen (2007). We recorded whether each individual was a survivor of management (based on estimated tree age relative to management date) or if it had established post-management, i.e., had reinvaded.

At each plot, we recorded several environmental variables, following Hurst and Allen (2007), including slope, aspect, and elevation. We took 332 cm³ soil samples at five locations within each plot (each corner and the centre) using a 65 mm diameter, 100 mm long soil corer. We recorded soil moisture using a Delta-T HH moisture meter at each of the five soil sample locations, and calculated the mean value to compare relative differences between plots with varying historical pine invasion stages. Weather conditions

were consistent with no rainfall during the sampling period, the homogeneous conditions across sites allowed for this to be used as a measure for spot comparisons enabling us to determine relative spatial differences, noting that this is not an absolute measure of soil moisture and so can only be interpreted in terms of relativity. Soil physicochemical analyses were conducted using the pooled samples per plot, by the commercial laboratory Hill Laboratories, Hamilton, New Zealand. We took hemispherical photos at 1 m height, at the centre of each plot and used the R package ‘Hemiphot’ to analyse the images and calculate canopy openness (ter Steege, 2018).

2.2.3 Data analysis

All analyses were conducted in R version 4.5.0 (R Core Team, 2025). All Pinaceae species were removed from the species data prior to analysis because all analyses were designed to determine community responses to current and historical pine invasion stage. We tested for spatial autocorrelation between plot location and environmental variables (principal components), and between plot location and plant communities (NMDS axes), using the ‘mantel’ function in the R package ‘vegan’ (Oksanen et al., 2013). All tests were non-significant, indicating no spatial autocorrelation.

2.2.3.1 Pine legacy effects on environmental conditions

We used general linear models to compare six key environmental variables to historical pine invasion stage, and time since management. The environmental variables were soil moisture, Olsen phosphorus, potentially available nitrogen, total carbon, pH, and canopy openness. Due to correlation between some of the variables, we then used a Principal Component Analysis (PCA) implemented using the ‘princomp’ function in the R package ‘vegan’ (Oksanen et al., 2013) to characterise the relationships among these environmental variables. We used the results of the PCA to test for the correlation between plot principal component scores and time since management using Pearson’s correlation coefficient, and one-way analysis of variance (ANOVA) to test the relationship between plot principal component scores and historical pine invasion stage.

2.2.3.2 Impact of historical pine invasion and management on plant community structure

To describe spatial patterns within the plant community we carried out non-metric multidimensional scaling (NMDS) on Bray-Curtis dissimilarities of species’ cover scores within plots after a square root transformation and a Wisconsin double standardisation (Faith et al., 1987; McCune & Grace, 2002). Species scores were calculated as weighted averages (proportional to species abundance), based on plot scores (ter Braak & Looman, 1986). Analyses were carried out using the R package ‘vegan’ (Oksanen et al., 2013).

We used generalised linear models to test whether native and non-native species percent cover and species richness differed across plot groups, split by historical pine invasion stage. Multiple pairwise comparisons were corrected using Tukey’s test (Cui et al., 2021; Dunn & Smyth, 2018). For species percent

cover, a negative distribution with a binomial link function was used, and for species richness we used a Poisson distribution with a log link function (Dunn & Smyth, 2018).

To quantify the structural change in plant communities we compared the proportional cover of each growth form (i.e., fern, forb, graminoid, orchid, shrub, tree, vine) separated by bio status (i.e., native vs. non-native) within each historical pine invasion stage. Proportions were calculated by summing the total cover of each growth form and dividing it by the total cover across all plots. We used a generalised linear model with a beta distribution and a logit link function, and corrected for multiple comparisons using Tukey's test using the R package 'multcomp' (Hothorn et al., 2008).

To assess pine reinvasion in plots, we totalled the counts of live pine individuals in two broad categories. The first category comprised counts of individuals that had survived management (survivors), this was estimated by assessing the age of the individual in relation to the timing of control or if any signs of herbicide damage were visible. The second category compared counts of individuals that had established post-management (reinvansion). For the reinvading individuals we also compared counts of individuals based on whether or not there was at least one coning pine tree inside the plot.

2.2.3.3 Testing species-environment relationships using hierarchical modelling of species communities

We used hierarchical modelling of species communities (HMSC) to analyse the impacts of environmental covariates, plant traits, and phylogenetic relationships to Family-level, on species' presence-absence (Ovaskainen & Abrego, 2020). Native and non-native species were modelled separately because earlier results and previous studies showed they are likely to respond differently (Seabloom et al., 2015). We also ran a model for all species to assess the residual species co-occurrences between all species. We modelled presence-absence of 42 species (25 native and 17 non-native species) that were not rare (i.e. occurred in at least 10% plots, or had at least one occurrence $> 1\%$ cover). We excluded rare species to ensure that we were not modelling species whose occurrences were more due to chance than biotic or abiotic interactions (Crisfield et al., 2024; Rabinowitz et al., 1984). Again, we excluded pine species from the response variable data because we were interested in the post-management plant communities. This allowed us to examine relationships between the residual plant community and abiotic legacies of pine invasion, rather than differences driven by the occurrence of the managed species. Pine invasion and management history were subsequently used to aid interpretation of the inferred community patterns.

We estimated model parameters using Markov chain Monte Carlo (MCMC) sampling implemented in the R package 'HMSC' (Tikhonov et al., 2020). We modelled environmental effects by using the plot scores from the first three principal components of the environmental variable PCA and used growth form as a trait, model details provided in Appendix A.1 (S2.1).

2.3 Results

2.3.1 Pine legacy effects on environmental conditions

Abiotic variation among plots was consistently related to invasion history, driven largely by shifts in soil nutrients, soil moisture and canopy structure. In particular, plots with a later historical pine invasion stage had increased soil moisture and less open canopies, soil moisture also declined with time since management (Figures 2.1 and 2.2). Principal components analysis summarised these environmental gradients, with the first three axes explaining 45.6%, 30.3%, and 12.6% of the variation among plots, respectively (Figure 2.3; Table S2.2). The first component was positively associated with soil moisture and Olsen phosphorus and negatively correlated with canopy openness and pH. The second component was positively associated with available nitrogen and total carbon, and negatively associated with Olsen phosphorus. The third component was positively associated with pH and Olsen phosphorous and negatively associated with total carbon. Historical pine invasion stage was positively correlated with PC 1, indicating that later-stage pine invasions were associated with moister, more phosphorus-rich and less open conditions. Similarly, PC 1 scores were negatively correlated with time since management (Table S2.2). Neither pine invasion stage nor time since management were related to PC 2; however, time since management was negatively correlated with PC 3.

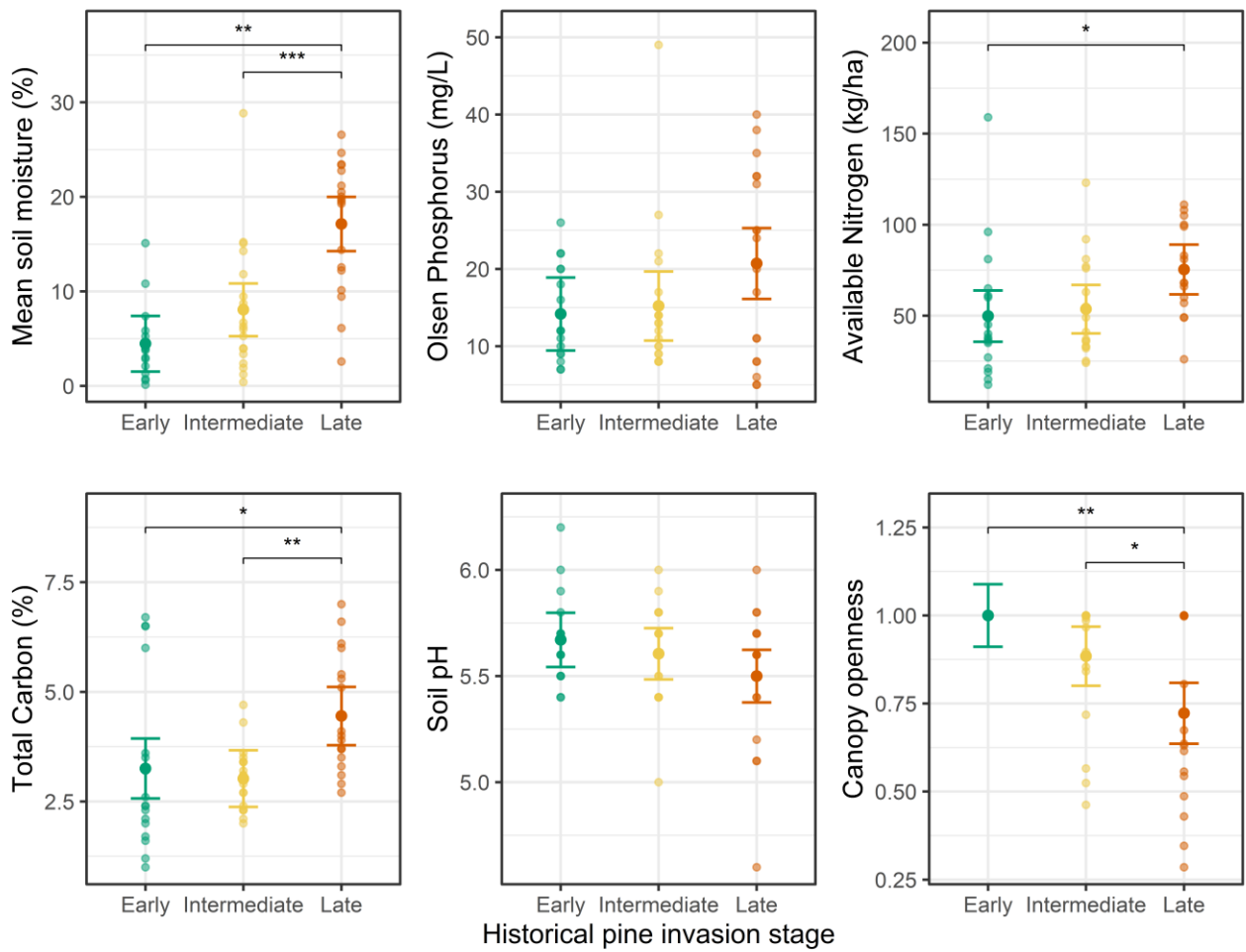


Figure 2.1 General linear models for each of the key environmental characteristics, showing the relationship with historical pine invasion stage. Points differ in colour by historical pine invasion stage (green = early, yellow = intermediate, orange = late). The larger central point is the model estimated mean, error bars show 95% Confidence Intervals. Horizontal brackets are pairwise comparisons between historical pine invasion stage. Stars show significance * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

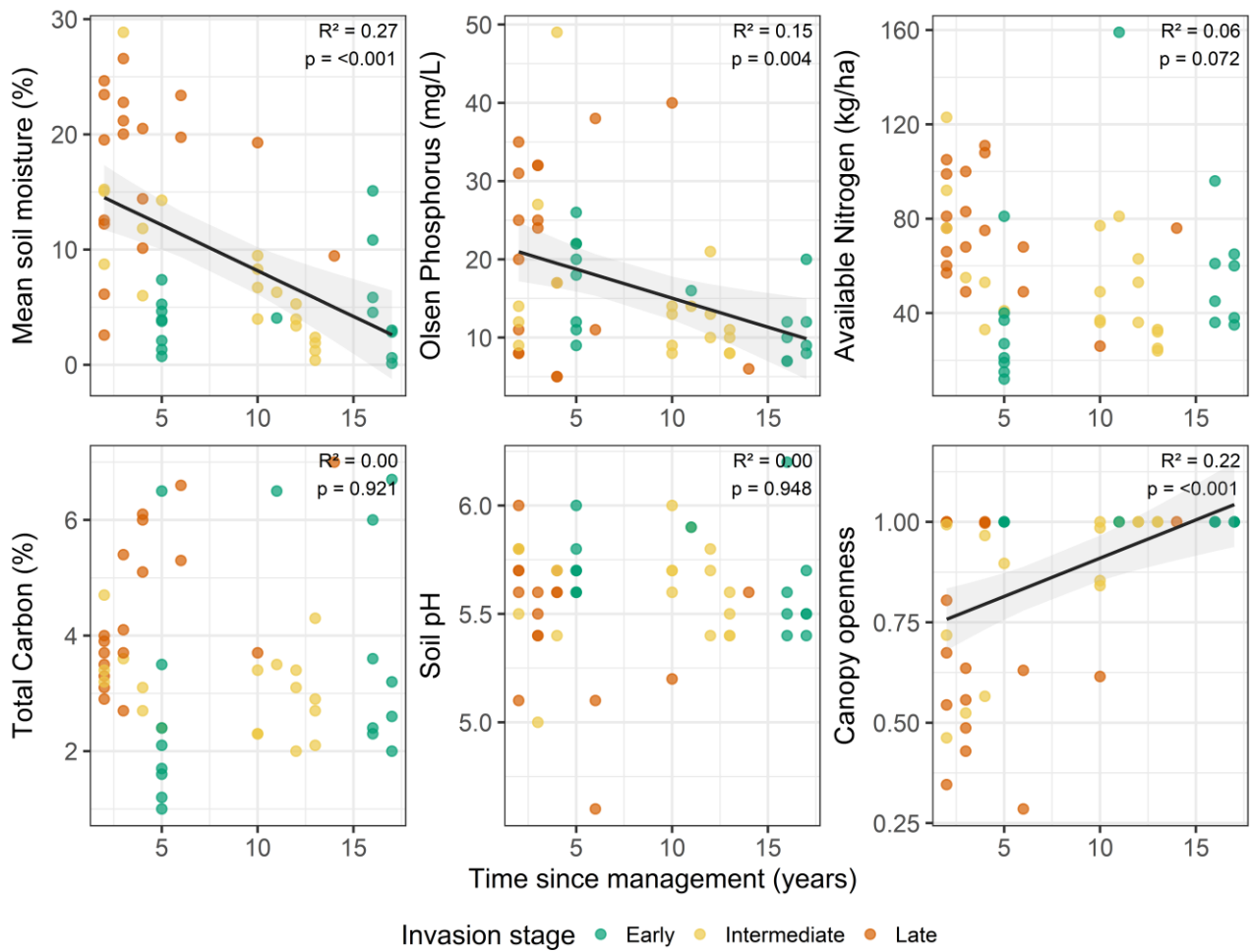


Figure 2.2 General linear models for each of the key environmental characteristics, showing the relationship with time since management. For significant relationships ($p < 0.05$), the black line shows the predicted relationship, and the grey shading is the 95% Confidence Interval. Points differ in colour by historical pine invasion stage.

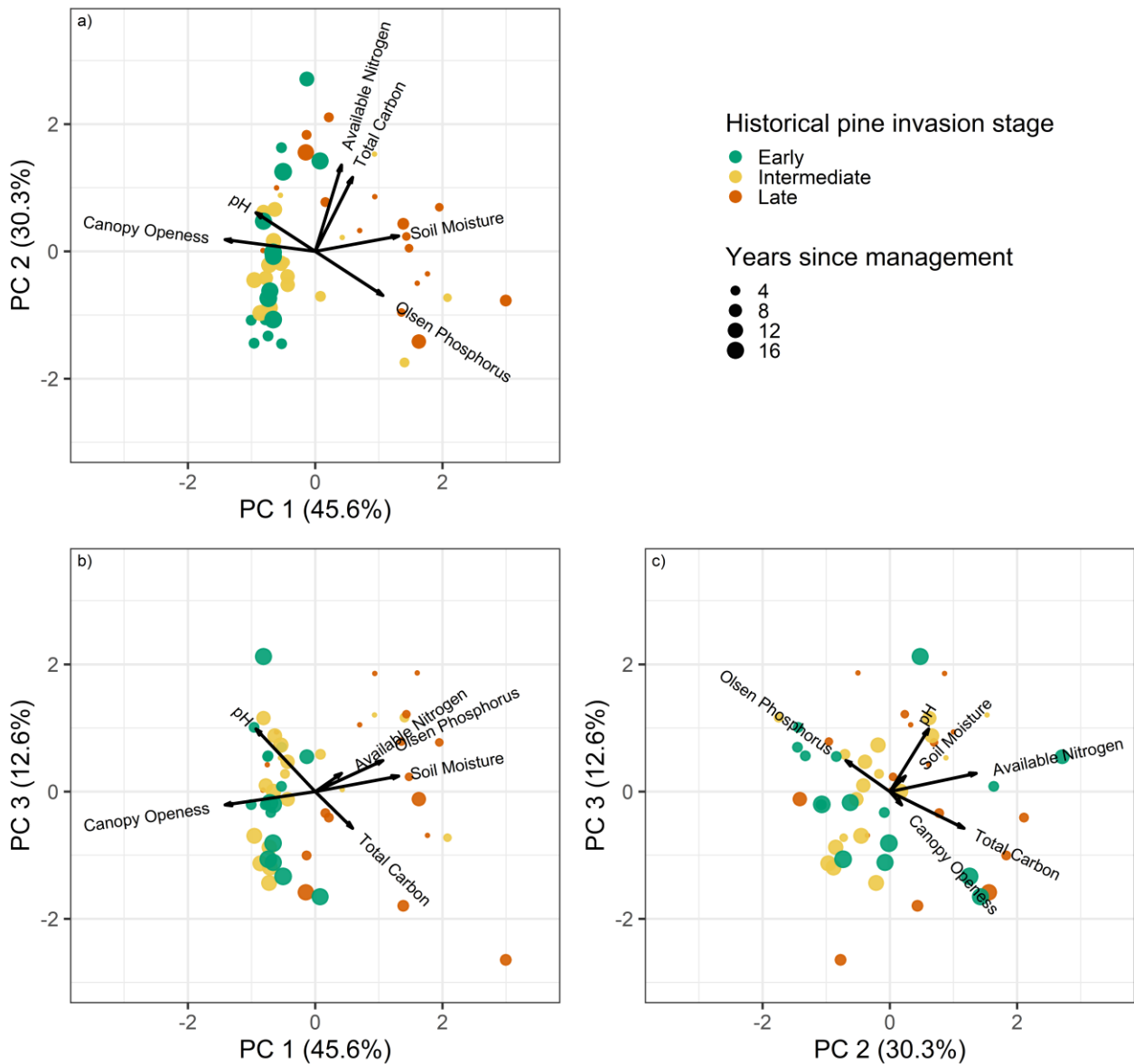


Figure 2.3 Principal Components Analysis (PCA) biplots showing how sampling plots (points) varied in their environmental characteristics (arrows). Plots are coloured by historical pine invasion stage, and their size is proportional to time in years since pine management was undertaken. All relationships shown are statistically significant ($p < 0.01$), and the length of the arrows is proportional to the strength of the relationship. The variance explained by each principal component (PC) is given as a percentage on the relevant axis. Plot a) compares the relationship between PC 1 and PC 2; b) the relationship between PC 1 and PC 3; and c) the relationship between PC 2 and PC 3.

2.3.2 Impact of historical pine invasion and management on plant communities

2.3.2.1 Plant cover

The plant community plots were dominated by a few species with most other species occurring infrequently (Figure 2.4; Table S2.3). The four most frequently observed species were all non-native, dominating the plant cover across all plots. For example, two non-native grasses *Anthoxanthum odoratum* and *Agrostis capillaris* occurred in 53 out of the total 54 plots, with a mean cover of 27% and 17%, respectively. Of the 72 species that were rare (i.e., occurred in less than 10% of plots and had a maximum cover of 1%), half (36 species) were native. There were few non-native woody species other than pine.

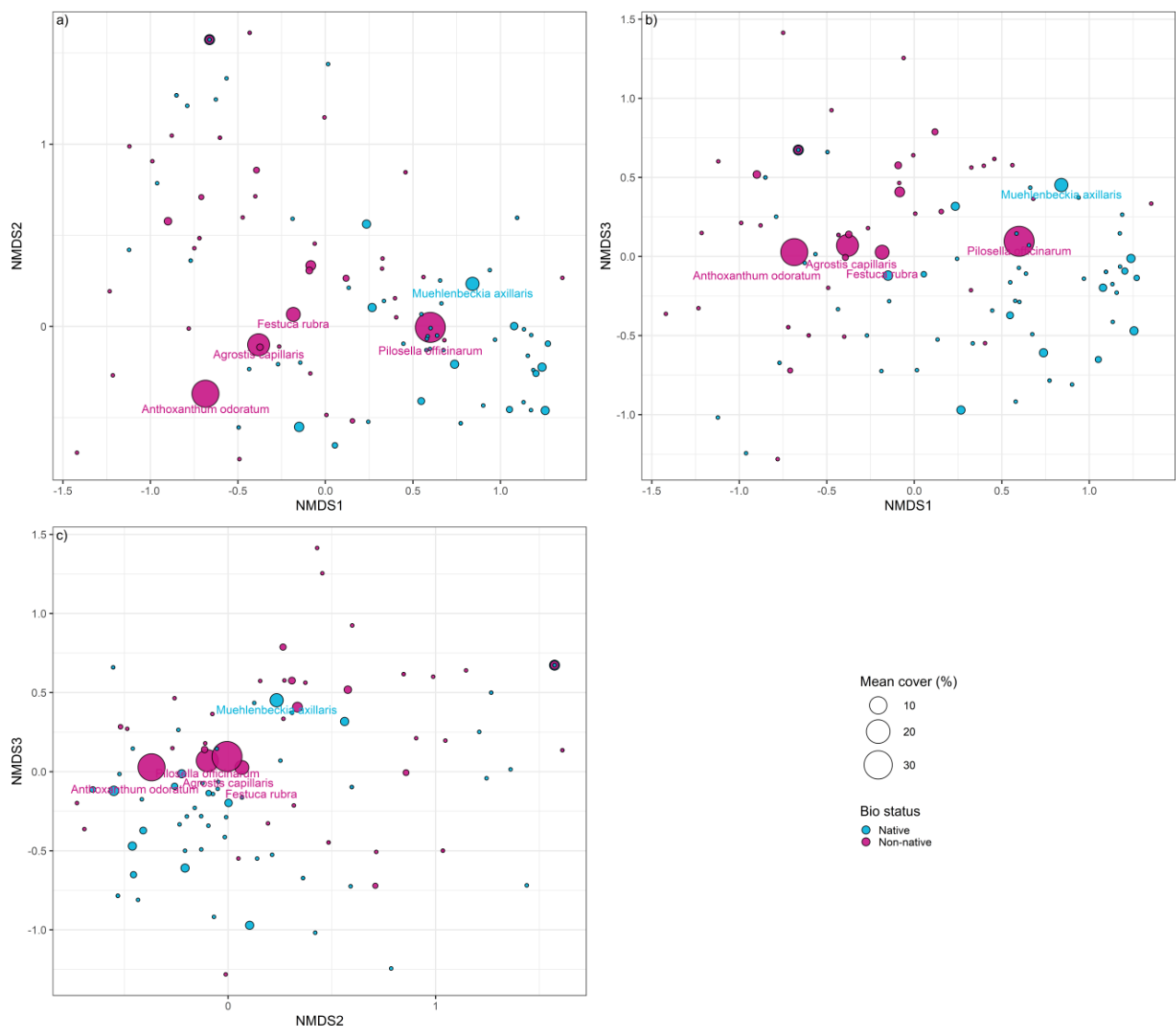


Figure 2.4 Non-metric Multidimensional scaling (NMDS) ordinations for three dimensions, showing the distribution of species recorded in plant community plots. Plot a) shows axes 1 and 3; b) axes 1 and 3; and c) axes 2 and 3. Non-native species are pink and native species are turquoise. Point size is proportional to mean species cover when present. The names of the five most abundant species are displayed. Pine species were excluded from the analysis.

Native and non-native species cover differed significantly at all three historical pine invasion stages, with non-native cover being 6.6 times greater at early stages of invasion, 15.3 times greater at intermediate stages and 18.8 times greater at late stages of invasion (Table 2.1). Native species also had lower mean percentage cover with higher historical pine invasion stages; with significant declines from early to both intermediate and late stages (Figure 2.5; Table S2.4). Non-native species cover in plots did not differ among historical pine invasion stages, although there was high variability among the late invasion stage plots. This variation was related to canopy openness, which was a measure of standing dead and live trees (Figure S2.2).

Table 2.1 Generalised linear model comparisons showing differences in species richness and percent cover between native and non-native species at different historical pine invasion stages. Stars show significance * $p < 0.05$, ** $p < 0.01$, * $p < 0.001$.**

<i>Comparison</i>	<i>Historical pine invasion stage</i>	<i>Estimate</i>	<i>Rate ratio</i>	<i>Standard error</i>	<i>z value</i>	<i>p value</i>	<i>Significance</i>
<i>Percent cover</i>	Early	1.89	6.64	0.20	-9.43	< 0.001	***
	Intermediate	2.73	15.32	0.20	-13.40	< 0.001	***
	Late	2.93	18.81	0.23	-12.96	< 0.001	***
<i>Species richness</i>	Early	-0.31	0.74	0.12	2.52	0.114	
	Intermediate	0.61	1.84	0.13	-4.68	< 0.001	***
	Late	1.09	2.98	0.18	-5.97	< 0.001	***

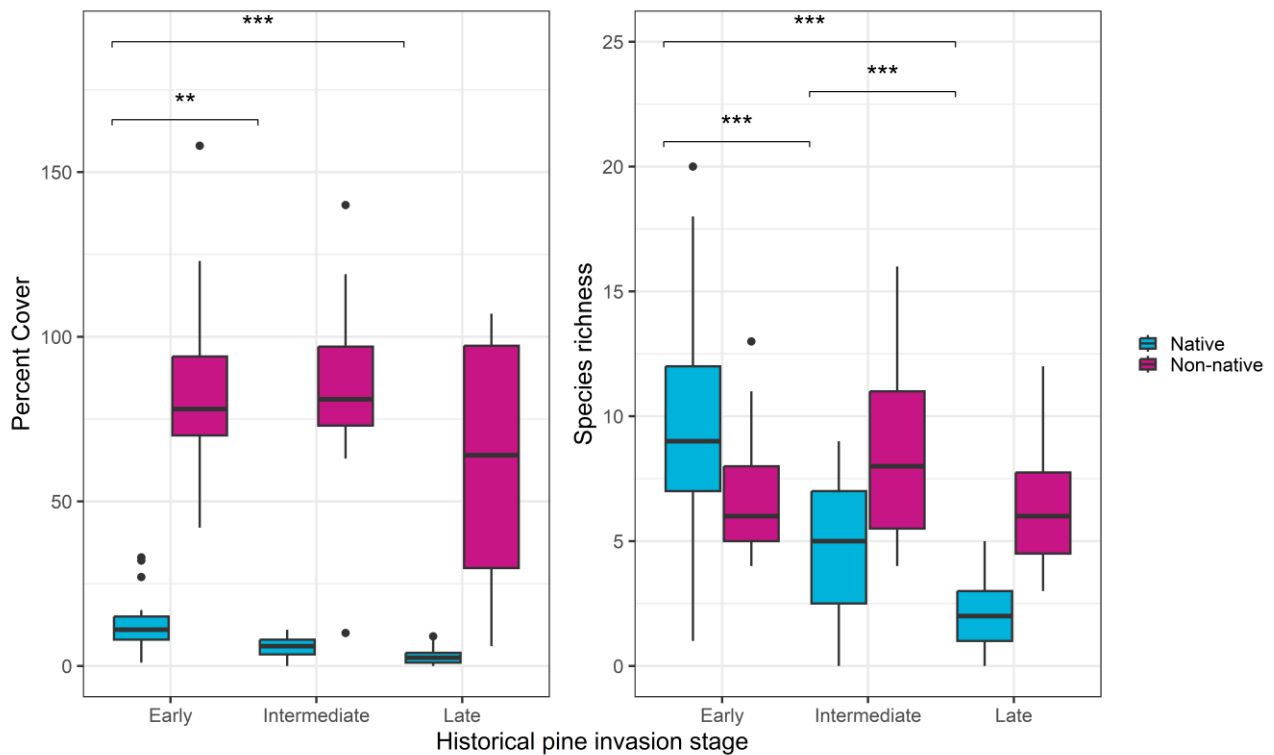


Figure 2.5 Distribution of (a) percent cover and (b) species richness across plots, categorised by the invasion stage of *Pinus contorta* at time of management. The horizontal line inside each box represents the median, the box spans the interquartile range (25th–75th percentile), and the whiskers extend to the smallest and largest values within $1.5 \times$ the interquartile range. Points beyond the whiskers are plotted individually as outliers. Horizontal brackets are pairwise comparisons between historical pine invasion stage for native species only. Stars show significance * $p < 0.05$, ** $p < 0.01$, * $p < 0.001$. There were no significant differences between historical pine invasion stages for non-native species.**

2.3.2.2 Species richness

We observed 117 plant species, of which 57 were non-native species and 60 native species, richness ranged from 3 – 26 species per plot. Native plant species richness was significantly lower in plots at later historical pine invasion stages. Compared to early stage invasion plots, there were half the number of native species in intermediate stage invasion plots, and a quarter in late stage invasion plots (Figure 2.5; Table S2.4), showing a major loss of biodiversity at the plot scale. In contrast, non-native species richness did not significantly differ among historical pine invasion stages. Non-native species richness was significantly higher than native species richness at intermediate (84%) and late (198%) pine invasion stages, but was not significantly different at early stages of invasion (Table 2.1).

Native and non-native plant species responded differently to environmental variation. The hierarchical modelling of species communities (HMSC), each based on species-level presences and absences, predicted the likelihood of occurrence for each species and the resulting species richness for each bio status category (native and non-native). The native species model showed a significant negative

relationship between predicted species richness and PC 1, with the 95% posterior credible interval below zero (Figure 2.6). In contrast, the non-native species model showed no significant relationships between total predicted species richness and any principal components (Figure S2.3). Variance partitioning of the HMSC indicated that the native species model explained 42.4% of the variation in species occurrences, and the non-native species model explained 35.2%. Overall, PC 1 (positively correlated with historical pine invasion stage and negatively with time since management) was the strongest explanatory environmental predictor with 61.3% of explained variation in native species occurrences, and 30.3% of explained variation in non-native species occurrences. PC 3 (negatively correlated with time since management) explained 16.8% for native species and 32.2% for non-native species, while PC 2 explained 12.3% for native species and 19.3% for non-native species (Figure S2.4). Bayesian posterior inference showed that individual native species that had significant responses to environmental variables predominantly had a negative relationship, while non-native species had a more variable response (Figure S2.5). Model fit statistics are provided in Table S2.5.

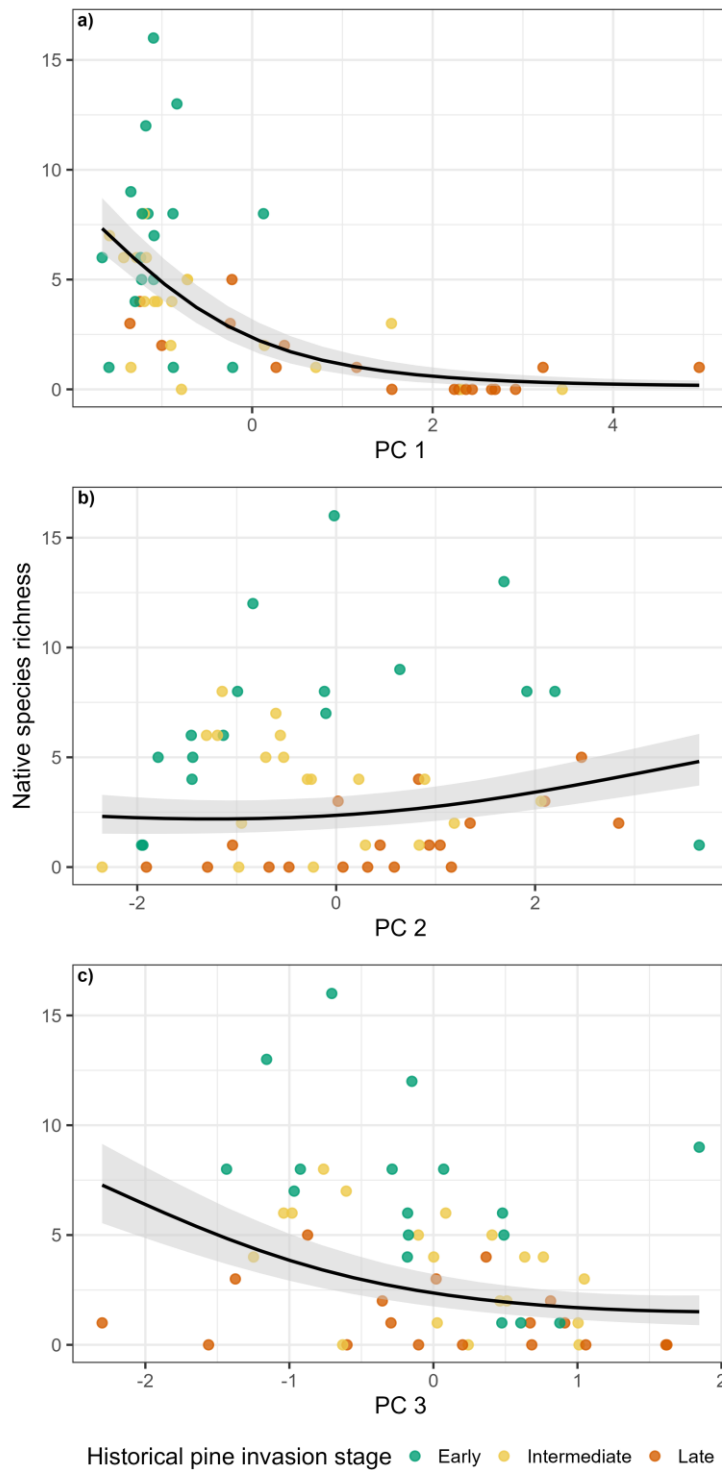


Figure 2.6 Hierarchical modelling of species communities (HMSC) comparing the relationship between predicted native species richness and plot principal component scores (black line) with 90% confidence interval (grey shading). The measured plot values are shown as points are coloured based on historical *Pinus contorta* invasion stage. Plot a) shows the relationship with Principal Component 1 (positively associated with historical pine invasion stage, soil moisture and Olsen phosphorus; negatively associated with time since management, canopy openness and pH); b) Principal Component 2 (positively associated with available nitrogen and total carbon; negatively associated with Olsen phosphorus); and c) Principal Component 3 (positively associated with pH and Olsen phosphorus; negatively associated with time since management and total carbon).

2.3.2.3 Variation among growth forms

Plant cover varied by growth form across historical pine invasion stages. Non-native grasses dominated overall plant cover, accounting for 60% of total non-native cover across all historical pine invasion stages (Figure 2.7), and their proportional cover was highest in plots at later historical pine invasion stages (Table S2.6). In contrast, the proportion of non-native herbaceous species was lower in plots at a later historical pine invasion stage. Among native species, woody plants accounted for 34% of total native cover in early stage pine invasion plots, but only 5% of total native cover in late stage invasion plots. Native orchids were present at both early (23% of total native cover) and intermediate (21% of total native cover) historical pine invasion stages, but were rare in late stage invasion plots. Native ferns were absent in plots at early stages of historical pine invasion but comprised 12% and 14% of total native cover in plots at intermediate and late stage pine invasions, respectively. These patterns among growth forms are consistent with the HMSC results, which showed that predicted species richness varied with environmental gradients (PC axes) for both native and non-native species across different growth forms (Figure 2.8).

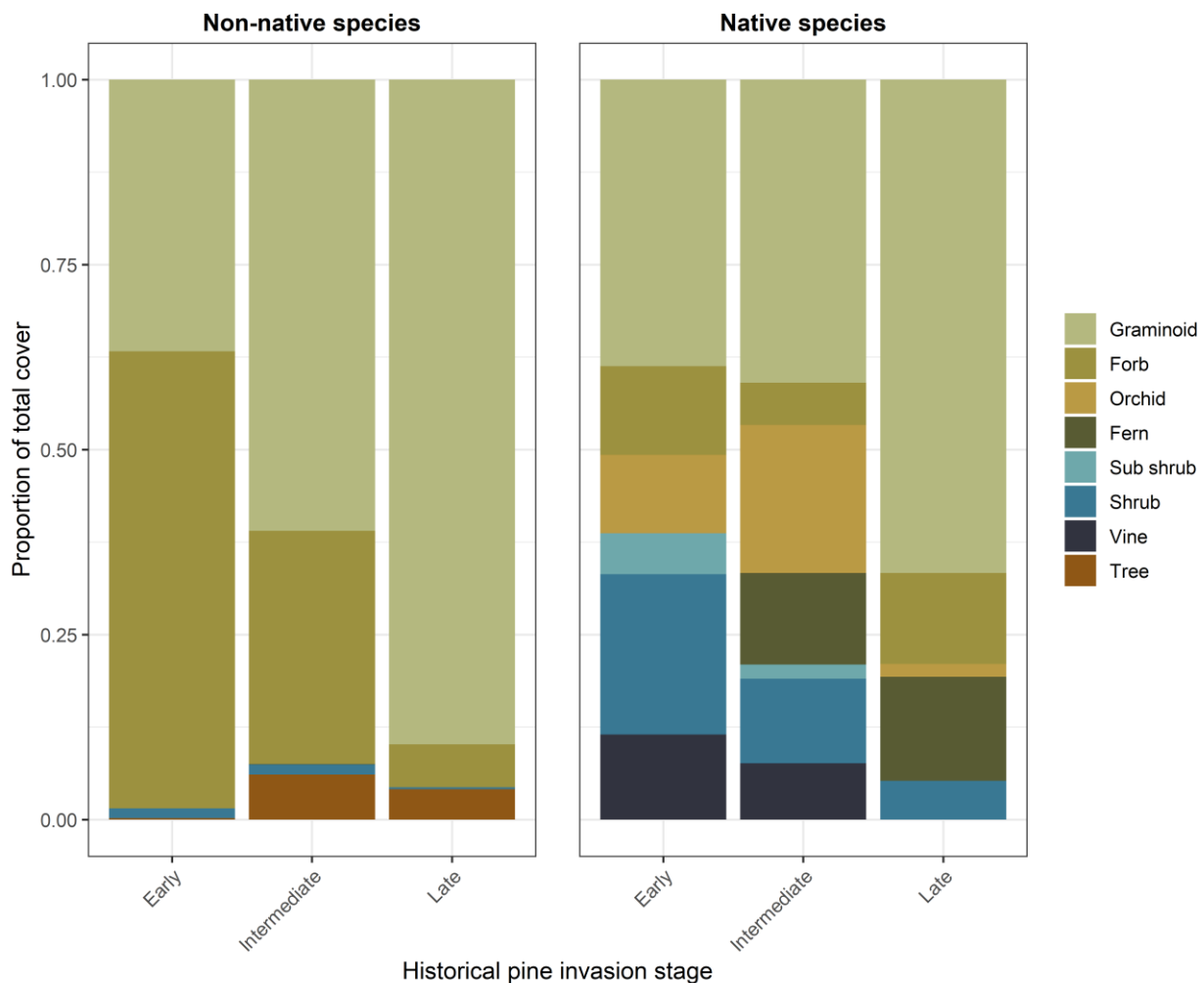


Figure 2.7 Proportion of total plant cover for non-native and native species, by growth form in plots that varied in their historical pine invasion stage.

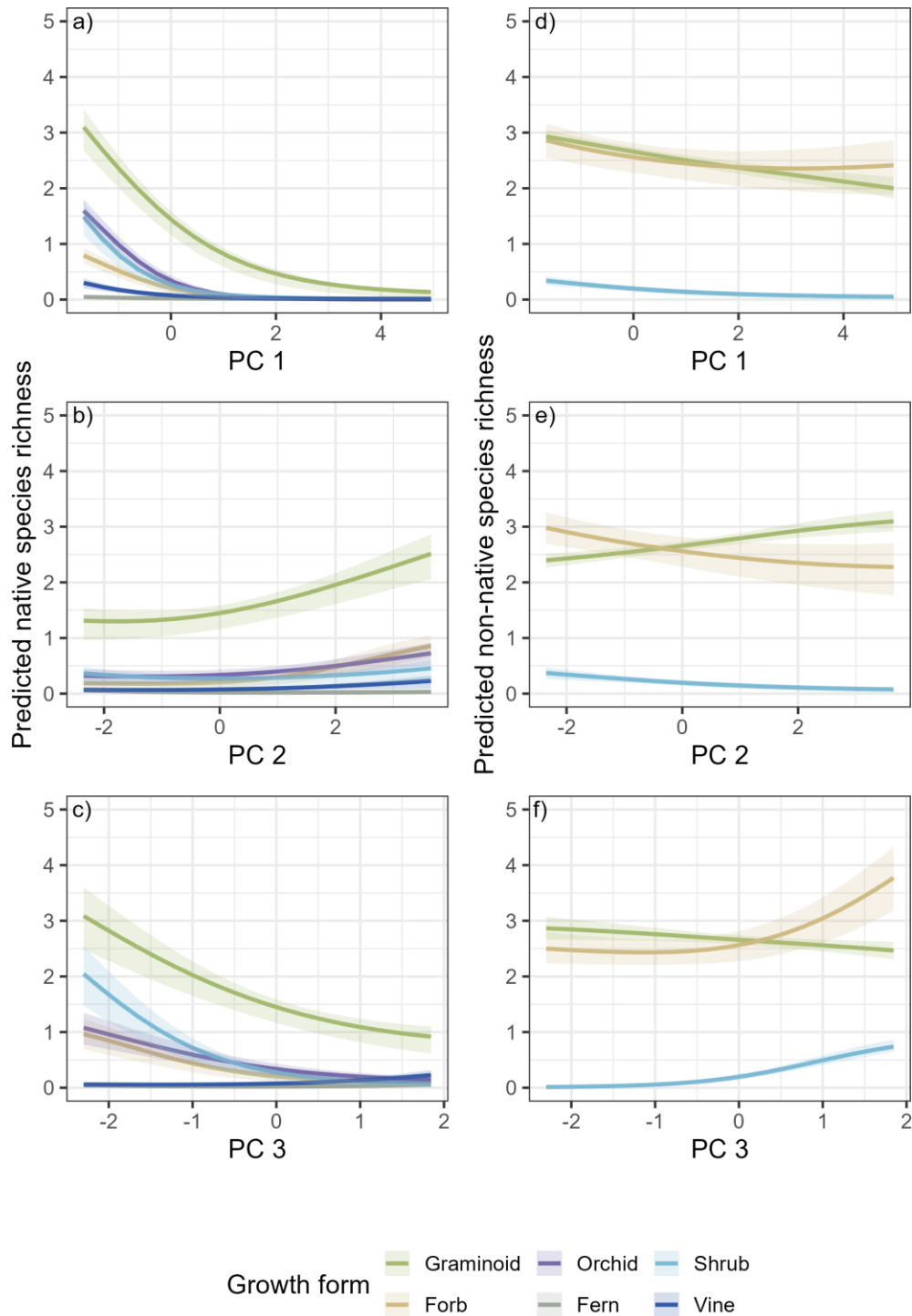


Figure 2.8 Hierarchical modelling of species communities (HMSC) results comparing the relationship between predicted species richness by growth form correlated with each of three principal components (solid lines), with 90% confidence interval (shading). Plots a-c) show predictions for native species for each of the principal components; and plots d-f) show predictions for non-native species for each of the principal components.

2.3.3 Reinvasion

Pine reinvasion was highly variable across sites, with reinvading pines occurring in fewer plots but at higher densities than surviving pines (Table 2.2). Reinvading pines made up 64% of all live pines recorded, while the remaining 36% were survivors of the original management treatment. Most reinvasion occurred in plots containing surviving coning pine trees, which accounted for 96% of all newly invading individuals. Reinvasion occurred in 13 of the 54 plots, but 93% of the total observed reinvading individuals occurred in only four plots. In contrast, surviving pines were more widely distributed, occurring in 22 plots with between zero and 30 individuals in each plot.

Table 2.2 Distribution of reinvading and surviving pines by historical pine invasion stage. Reinvaders were individuals that have established post-management, and survivors were individuals that were not killed by the management. Reinvasion counts are displayed separately for plots where a coning tree was present in the 10 x 10 m plot (In plot) or not (Out of plot).

Pine type	Invasion stage	Location of coning individuals	Count of individuals	
			Range	Mean (SD)
Reinvasion	Early	In plot	0	0.00 (0.00)
		Out of plot	0-3	1.00 (1.73)
	Intermediate	In plot	0-259	44.83 (105.00)
		Out of plot	0-8	2.67 (4.62)
	Late	In plot	0-8	1.33 (3.27)
		Out of plot	0-1	0.17 (0.41)
Survivor	Early	N/A	0	0.00 (0.00)
	Intermediate	N/A	0-30	7.50 (10.27)
	Late	N/A	0-29	8.11 (11.26)

2.4 Discussion

Our study demonstrates that previous invasion by *Pinus contorta* alters plant communities and increases resource availability for at least a decade following management. Moreover, later stages of historical invasion stage drove multiple belowground changes such as elevated Olsen phosphorus and total soil carbon, and lower pH. These findings are consistent with previous studies that report that concentrations of total carbon, available phosphorous, and available nitrogen are known to be higher, and pH lower, under both planted and wilding pine stands compared to adjacent grassland (Chen et al., 2000; Dickie et al., 2011). These soil legacies are likely to be driven by pine associations and effects on belowground biota (Sapsford & Dickie, 2023) such as shifting from bacterial to fungal functional dominance (Elgersma et al., 2011; Sapsford et al., 2022; Stinson et al., 2006). Biotic and biogeochemical changes are both linked to the stage of the

invasion (Dickie et al., 2011; García et al., 2023; Sapsford et al., 2022) and could promote reinvasion, secondary invasion, or failure of native species to recover through multiple mechanisms. However, how these long changes in soil communities and resources persist was previously unknown. Our findings support the view that invasions exert enduring legacy effects on ecological communities and ecosystems following their management.

Declines in native plant species richness and cover, and shifts in overall plant community composition, were strongly related to the invasion stage of pine invasion at the time of management. The dramatic decrease in native cover and richness with advancing invasion stages implies that there is an early threshold for limiting the impact of pine invasion on native plant communities. This is likely to be in relation to tree age and density, i.e., once trees are coning and a closed canopy has formed (Franzese et al., 2017). Although thresholds are recognised as crucial in managing invasions, they are often not quantified in a manner to guide intervention strategies (Ahmed et al., 2022; Hobbs & Humphries, 1995). These thresholds could be explicitly tested by conducting experimental management along a gradient of measured pine invasion stages and following the native community trajectory to determine the tipping point at which lasting impacts occur, which can then inform data-driven management decisions.

Historical invasion shifted plant communities from dominance by forbs and grasses with scattered shrubs, to communities dominated by few non-native grasses with scattered forbs and ferns. This change in the dominance of growth forms can be linked to species-specific responses to the alteration in soil biogeochemical processing; for example, high available phosphorous levels favour non-native grasses over native species, which are adapted to infertile soils (Dickie et al., 2014; Wardle, 1985). The reduction of herbaceous species at later historical pine invasion stages may be related to shade tolerance; we observed a negative relationship between pine invasion stage and canopy openness, indicating that standing dead and live trees continue to provide shade (Brown et al., 2015). In addition, native species declined in both richness and abundance at later historical pine invasion stages, whereas non-native grasses increased in abundance; these responses were exacerbated by later pine invasion stage prior to management, consistent with previous studies (Franzese et al., 2017; Mesacasa et al., 2022). Overall, pine invasion caused plant communities to become less species rich, more similar, and non-native -dominated, presaging ecosystem homogenisation (García et al., 2018; Olden et al., 2004).

The legacy effects of pines are driving plant community structure, in terms of both habitat suitability and biotic interactions, as shown by the modelling of species communities. Our results indicate that pines are both suppressing native species, and indirectly facilitating non-native grasses by changing the environment in a manner which is favourable, thus enabling secondary invasion. In addition to these indirect processes, direct competition between non-native grasses and native species may also be occurring. This supports a recent revision of the invasional meltdown hypothesis that proposes multiple mechanisms of meltdown, including that a single keystone invader may alter resource availability, triggering facilitation of multiple non-native species (Ricciardi & Simberloff, 2025; Simberloff & Von Holle, 1999). This is also consistent

with other studies, where pines invade and change the abiotic environment, specifically biogeochemical processing (García et al., 2023; Sapsford et al., 2022).

Reinvasion of pines following management is rapidly becoming a major concern (Dickie et al., 2022; Kremer et al., 2014). Our results demonstrate that rather than being directly related to historical invasion stage, pine reinvasion primarily occurred where some trees were not killed as part of the management effort. This suggests that management efforts should prioritise successfully removing all mature individuals to limit reinvasion. Secondary invasions by other non-native species, related to historical pine invasion stage, were more consistently observed among sites and were associated with greater influence on native plant community changes than pine reinvasion. Secondary invasion by other Pinaceae species is also a concern, as these species appear to benefit from the soil legacy effects of *P. contorta* (Dudenhöffer & Hulme, 2025b). For example, one of our plots had secondary invasion by *Pseudotsuga menziesii* and another with *Pinus sylvestris*. These findings add to the growing recognition that dominant invasive species exert a range of both direct and indirect effects in ecosystems, creating new issues for managers such as considering reinvasion, secondary invasion, or co-invasion as part of management planning (Brandt et al., 2023; Dickie et al., 2022; Zavaleta et al., 2001).

Managing invasive species in ecosystems facing multiple threats, or where invasive species may be generating a range of potential ecological outcomes, is inherently challenging (Brandt et al., 2023; Day et al., 2023; Suding et al., 2024). For example, this study has highlighted that legacy effects will continue to shape future tussock grassland plant communities, and these effects need to be considered when planning management actions (Corbin, 2025). For the ecosystem studied here, several potential management goals are possible, including managing the invasion, focussing on protecting native species, or aiming to restore the ecosystem to a pre-determined state, each of which presents unique challenges (Dickie et al., 2022). Maintaining a tussock grassland ecosystem under pine invasion requires more intensive management than, for example, a woody plant community, which are more resistant to re-invasion and would have previously existed at these sites (Dickie et al., 2022; Taylor et al., 2016b). If restoration is a goal, native shrubs are likely to be successful in re-creating a native-dominated shrubland in these dryland ecosystems and have been shown to have faster growth rates than non-native shrubs even in areas with altered nutrient and soil moisture levels (Cieraad et al., 2015). However, more initial effort will be required to re-establish woody species, particularly in highly-modified systems where native species are likely to be dispersal limited (Suding et al., 2004).

Our study of pine invasion, management and legacies for an ecosystem in which other non-native species were well established is, unfortunately, typical of many ecosystems undergoing complex changes (Day & Buckley, 2013; Suding et al., 2024). We demonstrate that past invasions exert major and lasting legacies through simplification of plant communities, losses of native species, increasing the abundance of non-native grasses, and elevating resource availability for at least 16 years following invader removal. The space for time design using past management efforts, coupled with complementary observational and

modelling approaches, provided new and generalisable insights into the duration and importance of biotic and abiotic legacies. Overall, our findings demonstrate that both biotic and abiotic legacies of invasive species determine whether the ultimate outcomes of management for invasions or biodiversity are achieved in practice.

Chapter 3

Invasion Legacies of *Pinus Contorta* Drive Successional Trajectories of Short-Tussock Grassland Plant Communities

3.1 Introduction

Widespread tree invasions can fundamentally reshape ecosystems (Martin et al., 2009; Rundel et al., 2014), yet the mechanisms through which persistent legacies influence native plant communities is poorly understood. Invasive trees are a global driver of biodiversity loss and ecosystem-level change (Linders et al., 2019; Simberloff, 2011). They often act as ecosystem engineers because of their large biomass, long lifespans, and capacity to alter ecosystem processes (Richardson et al., 2014). This can result in changes to soil abiotic properties and microbial communities, that often persist following their removal (Crooks, 2002; Ehrenfeld, 2010). The management of invasive plants is often undertaken with the assumption that removal leads to ecosystem recovery; however, recovery can often be slow, incomplete, or result in alternative vegetation types (Corbin & D'Antonio, 2012; Grove et al., 2015; Ogden & Rejmánek, 2005; Stephens et al., 2009).

Persistent legacy effects can influence the trajectories of native community recovery (Cuddington, 2011; Wardle & Peltzer, 2017). Previously invaded sites often do not simply revert to a pre-invasion state. Instead, communities may experience reinvasion by the same species or undergo secondary, “management-mediated” invasions in which other non-native species increase in abundance after the primary invader is removed (O'Loughlin & Green, 2017; Pyšek & Richardson, 2010; Simberloff & Von Holle, 1999). Sites within highly modified agricultural landscapes are particularly susceptible to secondary invasion due to high propagule pressure and altered disturbance regimes (Driscoll et al., 2013; Wiser & Buxton, 2008). In some cases, the legacy effects of the primary invader may continue to influence community assembly long after removal (Chang & HilleRisLambers, 2016). Persistent abiotic legacies can redirect successional pathways away from native recovery and toward novel or degraded community states (Flory & Clay, 2010). Following the targeted removal of a single species, biotic interactions are likely to be important in shaping trajectories (Prior et al., 2018), and re-invasion, secondary invasions, or recovery of native species are all possible outcomes (Pearson et al., 2016; Pyšek & Richardson, 2010; Zavaleta et al., 2001). Understanding these trajectories requires considering processes operating at both community and landscape scales (Catford et al., 2009; Chang & HilleRisLambers, 2016).

Non-native Pinaceae (pines) are invasive and cause ecosystem level change (Dickie et al., 2014; Nuñez et al., 2021). Invasive pines have become a dominant driver of ecological change in many New Zealand tussock grassland ecosystems (Peltzer, 2018). Their invasion and subsequent removal can cause both abiotic and biotic legacies that continue to influence plant community trajectories for many years after

management has been undertaken. This includes causing a long-term shift in soil nutrient cycling which promotes the growth of non-native grasses and herbs, even after pines have been removed (Dickie et al., 2014). Following invasion by pines native plant communities become simpler (i.e. declining richness and abundance), again this persists following management (Chapter 2). Soil legacies caused by invading pines are known to persist and are linked to initial invader abundance (Chapter 2), echoing patterns observed globally, particularly with the invasion of woody species (Franzese et al., 2017; Grove et al., 2015). However, the drivers underlying these patterns, and how they interact, are still largely underexplored.

Essential for understanding the trajectories of plant communities after the management of invasive woody species is disentangling both direct and indirect effects of the invasion. Of interest is determining whether an invasive species exerts influence on post-management communities through substantive changes to soil properties, or via biotic interactions, including competition from reinvading pines or secondary invaders such as non-native grasses, or both. There is a general lack of understanding of how legacy effects of plant invasions shape long-term native community structure, specifically how different effects interact, i.e., a whole system approach (Brandt et al., 2021; Zavaleta et al., 2001). This understanding is key for conservation management, specifically for reaching desired outcomes when the aim is to enhance conservation values and develop a system which is sustainable in the long term (Hobbs & Norton, 1996; Ruiz-Jaen & Mitchell Aide, 2005).

Here, we use a chronosequence of invasion and management to investigate such causal mechanisms. We assess the relative importance of historical pine invasion stage, soil legacies, secondary invasion and reinvader in shaping tussock grassland communities following invasion of *Pinus contorta* Loudon over three decades, and its subsequent management. Our overarching aim was to identify the pathways through which these factors influence successional trajectories and to identify the drivers. Specifically, we hypothesise that invasion legacies have the potential to alter successional pathways by influencing native plant community structure and species richness both directly, via the effects of competition across the full trajectory of invasion, and indirectly, through persistent soil legacies, competition from secondary invaders, or subsequent pine reinvader. Thus, our overall aim with this study was to identify the pathways through which these factors influence observed successional trajectories associated with the effects of long-term woody invasion in this grassland ecosystem.

3.2 Methods

3.2.1 Study area

We evaluated the impacts and legacies of pine invasions and removal in Te Manahuna / the Mackenzie Basin, within the South Island of Aotearoa / New Zealand, (WGS84 -44.22 S, 170.13 E). The area is a large glacial intermontane basin covering 269,000 ha at an elevation of 375 – 800 m a.s.l., and is predominantly of fans, moraines and outwash terraces (Espie et al., 1984; Peart & Woodhouse, 2020). The landscape is highly modified, and although it has been managed as a semi-productive landscape for over a hundred years, still

contains areas with high biodiversity value (Day & Buckley, 2013; Mark et al., 2013). The current vegetation is predominantly tussock grassland, with some shrubland (Duncan et al., 2001; Meurk et al., 2002). The Mackenzie Basin has been subjected to numerous waves of invasion by both mammals and plants, with the widespread invasion of pines having a significant impact (Mark et al., 2013). Pines started spreading from shelterbelts and subsequently scenic and commercial plantations, this was noticeable from the 1970s onwards, although invasions predominantly remained sparse (Belton & Ledgard, 1991). Invasions increased in density and became more widespread, expanding from the late 1990s onwards (Young, 2016).

3.2.2 Drivers of plant community change

To evaluate the mechanisms by which historical pine invasion and subsequent management have influenced native plant communities, we examined causal pathways using piecewise structural equation modelling (SEM) (Grace et al., 2010; Lefcheck, 2021). We evaluated the direct and indirect effects of historical pine invasion, soil legacies, reinvasion, and secondary invasion on native plant community composition and native species richness (Figure 3.1). The primary aim was to test whether native plant communities and native species richness are directly related to invasion history or mediated through indirect effects, based on *a priori* hypotheses (Table 3.1). In the modelling we incorporated measured biotic and abiotic variables in plant community plots and calculated long distance dispersal using a propagule pressure metric, as described below.

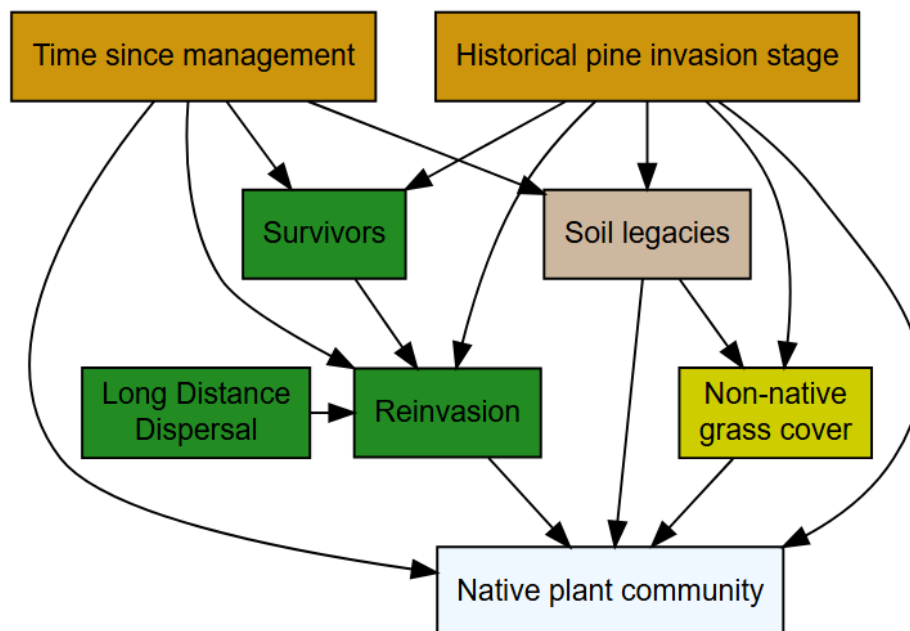


Figure 3.1 Structural Equation Model with potential pathways based on *a priori* hypotheses. Colours indicate causal mechanisms. Orange = direct pine effects, tan = soil legacies, dark green = reinvasion, olive = secondary invasion, pale blue = native plant community composition.

Table 3.1 Hypotheses and predictions of the drivers of native plant communities used in structural equation modelling, and the potential pathways through which these mechanisms act.

<i>Hypothesis</i>	<i>Prediction</i>	<i>Potential Pathways</i>
Historical pine invasion stage is the key driver of both biotic and abiotic factors, directly influencing native plant communities.	Invasion stage has a negative relationship with NMDS 1 and native species richness. Time has a positive relationship, showing community recovery.	Pine invasion stage + Time since management → NMDS 1 / Species richness
Soil legacies are related to historical pine invasion stage, and these legacies persist over time.	Invasion stage has a positive relationship with soil legacies because they are stronger after denser invasions; but there is no relationship with time indicating that the legacies persist.	Pine invasion stage + Time since management → PC 1
The native plant community is influenced by soil legacies from pine invasion.	Soil legacies have a negative effect on the native plant community.	PC 1 → NMDS 1/ Species richness
Secondary invasion by non-native grasses is directly related to historical pine invasion.	Soil legacies create conditions more suitable for non-native grass growth than for native plant species.	Pine invasion stage + Time since management → Non-native grass cover
Secondary invasion by non-native grasses is related to persistent soil legacies.	Increased nutrient availability from pine invasion promotes secondary invasion by non-native grasses, so we predict a positive relationship between PC 1 and grass abundance.	PC 1 → Non-native grass cover
Competition from non-native grasses influences resulting native plant communities.	Non-native grasses outcompete native species, having a direct negative effect.	Non-native grass cover → NMDS 1/ Species richness
Reinvasion is driven directly by propagule pressure from surviving trees and long-distance dispersal.	The number of invading individuals is positively related to both the number of surviving trees and propagule pressure from long distance dispersal.	Surviving trees and saplings + Long distance dispersal → New recruits
Reinvasion is driven directly by propagule pressure from standing dead trees immediately following management.	Dead trees continue to release seed creating a positive relationship with invasion stage and a negative relationship with time.	Pine invasion stage + Time since management → New recruits
Reinvasion by pines has limited influence on the plant community, unless it is more advanced than the initial invasion.	Reinvasion levels are generally low resulting in no relationship between the number of invading individuals and plant community outcomes.	New recruits → NMDS 1 / Species richness

3.2.3 Plant community plots

Within areas with known *Pinus contorta* invasion and management history we selected five study sites from across the Mackenzie Basin that had similar environmental characteristics (Chapter 2). The invasion stage of pines at the time of management had not been measured quantitatively, so we categorised sites into three levels based on a combination of density and the size of individuals, following standard definitions (Ministry for Primary Industries, 2014) ‘Late’ invasion stage, where trees had formed a closed canopy, with greater than 400 stems per ha; ‘intermediate’ invasion stage, where many small trees and saplings were present, but the canopy had not yet closed, with 20 – 400 stems per ha; and ‘early’ invasion stage, with scattered small individuals, and less than 20 stems per ha. Pines at all sites had been managed between 2006 – 2020 with herbicide as the primary means of killing individuals and managing their spread (Rolando et al., 2025). Within these sites we measured 54, 10 × 10 m plant community plots to quantify species composition, soil legacies and reinvasion (Chapter 2). For each plant community plot we derived the pine invasion stage at time of management and the time since management was undertaken, the count of pine individuals that survived the herbicide treatment (saplings and trees only, we excluded seedlings because they are not a seed source), the count of pine individuals that have established following treatment (i.e., reinvasion) and the cover of non-native grass species.

To investigate how historical pine invasion and subsequent management affects native plant communities we used data of species’ occurrences collected within the plant community plots to undertake non-metric multidimensional scaling (NMDS) of native species only. There were four plots that had no native species so did not contribute to the NMDS. We used Bray-Curtis dissimilarities of species’ cover scores within plots after a square root transformation and a Wisconsin double standardisation (Faith et al., 1987; McCune & Grace, 2002). Species scores were calculated as weighted averages (proportional to species abundance), based on plot scores (ter Braak & Looman, 1986). The first axis of the NMDS was used to represent native plant communities (Figure S3.1). To relate the native species ordination back to the full plant community, we compared the native-species ordination axis with the full community ordination based on all species except for pines by applying vector fitting using the ‘envfit’ function. To evaluate the degree to which the native-only ordination captured the structure of the full plant community we conducted a Procrustes analysis and tested the correlation between configurations using the ‘protest’ function with 9,999 permutations (Legendre & Legendre, 2012). Both tests were conducted using the R package ‘vegan’ (Oksanen et al., 2013).

As a metric of the pine abiotic legacy effects, we utilised the key soil variables identified in Chapter 2, namely soil moisture, Olsen phosphorus, potentially available nitrogen, total carbon, and pH. Due to correlation among some of the variables, we used a Principal Component Analysis (PCA) implemented using the ‘princomp’ function (Oksanen et al., 2013) to characterise the relationships among these environmental variables. The first principal component (PC 1) explained 39.5% of variation and was positively associated with soil moisture, total carbon, available nitrogen and Olsen phosphorous, and negatively associated with

pH (Figure 3.2). Correlation of PC 1 with historical pine invasion stage was positive and with time since management was negative. The second principal component (PC 2) explained 34.7% of variation and was positively associated with Olsen phosphorous and soil moisture, and negatively associated with pH, available nitrogen and total carbon. The third principal component (PC 3) explained 14.6% of variation, and subsequent components all explained less than 10% of variation.

All analyses were conducted in R version 4.5.0 (R Core Team, 2025), and data manipulation was carried out using the R package ‘dplyr’ (Wickham et al., 2019). Community analyses were carried out using ‘vegan’ (Oksanen et al., 2013).

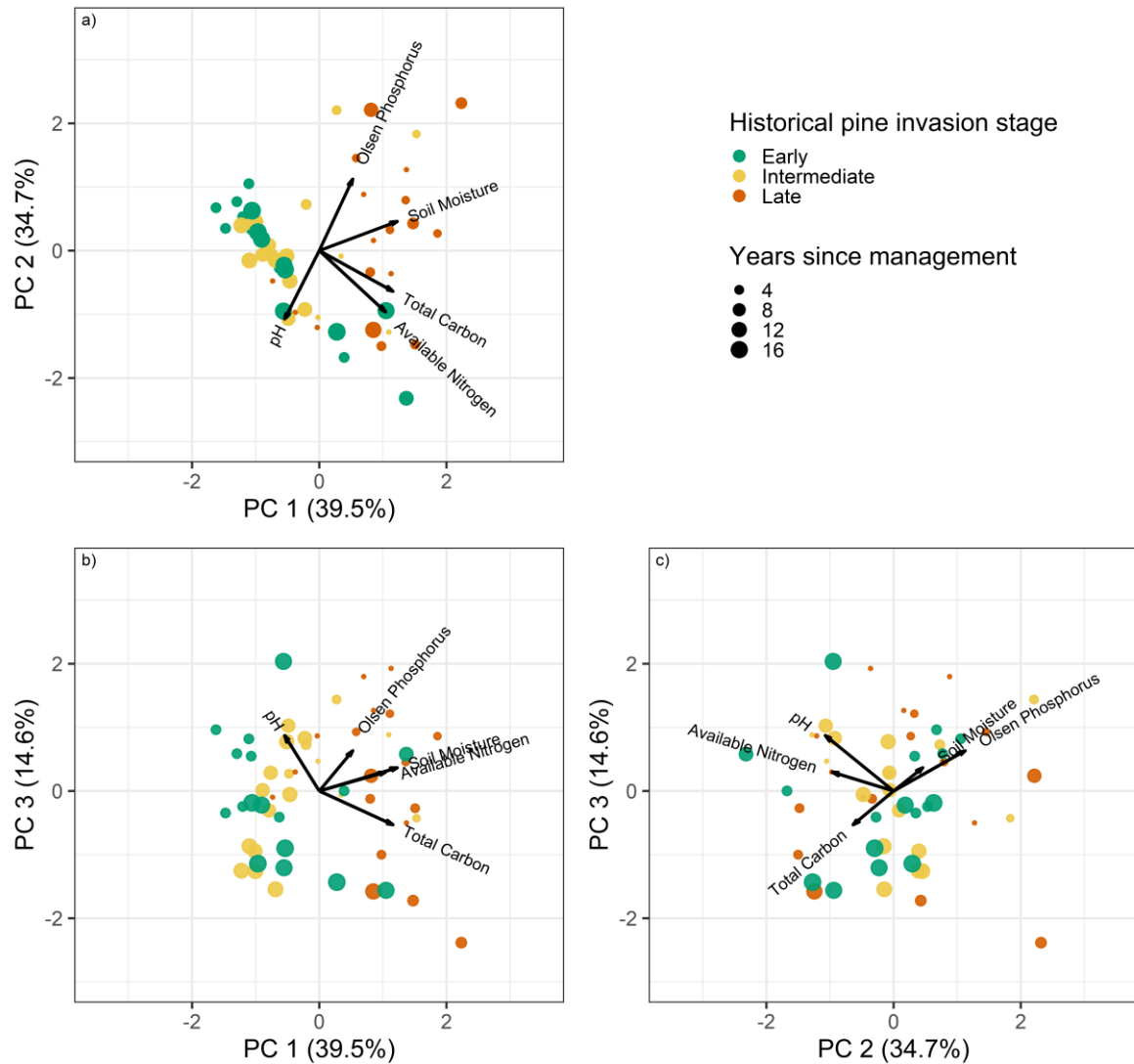


Figure 3.2 Principal Components Analysis (PCA) biplots showing variation among sampling plots (points) in relation to soil properties (arrows). Plots are coloured by historical pine invasion stage and their size is proportional to time in years since pine management was undertaken. All relationships shown are statistically significant ($P < 0.01$), and the length of the arrows is proportional to the strength of the relationship. The variance explained by each principal component (PC) is given as a percentage on the relevant axis. Plot a) compares the relationship between PC 1 and PC 2; b) PC 1 and PC 3; and c) PC 2 and PC 3.

3.2.4 Long distance dispersal

We estimated propagule pressure for each plot location using a mechanistic Wald Analytical Long-distance Dispersal (WALD) model (Katul et al., 2005; Thompson & Katul, 2008), which has been adapted in previous studies of pine dispersal in New Zealand (Caplat et al., 2012; Wyse & Hulme, 2021a). The WALD distribution is an inverse Gaussian model used to estimate seed dispersal distances, specifically the dominance of short distance dispersal with a tail of rare long distance dispersal events. The two parameters are the mean dispersal distance and a shape parameter to define the distance decay rate, which together characterise the physical processes and biological traits of seed dispersal by wind (Caplat et al., 2010). For the model parameters we utilised a combination of data from plant community plots, aerial image analysis and supplemented this with data available from relevant literature (Table 3.2).

Table 3.2 Parameters used in the WALD dispersal model to estimate relative propagule pressure for each plant community plot.

<i>Parameter</i>	<i>Value</i>	<i>Specification</i>	<i>Data source</i>
<i>Mean horizontal wind speed ($\bar{U}$)</i>	3.72 m/s	Lake Tekapō climate data	(Macara, 2016)
<i>Variance in vertical wind speed (σ_w)</i>	0.2 m/s	Sensitivity analysis	Based on values from (Caplat et al., 2012)
<i>Turbulence co-efficient (κ)</i>	0.4 m/s	Von Karmen constant	(Caplat et al., 2010; Katul et al., 2005)
<i>Seed terminal velocity (v_{t_s})</i>	0.68 m/s	<i>Pinus contorta</i> specific value	(Wyse & Hulme, 2021a)
<i>Seed release height (h_r)</i>	24.5 m	<i>Pinus contorta</i> specific value	Mean height from NZ traits database
<i>Surrounding vegetation (h_c)</i>	Mean top height per plot (m)	Mackenzie Basin data	Chapter 2

Parameterising the dispersal kernel component of the WALD model involved assigning *P. contorta* specific values for seed terminal velocity and seed release height (mean maximum species height), mean horizontal wind speed, and plot-specific canopy height (Table 3.2). The shape parameter of the kernel incorporated vertical wind speed variability and turbulence; data for vertical wind speed was not available at this location, so we conducted a sensitivity analysis using the range of values recorded in (Caplat et al., 2012) at 0.1 m/s intervals to find the inflection point.

We first identified the distance at which 99% of seeds would be expected to land based on a WALD dispersal kernel, following Wyse and Hulme (2021a). We set an initial upper distance of 10 km because, while most *P. contorta* dispersal occurs within 100 m of the parent tree, long-distance dispersal is recorded at 8 – 10 km but increasingly rare at longer distances (Ledgard, 1988; Ledgard, 2001; North & Ledgard, 2005). The model identified that for our parameters the distance that 99% of seeds would land within for any of our plant community plots was 259 m.

3.2.4.1 Pine tree locations

To identify locations of pine trees that were a contributing seed source, we used aerial imagery (LINZ 2021) within a 1 km radius of each plant community plot. This distance was selected based on the WALD dispersal kernel results, which indicated that trees beyond 1 km have a minimal contribution as a seed source, and therefore contribute little explanatory value to the final dispersal model. We identified raster cells that were likely to be pine trees by creating an RGB-based spectral mask based on values from training polygons and refining the mask with green-difference and texture filters to ensure that tree patches were extracted with a high level of accuracy. We resampled the raster to approximate the size of tree crowns, converted these to point locations and filtered these points using land cover types to minimise mis-classification (Figure 3.2).

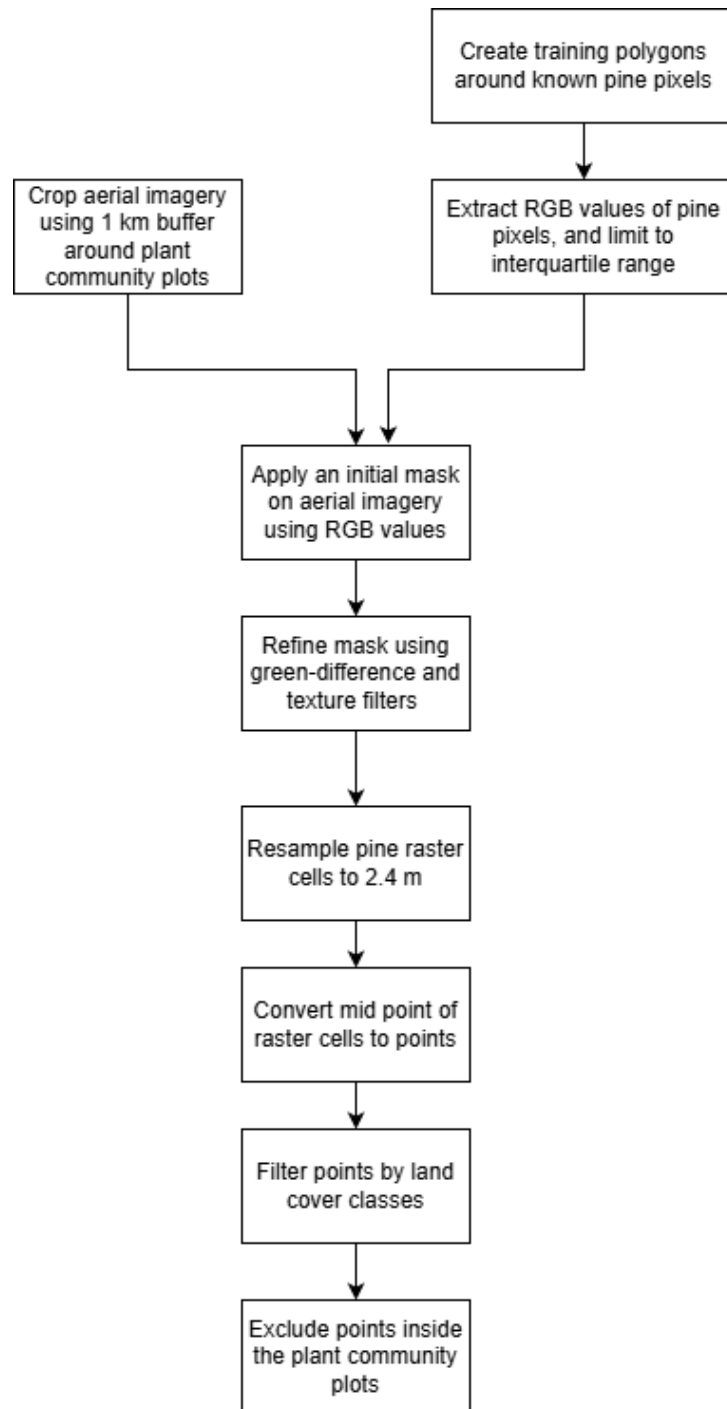


Figure 3.3 Workflow for creating point locations of pine trees from aerial imagery. Training polygons were created in ArcGIS Pro, all subsequent steps were undertaken in R using the ‘terra’ package.

To develop a training dataset to identify pines, first, we hand-digitised 183 training polygons representing known pine canopies on aerial imagery to a distance of 3 km from plot locations to ensure we were sufficiently sampling variation in pine spectral characteristics (Foody et al., 2006). These polygons provided representative pine pixels from which we extracted the distribution of RGB values characteristic of pine canopies. For the area within each 1 km buffer, we created a mask by applying three criteria. First we

generated an initial pine mask by filtering the pixels to retain those within the identified RGB spectral ranges (Upadhyay et al., 2016). We visually compared masks produced using different percentile thresholds (e.g., retaining between 30–70% and 10–90% of the training sample RGB values, in 5% increments) to assess over and under classification relative to the imagery. Based on this inspection, we selected the interquartile range (25–75%) of RGB values as the optimal threshold for identifying pine-coloured pixels.

To improve the discrimination of pine trees from other vegetation in the imagery, we combined the RGB-based mask with two additional spectral and spatial features: A green difference index to capture the darker green colour characteristic of pine, and a local texture measure to distinguish between the uneven canopy of trees compared to the smoother texture of grassland (Dong et al., 2025; Lu & Weng, 2007). We calculated a green difference index for each pixel, defined as $G-(R+B)/2$, and excluded all pixels with index values below the 25th percentile of those observed in the pine training samples (Signorelli et al., 2025). Canopy texture was incorporated by computing the local standard deviation of the green band within a 3×3 moving window (Culbert et al., 2012; Szantoi et al., 2013). Pixels with texture values below the 25th percentile of pine samples were removed, as these low-variation areas are more typical of grass (Wood et al., 2012). All thresholds were derived directly from the distribution of values in the training polygons using interquartile-range-based selection. The final pine mask retained only pixels that satisfied all three criteria of RGB range, green difference and texture. Incorporating the green difference and texture criteria substantially improved classification performance relative to RGB filtering alone, particularly by reducing misclassification of high-producing grassland, shrubland, and non-pine species of trees.

To convert the raster cells identified as pine trees into point locations we resampled the raster to a resolution matching a minimum-detectable tree-crown size (2.4 m), following Sprague et al. (2019), who found that most *P. contorta* trees with canopies larger than 2.5 m were identifiable. They also found that nearly 80% of trees were coning at this size, which matches our goal of quantifying propagule pressure. During resampling each new cell was assigned a pine or non-pine label based on the dominant value of the underlying pixels; in cases where pine and non-pine pixels were equally represented, the cell was assigned as non-pine to minimise the incidence of lone pixels, thus reducing noise (Coulston et al., 2014). After resampling, each raster cell represented an individual tree, and we converted the centroid of each cell to a point to produce a spatial point dataset of tree locations. We then excluded tree points falling in New Zealand land cover classes (LCDB v6(Manaaki Whenua - Landcare Research, 2025a) that were not classed as vegetation (specifically, "Gravel and Rock", "Lake or Pond", "River", or "Transport Infrastructure"), and those from "Deciduous hardwoods" which are unlikely to be pine and instead were misclassifications based on similar spectral signatures that we were unable to resolve with the masking process. The LCDB classification did not match the aerial imagery in one location, so we reclassified this area from 'low producing grassland' to 'deciduous hardwoods'. This process of filtering based on land cover resulted in discarding 10,436 points (0.05%). We then excluded points within a 7.07 m radius of each plot centre, because for short distance dispersal we utilised the tree count data from within the plots instead of the

modelled pine locations. The remaining points were the final tree locations used in the propagule pressure calculations (Figure S3.2).

We carried out an accuracy assessment of the pine classification by randomly selecting 50 tree points, and also randomly generating 50 points in areas classified as non-pine. We then visually inspected the pixels from the aerial image to assign a class of pine or non-pine to each point and compared this to the calculated classification (Congalton, 1991). The accuracy assessment showed 90% of points correctly classified as pine and 92% correctly classified as non-pine, suggesting that our image processing and filtering procedures were producing an adequate representation of pine source areas. Spatial data were analysed using the R package ‘terra’ (Hijmans et al., 2022).

3.2.4.2 Propagule pressure

We calculated a relative measure of propagule pressure for each plot based on the probability of long-distance dispersal. For each plant community plot, we calculated the distance from the plot to every tree point identified from the aerial imagery within a 1 km buffer. We applied the WALD dispersal kernel with site and species-specific parameters (Table 3.2) for each location to give the contribution of each tree to propagule pressure for that plot. Contributions from all trees were summed to give a relative propagule pressure value, reflecting the weighted likelihood of seed arrival at each plot.

The relative propagule pressure values ranged between 0 and 27.14. The dominant input influencing the outcome of the model was the tree locations. To test if these results were plausible, we compared the plot-based propagule pressure metrics against an independently generated supervised pixel-based vegetation image classification (detailed in Chapter 3) by creating a 1 km buffer around the plant community plots to extract a comparable dataset. We then calculated the percentage of pixels classified as pine trees within these buffers. We compared the percent cover of pine from the prior image classification against the propagule pressure metric to see if they aligned. The correlation was high (Pearson’s $r = 0.76$), indicating that our method for extracting tree locations was plausible (Figure S3.3). Variation is expected because the WALD kernel takes into account distance whereas our estimate of tree cover is a single value within the buffer.

3.2.5 Structural equation modelling

We identified the potential causal pathways based on *a priori* hypotheses (Table 3.1) and set up five linear models to incorporate into the overall structural equation model. We set up two separate structural equation models, one with plot scores on NMDS 1 as the primary response variable, which was a measure of native plant community composition, and a second model with native species richness in plots as the primary response variable. The four plots with no native species did not contribute to the community composition model, but these plots did contribute to the species richness model.

For both plant community and richness SEMs, we included the same set of related models (i.e., the ‘pieces’ in the piecewise SEM) using the following response variables: PC 1 as a measure of soil legacies, number of new recruits as a measure of reinvasion, counts of trees and saplings that had survived

management as a measure of short distance dispersal, and non-native grass cover as a measure of secondary invasion. For soil legacy effects we used plot-level principal component scores from the first principal component. When we tested PC 2 in an additional analysis, it did not contribute substantially to the variance explained by the overall model, so it was not included in the models presented here. The explanatory variables included were historical pine invasion stage as a factor with three levels (early, intermediate or late), the number of years since herbicide treatment (management) was undertaken, and the propagule pressure metric (calculated in section 2.3) as a measure of long-distance dispersal.

Prior to specifying the final models, we conducted tests on these metrics to assess if any non-linear terms were required to represent the modelled relationships (Figure S3.4). We assessed the relationships between key variables to confirm if they were linear. The relationships between NMDS 1 and non-native grass cover; and between reinvasion and time since management were unimodal, so we included a centred quadratic term for non-native grass cover and time since management in the relevant models (Fahrmeir et al., 2022; Grace & Keeley, 2006).

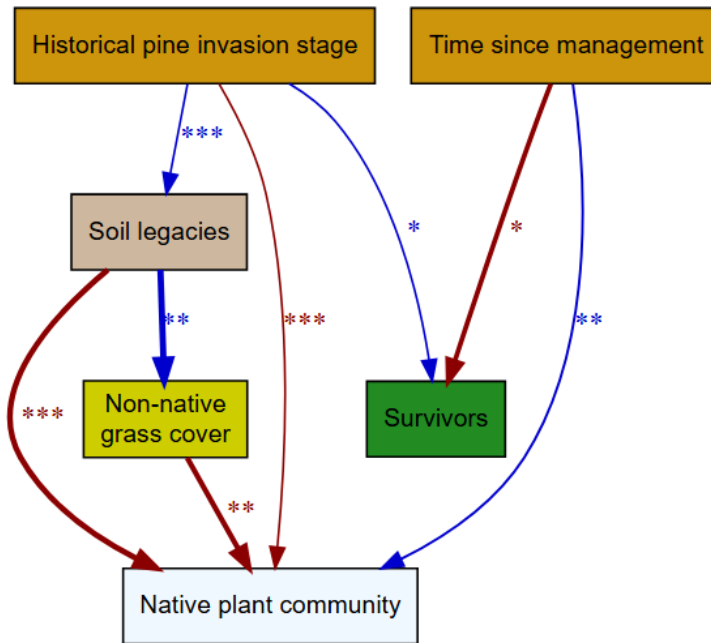
To design the SEM, we first set up each of the piecewise models with all potential explanatory variables based on our hypotheses. For each response variable we tested a model with the full suite of hypothesised explanatory predictors against a set of simpler plausible models with fewer predictors. In this comparison, we also modelled both linear and non-linear relationships to confirm that those relationships initially identified as non-linear remained so after accounting for all other variables. We used AIC to select the model with the best fit for inclusion into the piecewise SEM (Burnham & Anderson, 2002). We assessed each component model for overdispersion and multicollinearity (Lefcheck, 2016).

For each response variable within the SEM where historical pine invasion stage was shown to be significant, we conducted post-hoc tests of differences among the means of each factor level to show the direction and significance of the relationship between invasion stage, with Tukey correction for multiple comparisons (Fahrmeir et al., 2022; Lefcheck, 2021). The structural equation modelling was carried out using ‘piecewiseSEM’ (Lefcheck, 2016), and post-hoc testing was carried out using ‘emmeans’ (Lenth, 2023). Path diagrams were created using ‘DiagrammeR’ (Iannone & Roy, 2016).

3.3 Results

Pine invasion and management history influenced native plant communities and native species richness through both direct and indirect mechanisms, as shown in the structural equation models (Figure 3.4). Variation in the native plant community (NMDS 1) was directly explained by both historical pine invasion stage (plant community plots with early stage invasions differing significantly from intermediate and late-stage plots), and by a positive effect of time since management (Table 3.3; Table 3.4). The native plant community also showed a strong negative relationship with soil legacy effects (PC 1) and with non-native grass cover. Together, these predictors explained 80% of the variation in NMDS 1. In contrast, the level of reinvasion did not explain additional variation in the native plant community.

a)



b)

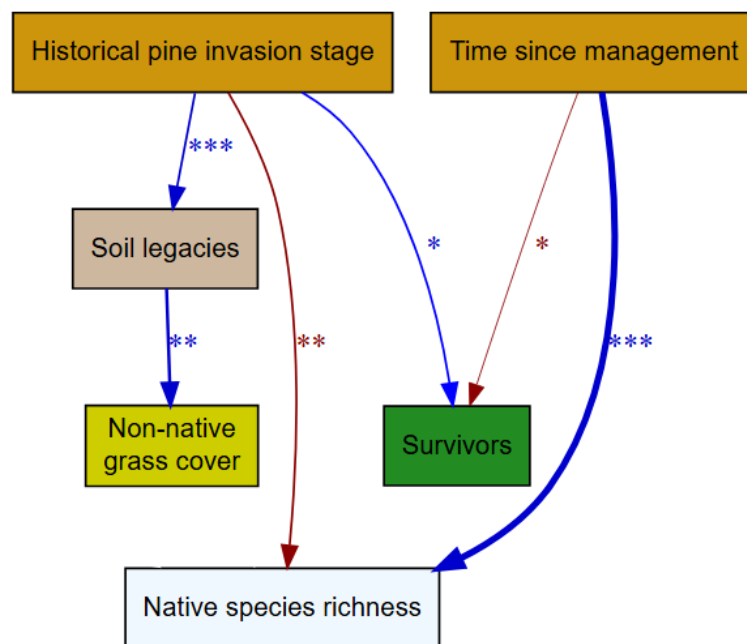


Figure 3.4 Structural Equation Model (SEM) diagram showing a) significant paths for the native Plant community composition (native NMDS) model; b) significant paths for the native species richness model. Stars show significance * $p < 0.05$, ** $p < 0.01$, * $p < 0.001$. Arrow widths are proportional to the strength of the standard coefficient. The exception is invasion stage which has no standard coefficient, so linewidth is set at 1. Blue arrows indicate positive relationships, and red arrows indicate negative relationships. Model explanatory power for endogenous variables: Soil legacies ($R^2 = 0.43$), Non-native grass cover ($R^2 = 0.13$), Survivors ($R^2 = 0.27$), Native plant community ($R^2 = 0.80$), Native species richness ($R^2 = 0.56$).**

Table 3.3 Structural Equation Model (SEM) results for the model with native species community composition (NMDS 1) as the primary response variable

<i>Response</i>	<i>Predictor</i>	<i>Estimate</i>	<i>Standard error</i>	<i>df</i>	<i>Critical value</i>	<i>p value</i>	<i>Standard estimate</i>
<i>Native plant community (NMDS 1)</i>	Non-native grass cover	0.00	0.00	47	-2.56	0.014	-0.19
	Non-native grass cover squared	0.21	0.06	47	3.30	0.002	0.33
	Time since management	0.03	0.01	47	3.13	0.003	0.24
	Soil legacies (PC 1)	-0.16	0.04	47	-3.80	0.000	-0.34
	Invasion stage	NA	NA	2	10.20	0.000	NA
	Invasion stage = Early	0.34	0.09	47	3.92	-	0.52
	Invasion stage = Intermediate	-0.04	0.08	47	-0.47	-	-0.05
	Invasion stage = Late	-0.28	0.09	47	-2.99	-	-0.43
<i>Soil legacies (PC 1)</i>	Time since management	-0.01	0.03	50	-0.42	0.675	-0.05
	Invasion stage	NA	NA	2	12.72	0.000	NA
	Invasion stage = Early	-0.77	0.29	50	-2.70	-	-0.55
	Invasion stage = Intermediate	-0.48	0.25	50	-1.88	-	-0.34
	Invasion stage = Late	1.24	0.29	50	4.30	-	0.87
<i>Reinvasion</i>	Survivors	-0.25	1.02	49	-0.25	0.807	-0.04
	Propagule pressure	0.46	0.44	49	1.03	0.308	0.14
	Invasion stage	NA	NA	2	2.64	0.081	NA
	Invasion stage = Early	0.67	5.02	49	0.13	-	-0.24
	Invasion stage = Intermediate	14.00	4.59	49	3.05	-	0.44
	Invasion stage = Late	0.65	4.51	49	0.14	-	-0.24
<i>Survivors</i>	Time since management	-0.17	0.08	50	-2.19	0.033	-0.31
	Invasion stage	NA	NA	2	4.93	0.011	NA
	Invasion stage = Early	0.52	0.66	50	0.79	-	-0.46
	Invasion stage = Intermediate	3.18	0.58	50	5.44	-	0.47
	Invasion stage = Late	1.66	0.66	50	2.50	-	-0.06
<i>Non-native grass cover</i>	Soil legacies (PC 1)	8.85	3.18	52	2.78	0.008	0.36

Table 3.4 Post-hoc pairwise comparisons of Structural Equation Model (SEM) results to show the significance of the different historical pine invasion stage in relationships that were significant in the overall SEM for both native plant community composition and species richness.

<i>Model</i>	<i>Contrast</i>	<i>Estimate</i>	<i>Standard error</i>	<i>df</i>	<i>t value</i>	<i>p value</i>	<i>Standard estimate</i>
<i>Native plant community (NMDS 1)</i>	Early - Intermediate	0.37	0.11	47	3.38	0.00	0.57
	Early - Late	0.62	0.14	47	4.28	0.00	0.95
	Intermediate - Late	0.24	0.13	47	1.87	0.16	0.38
<i>Native species richness</i>	Early - Intermediate	3.84	1.12	48	3.43	0.00	0.84
	Early - Late	4.32	1.51	48	2.86	0.02	0.95
	Intermediate - Late	0.48	1.36	48	0.35	0.94	0.10
<i>Soil legacies (PC 1)</i>	Early - Intermediate	-0.30	0.38	50	-0.79	0.71	-0.21
	Early - Late	-2.01	0.44	50	-4.61	0.00	-1.42
	Intermediate - Late	-1.71	0.39	50	-4.38	0.00	-1.21
<i>Survivors</i>	Early - Intermediate	-2.66	0.87	50	-3.07	0.01	-0.92
	Early - Late	-1.14	1.00	50	-1.13	0.50	-0.39
	Intermediate - Late	1.52	0.90	50	1.69	0.22	0.53

Soil legacies (PC 1) were positively associated with historical pine invasion stage, with late invasion stage plots differing significantly from early and intermediate-stage plots. In contrast, PC 1 showed no significant relationship with time since management. The model explained 43% of the variation in PC 1. Non-native grass cover increased with PC 1, indicating that soil legacies promote non-native grass abundance. However, the model for non-native grass cover explained only 13% of the variation.

Reinvasion did not have a significant effect on the native plant community (NMDS 1). Reinvasion patterns were strongly influenced by two outlier plots; these are intermediate invasion stage sites with high reinvasion levels due to surviving coning trees producing large numbers of seedlings. Reinvasion was not explained by the historical pine invasion stage, or by either the number of surviving pine individuals or long-distance dispersal, and the model only explained 14% of the variation. When the SEM was rerun without the two outlier plots, results showed that recruitment had a highly significant relationship with long distance dispersal, and model performance was vastly improved, explaining 42% of the variation. Number of surviving pines was moderately explained by invasion stage (with early invasion stage plant community

plots differing significantly from intermediate and late-stage plots), and by time since management. However, the model only explained 27% of variance, indicating that additional factors influence survivor abundance.

Variation in species richness was explained by a similar set of explanatory variables as the plant community. Both historical pine invasion stage (with early stage plant community plots differing significantly from intermediate and late-stage plots), and time since management were significant predictors (Table 3.4; Table 3.5). In contrast to the native community model, soil legacies and non-native grass cover did not directly influence species richness. The model explained 56% of the variation in species richness.

Table 3.5 Structural Equation Model (SEM) results for the model with native species richness as the primary response variable.

<i>Response</i>	<i>Predictor</i>	<i>Estimate</i>	<i>Standard error</i>	<i>df</i>	<i>Critical value</i>	<i>p value</i>	<i>Standard estimate</i>
<i>Native species richness</i>	Non-native grass cover	0.01	0.01	48	0.64	0.528	0.07
	Time since management	0.39	0.10	48	3.88	0.000	0.44
	Soil legacies (PC 1)	-0.22	0.43	48	-0.50	0.618	-0.07
	Invasion stage	NA	NA	2	6.73	0.003	NA
	Invasion stage = Early	8.14	0.89	48	9.11	-	0.61
	Invasion stage = Intermediate	4.30	0.78	48	5.53	-	-0.23
	Invasion stage = Late	3.83	0.98	48	3.90	-	-0.33
<i>Soil legacies (PC 1)</i>	Time since management	-0.01	0.03	50	-0.42	0.675	-0.05
	Invasion stage	NA	NA	2	12.72	0.000	NA
	Invasion stage = Early	-0.77	0.29	50	-2.70	-	-0.55
	Invasion stage = Intermediate	-0.48	0.25	50	-1.88	-	-0.34
	Invasion stage = Late	1.24	0.29	50	4.30	-	0.87
<i>Reinvasion</i>	Survivors	-0.25	1.02	49	-0.25	0.807	-0.04
	Propagule pressure	0.46	0.44	49	1.03	0.308	0.14
	Invasion stage	NA	NA	2	2.64	0.081	NA
	Invasion stage = Early	0.67	5.02	49	0.13	-	-0.24
	Invasion stage = Intermediate	14.00	4.59	49	3.05	-	0.44
	Invasion stage = Late	0.65	4.51	49	0.14	-	-0.24
<i>Survivors</i>	Time since management	-0.17	0.08	50	-2.19	0.033	-0.31
	Invasion stage	NA	NA	2	4.93	0.011	NA
	Invasion stage = Early	0.52	0.66	50	0.79	-	-0.46
	Invasion stage = Intermediate	3.18	0.58	50	5.44	-	0.47
	Invasion stage = Late	1.66	0.66	50	2.50	-	-0.06
<i>Non-native grass cover</i>	Soil legacies (PC 1)	8.85	3.18	52	2.78	0.008	0.36

The structural equation models showed good overall fit. Chi-squared values (25.6.9 and 17.59 respectively) and Fisher's C statistics (38.3 and 28.3 respectively), all with non-significant *P*-values indicated that both models adequately captured the observed covariance structure. Directed separation tests revealed no plausible missing significant conditional dependencies in either the plant community or species richness models, indicating that they were both well specified.

To relate the structural equation model results back to the full plant community, we compared the first native species ordination axis (native NMDS 1) with the second axis from the full species community ordination (all species NMDS 2). Vector fitting confirmed a relationship between native NMDS 1 scores and the overall community NMDS 2 scores (envfit $r^2 = 0.53$, $P = 0.001$), indicating that variation in native species composition represented a substantial gradient within the broader plant community structure. Procrustes analysis shows a moderate correlation ($r = 0.59$), indicating that there is structural similarity with native species representing a significant component of the variation in the full species community, although there was also additional structural variation attributed to non-native species (Legendre & Legendre, 2012). We calculated ellipses with 95% confidence intervals to visualise distinct community groups within the full species NMDS (Figure 3.4). Along the full species NMDS 2 (which had a negative relationship with the native NMDS 1 gradient) the community composition shifted from tussock grass species, to shrubland, and finally to communities characterised by ferns. These three clusters represent: Short tussock grasslands with native vines/shrubs commonly occurring in sites that historically had early stage pine invasions; degraded short tussock grasslands often dominated by non-native grass species; sparsely vegetated communities characterised by ferns occurring under recently managed late-stage pine invasion sites.

3.4 Discussion

Our study demonstrates that pine invasion and management history exert long lasting influences on native plant communities, in terms of both community composition and species richness, through both direct and indirect mechanisms. These findings support the theory that invaders acting as ecosystem engineers can leave persistent legacies that shape community trajectories long after removal (Ehrenfeld, 2010; Sapsford et al., 2020). By utilising structural equation modelling we show that both biotic and abiotic legacies interact to determine long-term outcomes for native plant communities, exemplifying the potential of pine invasions to have long-lasting influence on grassland ecosystems.

The native plant communities were influenced both directly by invasion history, and indirectly by persistent soil legacies. Historical pine invasion stage has played an important role, with sites that had historically late stage pine invasions exhibiting distinct soil conditions and altered plant communities. This is consistent with the expectation that dense, mature invasions generate stronger ecosystem-level modifications, although the relationship is often non-linear (Elgersma & Ehrenfeld, 2011). Whilst soil legacies were directly related to historical pine invasion stage, they showed no significant relationship with time, suggesting that changes in soil nutrient cycling persist. The strong negative influence of soil legacies on native community

composition (NMDS 1) highlights how altered nutrient cycling can continue to shape community assembly long after invader removal (Corbin & D'Antonio, 2012). The lack of response in species richness to soil conditions differs from our hypotheses, but is consistent with findings of other studies showing persistent soil legacies following invader removal have species-specific responses, with some native species being highly sensitive while others appear to be relatively unaffected (Jordan et al., 2008).

The native plant community was influenced by non-native grass cover, but species richness was not. This indicates that secondary invasion by these grasses alters community composition by competitively suppressing particular native species rather than reducing overall richness. Non-native grasses appear to occupy empty space rather than directly displacing most native species. This is supported by weak correlations between non-native cover and native species richness ($r = 0.25$) or native species cover ($r = 0.18$) as well as between native species cover and bare ground ($r = 0.38$), but a strong correlation between non-native species cover and bare ground ($r = 0.88$) (Figure S3.5). This is consistent with other observational studies in tussock grassland communities, which quantified the impacts of hawkweed species (*Hieracium* and *Pilosella*, Asteraceae), widespread non-native forbs, finding that they have little direct competitive effect on native species (Radford et al., 2010; Walker et al., 2016).

Higher non-native grass cover was associated with soil legacies, indicating that as predicted altered soil conditions may favour fast-growing non-native grasses (Dudenhöffer & Hulme, 2025b). However, the model explained little variation in non-native grass cover, indicating that additional factors contribute to non-native grass abundance. This is likely to be because, while an increase in nitrogen availability does promote grass growth (Yelenik et al., 2004), other nutrients such as available phosphorous and pH are also influential (Dickie et al., 2014; Dickie et al., 2011). These variables correlated with the second principal component (PC 2), which was not included in the SEM presented here. When we included PC 2 in an additional SEM analysis, a further 26% of variation in non-native grass cover was explained; however, this did not contribute substantially to the variance explained by the overall model. Together, these results indicate that pines and their persistent soil legacies negatively affect native species while promoting the abundance of a small number of non-native grass species. These grasses may fill vacant space, directly outcompeting only a subset of native species (Figure S3.5); however, this influence is sufficient to alter the overall community structure.

Time since management was also an important driver of native plant community structure, directly influencing both native community composition and species richness. This suggests that while native species recovery was underway in the study areas, it is a gradual process. The influence of both invasion stage and time indicates that pine invasion and management reduce native species richness and changes the community structure. Native species richness may increase over time, but the structure within the community remains altered. The trajectory of native communities depends not only on the magnitude of historical impacts, but also on the time elapsed since management.

Reinvasion dynamics were more complex, and the underlying processes are generally not well understood (Banks et al., 2018; Gabler & Siemann, 2012). Reinvasion did not influence native community

composition or richness; likely because reinvasion occurred at levels lower than the original invasion and had not yet reached levels where its effect would outweigh the legacy of the primary invasion. Initial models explained little of the variation in levels of reinvasion. The presence of two plots that were significant outliers, where surviving coning trees produced large seed cohorts, indicates that reinvasion is highly context-dependent and is likely to be influenced more by short distance dispersal than by propagule pressure at a landscape scale. When these outliers were removed, long-distance dispersal became a strong predictor of reinvasion, indicating that, as expected, propagule pressure is a key determinant of reinvasion risk (Gabler & Siemann, 2012). Historical pine invasion stage was not related to the number of reinventing individuals, indicating that although dead trees continue to release seed (Carlin et al., 2025a), this was not a significant driver of reinvasion in our study. Only a small proportion of the variation in surviving pine abundance was explained by the model, suggesting that, in addition to historical pine invasion stage and time since management, other factors, such as the quality of the management effort, have a larger effect on the number of survivors. These results show that successful pine management is essential for limiting reinvasion.

Our findings align with global evidence that invasive trees, particularly pines, act as ecosystem engineers whose impacts persist long after removal (Dickie et al., 2014; Sapsford & Dickie, 2023). Other studies have shown that pine invasion exerts ecosystem level changes that are related to invasion stage, and that these changes persist following removal, influencing native plant community recovery (Franzese et al., 2017; Mesacasa et al., 2022). This is also consistent with research of other invasive tree and shrub species, particularly nitrogen fixing species (Grove et al., 2015; Nsikani et al., 2018). Our results contribute to a growing global understanding that the trajectory of post-invasion recovery depends not only on invader removal but also on the strength of ecosystem legacies and the presence of secondary invaders (Corbin, 2025; Prior et al., 2018; Reynolds et al., 2017). In addition to this, we provide a unique insight into the drivers at an ecosystem level.

By relating the SEM results to the patterns in the full community ordination, we show that these legacy effects determine the structure of plant communities. The relationship between native NMDS 1 and the second axis of the full-community NMDS shows that native species drive a substantial portion of community variation; however, there was additional structural variation attributed to non-native species, indicating that native and non-native species respond differently to environmental variation (Li et al., 2018). The gradient from tussock grasslands to shrublands and finally to fern-dominated communities reflects a continuum of invasion impact and recovery potential. Early stage invasion sites retain community characteristics typical of intact short tussock grasslands, whereas late stage invasion sites transition toward sparse, fern-dominated assemblages. These patterns suggest that pine invasion can push ecosystems toward alternative states, with recovery trajectories dependent on both the intensity of historical invasion and the time elapsed since management.

The management implications of our results depend on conservation goals. If the aim is simply to maintain native species richness, and community structure is less of a priority, then soil legacies and

non-native grasses are less important compared with allowing sufficient time for native species to recover. However, if the goal is to restore community structure or protect specific native species, soil legacies become critical and active intervention may be required. Such actions may include soil amelioration, targeted non-native grass management, or native species reintroduction. Our results indicate that passive recovery may be insufficient where soil legacies and secondary invasions interact to shape community identity; this is consistent with studies which demonstrate that invasive pines leave persistent soil legacies that promote secondary invasion and inhibit native recovery even after removal (Dudenhöffer & Hulme, 2025a; Sapsford et al., 2022). While native species may eventually return, increasing richness, the structure and composition of the community can remain altered for decades.

Managing pines at early stages of invasion is therefore likely to reduce long-term impacts by preventing the development of strong soil legacies that favour non-native grasses. Managing invasions that have progressed to advanced stages is critical for limiting propagule pressure and preventing spread into currently uninvaded areas. While the densely invaded area will have already undergone significant change, it is still important to manage these areas for effective landscape scale management. Our findings highlight the need for integrated management strategies that address multiple pathways simultaneously. Soil legacies, secondary grass invasion and potentially reinvasion pressure all influence recovery, and focusing on only one factor may be insufficient to shift ecosystems toward desired states. Our results support a broader shift in invasion ecology toward managing invaded ecosystems as complex, feedback-driven systems rather than focusing solely on invader removal (Brandt et al., 2023; Zavaleta et al., 2001).

In conclusion, pine invasion continues to shape native plant communities following management, through both direct effects and indirect effects mediated by persistent soil legacies and competition from non-native grasses. Pine invasion history and management timing strongly influenced native community composition and species richness, while soil legacies and non-native grasses determined the type of community that re-establishes rather than the overall richness. These results highlight the role of pines as ecosystem engineers and demonstrate that both direct and indirect pathways must be considered when predicting long-term plant community outcomes. Understanding these legacies is essential for restoring invaded ecosystems and managing their future trajectories.

Chapter 4

Timing of Invasion Management Shapes Land Cover Trajectories Over Four Decades

4.1 Introduction

Grassland ecosystems contain high levels of biodiversity, support essential ecosystem services such as carbon storage, and underpin agricultural production (Bai & Cotrufo, 2022; Hopkins & Holz, 2006; Newbold et al., 2016). Despite their ecological and economic importance, grasslands are undergoing rapid transformation globally as woody plants expand into open landscapes through afforestation or biological invasions (Prangel et al., 2023; Stevens et al., 2017; Van Auken, 2009; Wieczorkowski & Lehmann, 2022).

Plant invasions often leave persistent ecological legacies that continue to shape these ecosystems long after invaders are removed, such as by altering fire regimes or soil biogeochemical processes (Corbin & D'Antonio, 2012; Ehrenfeld, 2010; Reynolds et al., 2017). The invasion of tree species into non-forested areas is particularly problematic due to the impact, not only on biodiversity, but also limiting potential future uses of that land (Peltzer, 2018; Richardson & Rejmánek, 2011). At the same time, many grassland ecosystems are also undergoing rapid land use change, adding further pressure to these systems (Leidinger et al., 2017; Schils et al., 2022). Biological invasion and land-use change are two of the most significant global drivers of biodiversity loss (Didham et al., 2007; Tylianakis et al., 2008), yet their combined influence on long-term ecosystem trajectories remains underexplored.

Among the most transformative woody invaders are non-native Pinaceae (hereafter termed ‘wilding pines’), which can rapidly alter ecosystem structure and function and create persistent legacy effects following their removal (Fuentes-Lillo et al., 2026; Sapsford & Dickie, 2023). Their capacity for long-distance seed dispersal and rapid population growth makes them particularly challenging to manage once established (Nuñez et al., 2017). The likelihood of a site to be invaded by pines is a combination of both propagule pressure and environmental factors, including the current land cover (Novoa et al., 2020; Richardson et al., 1994). In New Zealand, wilding pines represent one of the most significant biological invasions affecting tussock grassland ecosystems (Peltzer, 2018), and have spread across landscapes with high conservation values and land used for pastoral farming (Froude, 2011).

The timing of management is widely recognised as a critical determinant of invasion outcomes (Ahmed et al., 2022; Simberloff et al., 2013). Early intervention, including removing seedlings and saplings before they reach reproductive maturity is consistently identified as the most effective and least costly strategy for managing pine invasions (Buckley et al., 2005; Moyano et al., 2025; Peralta et al., 2020). In contrast, delayed management allows invasions to accelerate, increasing the spatial extent of spread and leaving behind dense stands whose legacies can persist for decades (Franzese et al., 2017; Fuentes-Lillo et

al., 2026). Although these principles are well established, there is limited empirical evidence demonstrating how management timing shapes long-term land-cover trajectories at a landscape scale.

The landscape scale of some plant invasions makes it difficult to effectively quantify the extent of change through ground-based monitoring. Remote sensing offers a powerful means of reconstructing historical land-cover change and tracking invasion dynamics across large spatial and temporal scales. High-resolution aerial imagery provides an opportunity to quantify invasion extent and identify management activities, including evaluating the effectiveness of management actions where long-term ground data are limited. Remotely sensed data complements field data and is particularly effective at detecting change in non-woody ecosystems (Sprague et al., 2019; Zhang et al., 2019). Remote sensing provides a pragmatic tool for monitoring invasion, reinvasion, and land-cover change across decades, particularly in remote areas (Francis et al., 2024; Martin-Gallego et al., 2020). Numerous studies have utilised satellite imagery to quantify tree invasions (Gavier-Pizarro et al., 2012; Nandasena et al., 2023; Sá et al., 2017). However, few studies have applied multi-decadal high-resolution aerial imagery analysis to assess invasion and management outcomes. In highly modified or fragmented landscapes, linking spatial pattern to ecological processes provides insight into how drivers, such as management timing, shapes long-term trajectories (Hobbs & Norton, 1996; Wiens et al., 1993).

Although the global spread of invasive conifers is well documented, less is known about how landscape-scale invasion dynamics interact with the timing of management interventions to shape long-term outcomes. In this study, we use four decades of aerial imagery and plot-based plant community data to reconstruct land-cover change in a tussock grassland, specifically in areas where pines have invaded and subsequently been managed. We quantified the extent and rate of wilding pine invasion and assessed how the timing of management influences long-term landscape outcomes. We evaluate the effectiveness of remote sensing for monitoring invasion trajectories, combining multi-temporal land cover classifications of aerial imagery with plot-based plant community data to evaluate whether landscape-scale changes detected from aerial imagery correspond to ecological community change on the ground.

4.2 Methods

4.2.1 Study area

Te Manahuna / the Mackenzie Basin is an intermontane basin in the central South Island of Aotearoa / New Zealand. It is a glacial landscape predominantly comprised of fans, moraines and outwash terraces (Espie et al., 1984). The basin covers 269,000 ha and ranges in elevation between 375 – 800 m a.s.l (Peart & Woodhouse, 2020). The Mackenzie Basin has a history of anthropogenically induced landscape scale change, with extensive burning and grazing (McGlone & Moar, 1998; Wardle, 1991), and multiple introductions of non-native animals and plants, resulting in a highly modified landscape (Mark et al., 2013; Meurk et al., 2002). Land is held under both private and public ownership, and the publicly owned land has

a range of different purposes from long-term agricultural leases to being managed for conservation (Brower et al., 2018). In more recent decades, tenure review of crown leasehold land has resulted in splitting the ownership into freehold agricultural land and public conservation areas (Brower & Page, 2017), leading to an increase in the use of irrigation and the conversion of some areas to high producing grassland which has substantially altered these landscapes (Brower et al., 2018; Peart & Woodhouse, 2020). There has also been extensive pine spread over recent decades, initially from historical plantations and shelterbelts, and increasing propagule pressure from maturing wilding stands (Ministry for Primary Industries, 2014; Young, 2016). The dominant species *Pinus contorta*, Loudon is one of the most invasive and widespread pine species in New Zealand (Ledgard, 2001; Lloyd et al., 2016); is shade intolerant and frequently invades open grassland (Richardson & Bond, 1991).

Landscapes within the Mackenzie Basin with known pine invasion and management history were identified (Chapter 2). Within these areas, five study sites with similar environmental characteristics were selected, specifically rainfall (300 – 700 mm/year), elevation (400 – 750 m), flat to moderate slope gradients (0 – 15°), predominately south-west facing aspects (150 – 272°), and soil types composed of greywacke gravels, loess, colluvium and till on moraine or outwash surfaces (Barrell et al., 2011). The study sites have varying land tenures, land uses and invasion history (Chapter 1, Table 1.1). The invasion stage of pines at the time of management had not been measured quantitatively, so we categorised sites into three levels based on a combination of density and the size of individuals, following standard definitions (Ministry for Primary Industries, 2014), with some sites containing more than one stage due to the natural invasion front. The invasion stage levels were: ‘Late’ stage invasion, where trees had formed a closed canopy, with > 400 stems per hectare; ‘intermediate’ stage invasion, where many small trees and saplings were present, but the canopy had not yet closed, with 20 – 400 stems per hectare; and ‘early’ stage invasion, with scattered individuals, and < 20 stems per hectare. All sites were managed with herbicide applications as the primary means of removal, predominantly either aerial broadcast spray for dense infestations, or ground-based herbicide application for sparse infestations (Rolando et al., 2025), with management occurring between 2006 – 2020. Sites varied in size from 19 ha to 244 ha. Within each of these five sites we then located a 2 × 2 km area of interest (AOI), centred around the plant community plots measured in Chapter 2 (Figure 4.1).

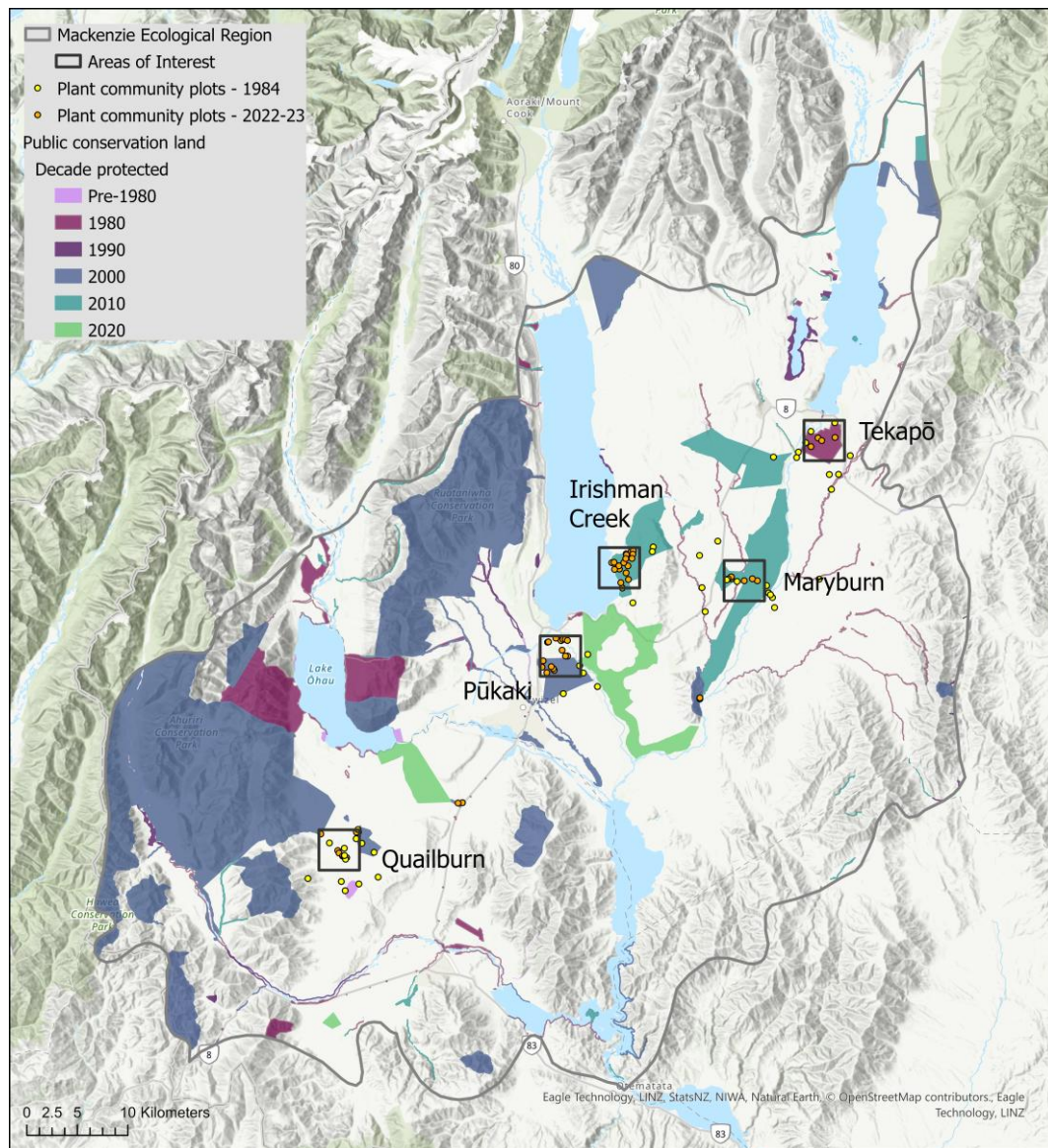


Figure 4.1 Location map showing the Areas of Interest (AOIs), the plant community plots measured and within the Mackenzie Basin. Public conservation land is that owned by the Crown and managed for conservation purposes; the decade protected indicates when either the ownership or the reserve purpose changed.

4.2.2 Image pre-processing and classification

To quantify where and how land cover has changed at a landscape scale, including re-constructing the history of pine invasion and management, we analysed historical aerial imagery from four time points (Table S4.1). Image processing and classification procedures were carried out using ArcGIS Pro (ESRI, 2025). The classification was based on modified land cover categories described within the Landcover Database for New Zealand (Dymond et al., 2017) (Table 4.1); an additional category was created for tree shadows to reduce mis-classifications (Movia et al., 2016). Plant functional types can be differentiated based on spectral signatures (Bradley, 2014), we selected categories based on land cover types with distinguishable spectral

signatures in the visible (RGB) bands, meaning that each category had unique colour combinations that were consistent enough to visually separate the classes (Foody, 2002; Upadhyay et al., 2016).

Table 4.1 Modified land cover categories used to assess land cover change. For the image classification a larger set of classes based on the LCDB classification were used (Dymond et al., 2017). Classes were subsequently merged into categories of interest for data analysis.

<i>LCDB class</i>	<i>Image classified class</i>	<i>Merged class</i>
<i>Exotic forest</i>	Pine	Pine
<i>Forest – Harvested</i>	Dead pine	Dead pine
<i>Deciduous hardwoods</i>	Deciduous hardwoods	Deciduous hardwoods
<i>Shrubland</i>	Shrubland	Shrubland
<i>High producing grassland</i>	High producing grassland	High producing grassland
<i>Low producing grassland</i>	Low producing grassland	Low producing grassland
<i>Depleted grassland</i>	Depleted grassland	Low producing grassland
<i>Herbaceous freshwater</i>	Herbaceous freshwater	Low producing grassland
<i>Built-up Area (settlement); Sand and Gravel; Transport Infrastructure; Gravel and Rock</i>	Bare	Bare
<i>Lake or pond; River</i>	Lake	Bare
<i>NA</i>	Shadow	Shadow

We obtained greyscale imagery from the 1980s and 1999, and colour imagery from 2008 and 2021 (Table S4.1). The colour (RGB) imagery was obtained as geo-referenced map tiles. We geo-referenced the greyscale imagery against clearly identifiable ground locations that were visible in both the imagery and either existing GIS based maps or more recent geo-referenced aerial imagery. To classify images according to the pre-specified land cover categories, supervised and unsupervised pixel-based classification methods were employed for colour and grey-scale imagery, respectively. We opted for an unsupervised method for the greyscale imagery because we could not reliably identify training pixels needed for a supervised classification approach. The greyscale images each encompassed the areas of interest, and only one image was required per AOI, while multiple colour images were required per AOI. Due to differences in spectral variability and light conditions between each of the colour image tiles we created training samples and ran the classification separately for each individual image.

The supervised classification of the colour images was carried out by creating training sample polygons of 11 pre-defined land cover classes based on a visual interpretation of the imagery (Table 4.1). A minimum of five training polygons per category were hand digitised for each image. A Support Vector Machine (SVM) classifier was trained using the training sample polygons (Foody & Mathur, 2004; Melgani & Bruzzone, 2004) and subsequently applied to each image to generate a thematic classification aligned with the 11 pre-defined land cover types. We merged the original list of land cover types into a subset of eight types that encompassed the major changes in land cover expected over four decades in the Mackenzie Basin based on previous studies (Day et al., 2023; Mark et al., 2013). Classification of the greyscale images was carried out using an automated unsupervised ISO Cluster classification method (Al-Zubaidi & Al Khafaji,

2024). Following classification, the resulting pixel clusters were then assigned to one of the eight land cover classes, often amalgamating the original classification into fewer classes.

Following classification, each classified raster was clipped to the 2×2 km bounding box denoting the area of interest. For the two datasets with multiple colour image tiles, we created a single raster by combining the individual classified raster files using an mosaicking procedure. We used the non-vegetation categories from LCDB v6.0 (Manaaki Whenua - Landcare Research, 2025a) to mask out areas that were: Built-up Area (settlement), Lake or Pond, Transport infrastructure, or River. We adjusted the polygons where they did not match the imagery, e.g. Lake Pūkaki extended further than the LCDB mask boundary.

To assess the accuracies of the classifications (Congalton, 1991; Foody, 2002) we generated cross-tabulations that compared land cover types identified at an independent set of validation point locations to types generated by our image classification procedures at those locations. To do this, for each site, we generated a set of 100 random sample locations and assigned a land cover class for each time step based on aerial imagery, plant community data and knowledge of the locations. We calculated the accuracy statistics using the R package ‘caret’ (Kuhn, 2008). These class assignments were then compared to the modelled classification type at those locations and used to generate the cross-tabulation matrix. From this matrix we generated four metrics of classification accuracy. The user’s reliability metric indicates the probability that each class was correctly classified, and was calculated as the proportion of correctly classified validation points relative to all points assigned to that class. The producer’s accuracy metric indicates the probability that pixels belonging to a given class are correctly classified and was calculated as the proportion of correctly classified validation points relative to the total number of points for that class. The overall accuracy, indicating how well the classifications performed across all classes, was calculated as the proportion of correctly classified validation points. Cohen’s Kappa coefficient indicates how much better the overall classification performed than would be expected by chance and was calculated using the marginal totals of the confusion matrix. Calculated accuracy metrics were combined to provide a single assessment for each site and year, then aggregated for all AOIs in a given year.

4.2.3 Plant community data

To assess dominant land cover types, we compiled data from measured plant community plots that were located within our five study sites. We analysed data from two comprehensive plant community surveys of the area, one during the early stages of invasion (1984) and following management (2022-23). We utilised 47 (10×10 m) plots measured in 1984 as part of the Mackenzie Ecological Region Protected Natural Areas (PNAP) surveys (Espie et al., 1984), sourced from the New Zealand National Vegetation Survey databank (NVS) (Manaaki Whenua - Landcare Research, 2025b). We also utilised 56 randomly located 10×10 m plots that were measured in January (austral summers) of 2022 and 2023 (those described in Chapter 2 plus two additional plots located in unmanaged pine invasions). Both datasets visually estimated the cover of individual vascular plant species, recorded as cover scores in 1984 and as percentages in 2022-23. We converted the cover scores to the percentage mid-point of each range.

In 2022-23, we counted dead pines in three size classes (seedling, sapling, tree). To include dead pine in the cover of each plot (i.e. to be comparable with the measured live species cover), we converted the counts to a percent cover by estimating a basal area–derived cover index. Basal area was calculated by selecting a representative DBH for each size class (2 cm for saplings and 10 cm for trees), calculating the basal area per individual and multiplying by the number of individuals in that size class and summing across classes. We then multiplied the basal area per plot by 100 to express this as an approximate percent cover (Buckley et al., 1999).

4.2.4 Data analysis

4.2.4.1 Aerial imagery

To assess the change in land cover across four decades we utilised the classified aerial images produced for each time point as described above. The final raster files from the image classification were saved in ArcGIS Pro and then imported into R 4.5.0 (R Core Team, 2025) for further analysis, using the R package ‘terra’ (Hijmans et al., 2022). Change in cover within 4 km² areas of interest was assessed between each of the four timesteps. First, we aligned the pixel sizes so that all four timesteps used the same (i.e. coarsest) image resolution of 17.6 m, then reclassified the finer resolution rasters by assigning each pixel to the most dominant classification for the original underlying pixels (Zhu, 2017). We calculated both the overall change in proportional area of each cover type and the pixel-based change.

To assess what land cover transitioned to over time, we calculated the number of pixels changing between each land cover class at a pixel level between each time step. To allow comparison between sites we converted the pixel counts to a percentage of the total pixels analysed (i.e. excluding masked areas) at each time step. We also assessed land cover change between time steps using a binary approach, i.e. did the cover class change for a given pixel between timesteps.

4.2.4.2 Plant community plots

To assign plant community plots to land cover classes, we first extracted the list of species and updated all names to the current accepted taxonomy using the NVS species list (Manaaki Whenua - Landcare Research, 2025b). We then assigned a land cover class to each species using growth form and bio-status information data from the NVS species list, supplemented with habitat preference information from the NZ Plant Conservation Network (Manaaki Whenua - Landcare Research, 2025b; NZPCN, 2026). Most species could be classified using a combination of growth form and bio status (Table S4.2). However, ferns were classified using their habitat preferences. Non-native grass species commonly used in pasture (Ministry for Primary Industries, 2013) were classified as high-producing grassland, with the exception of *Agrostis capillaris* which is common in low-producing grassland in these ecosystems. All other non-native grass species were classified as low-producing grassland.

We summed the species cover within each land cover type and calculated the proportion of the total cover in each type. Plots were then assigned to an overall land cover type based on the proportion of each class. For plots where cover of tree classes was >30 % then plots were assigned to the relevant tree class; for plots where shrubs made up > 30% cover then they were classified as shrubland. For all other land cover types, plots were assigned to the single most dominant class. We analysed the plant community data using the R packages ‘dplyr’ (Wickham et al., 2019) and ‘vegan’ (Oksanen et al., 2013).

4.2.4.3 Comparison of image-derived and plot-derived classification

To assess whether measured plot level change in plant community composition was concordant with remotely sensed landcover change, we generated cross-tabulations that compared land cover types derived from measured plant cover with the land cover types derived from the image classification for each plot area, using the image classification from the year most closely aligned to that of the plot measurement. We clipped the raster-based image classification to the extent of each plant community plot and calculated the proportion of each modified land cover class occurring at each plot location. We compared the proportional cover and the dominant land cover class from the image classification with the measured plot-based cover proportions and dominant classes and used this data to generate the cross-tabulation matrix. From this matrix we generated two metrics of classification accuracy; the overall accuracy and Cohen’s Kappa coefficient, both were calculated following the methodology used for the image classification accuracy assessment.

4.3 Results

Image classification shows the landscape scale changes across four decades, in particular the spread of invasive pines and their management, as well as an increase in high-producing grassland (Figure 4.2). While low-producing grassland remained the dominant land cover type across all sites, it declined from 94.7 – 99.7% of cover across AOIs in the 1980s, to 64.3 – 96.1% in 2021 (Figure 4.3). Over this time, other land cover types increased in abundance, notably pine (from 0 – 4.0% up to 0 – 10.1%), dead pine (from 0% up to 0 – 24.9%) and high producing grassland (from 0 – 1.0% up to 0 – 12.4%) (Figure 4.3). This change was particularly notable with pine and dead pine at Quailburn and Irishman Creek, and to a lesser extent the increase in irrigated farmland at Maryburn.

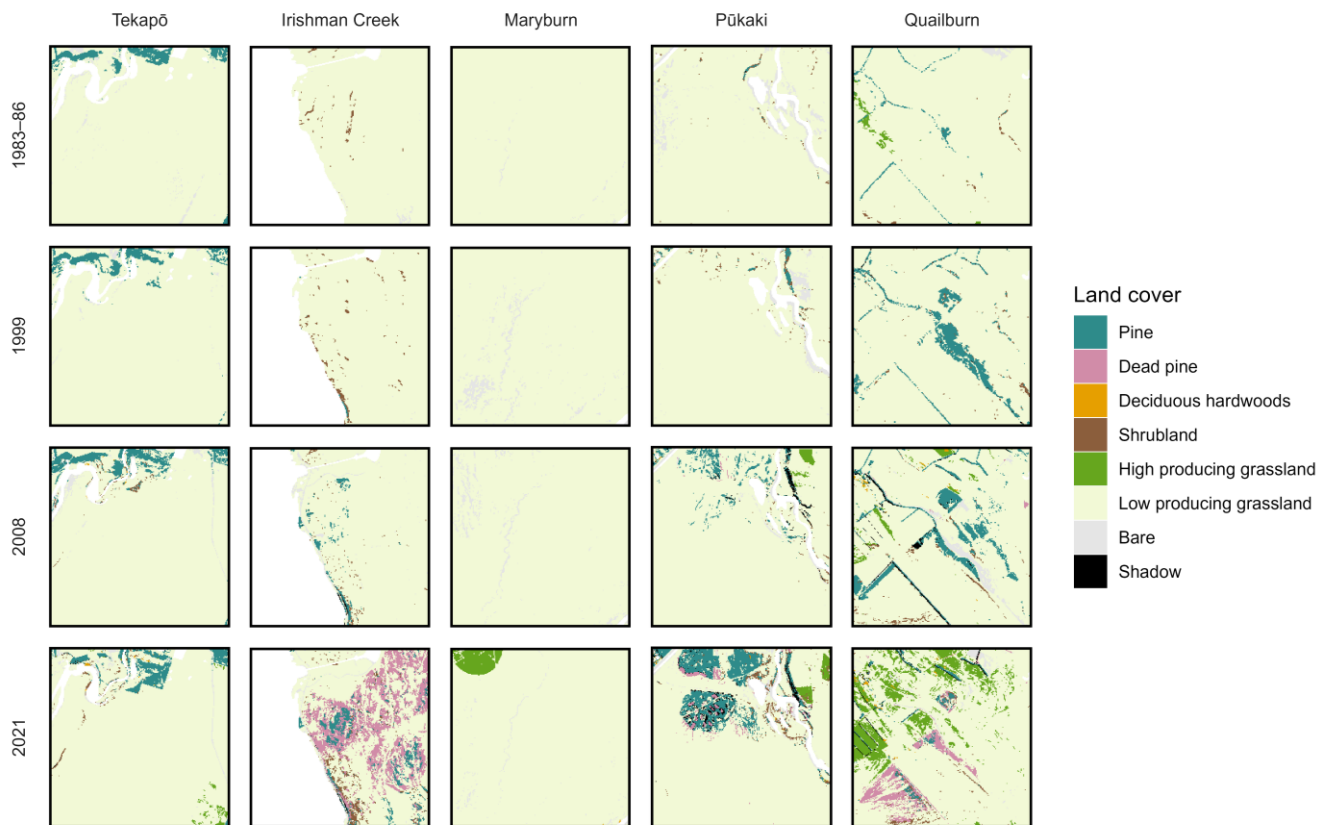


Figure 4.2 Pixel-based image classification within each of five Areas of interest (AOIs) at four timesteps. Land cover classification is based on merged LCDB types (Table 4.1).

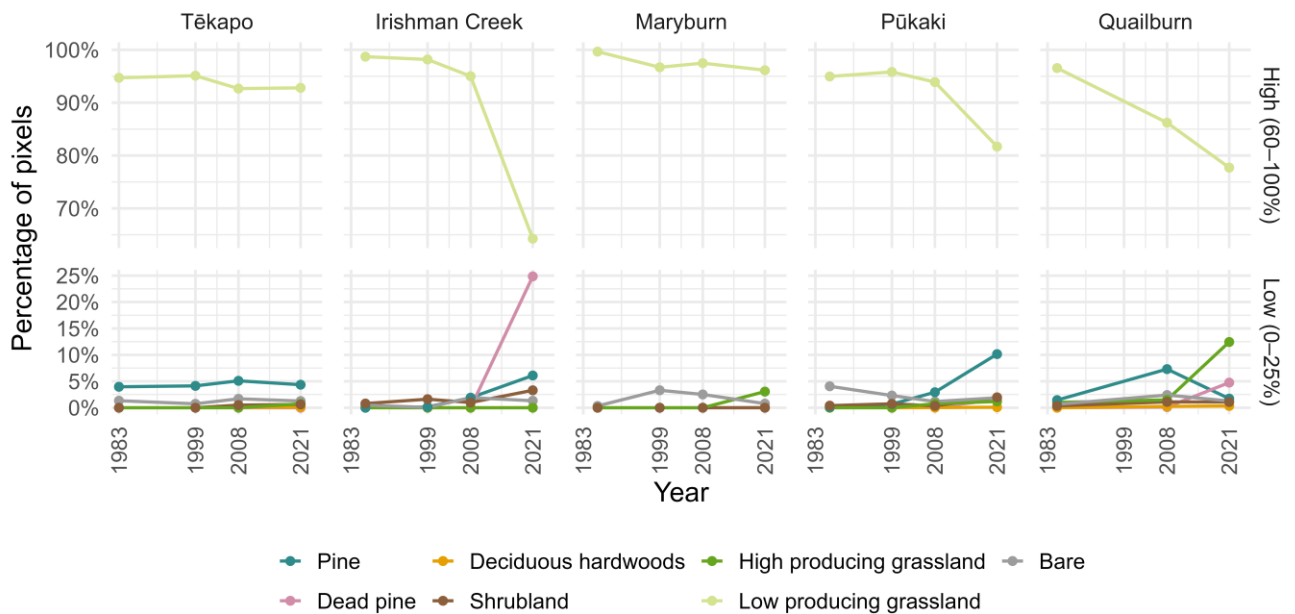


Figure 4.3 Change in the abundance of land cover types through time, shown as the percentage of the pixels classified for each Area of Interest (AOI) at each time step based on the pixel-based image classification.

Pine was present across the Mackenzie Basin as planted stands, predominantly shelterbelts, in the 1980s and spread was visible from 1999 onwards, although the spread and management of pine was site specific (Figure 4.4). Quailburn shows the earliest spread of pines, with sizeable areas present in 1999 and 2008, however by 2008, management was already underway and large areas of dead pine were visible by 2021. The spread of pines at other sites such as Irishman Creek and Pūkaki was more concentrated post-2008, with both widespread invasion and management visible by 2021. The invasion of pine was detected in the image classification for all sites except for Maryburn. This was an early-stage invasion site, and individual pines were managed as seedlings and saplings meaning that they never reached a size large enough to be visible in aerial imagery.

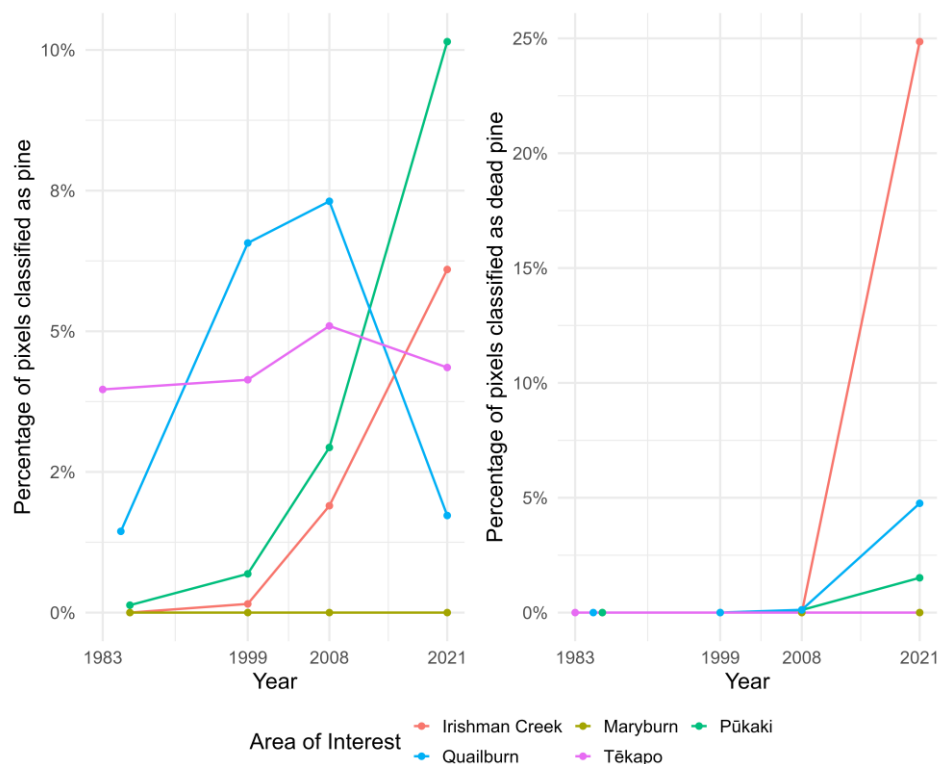


Figure 4.4 Change in the percentage of the pixels classified as a) live pine and b) dead pine within the five Areas of interest (AOIs).

The classification of imagery was satisfactory, the overall accuracy assessment was 0.94, and the mean Kappa, which is the estimated accuracy across all sites and years, was 0.72 (Table 4.2). There is some variability by year, with overall accuracy between 0.84 – 0.99 (Table S4.3). This variation is likely due to the differing image resolutions and by sites with more heterogenous sites being less accurately classified. Grassland and pine categories were accurately classified, while shadows were highly inconsistent.

Table 4.2 Aggregated confusion matrix showing accuracy assessment scores for the pixel-based image classification across all Areas of Interest (AOIs) and years

<i>Land cover class</i>	<i>Pine</i>	<i>Dead pine</i>	<i>Deciduous hardwoods</i>	<i>Shrubland</i>	<i>High producing grassland</i>	<i>Low producing grassland</i>	<i>Bare</i>	<i>Shadow</i>	<i>Total</i>	<i>User's accuracy</i>
<i>Pine</i>	59	2	1	1	0	3	0	4	70	0.77
<i>Dead pine</i>	0	24	0	1	0	0	0	0	25	0.69
<i>Deciduous hardwoods</i>	1	0	3	1	0	0	0	0	5	0.75
<i>Shrubland</i>	6	1	0	14	3	7	0	3	34	0.56
<i>High producing grassland</i>	0	0	0	0	25	3	0	0	28	0.52
<i>Low producing grassland</i>	9	6	0	8	20	1708	10	3	1764	0.97
<i>Bare</i>	0	0	0	0	0	31	27	0	58	0.73
<i>Shadow</i>	2	2	0	0	0	0	0	12	16	0.55
<i>Total</i>	77	35	4	25	48	1752	37	22	2000	
<i>Producer's accuracy</i>	0.84	0.96	0.60	0.41	0.89	0.97	0.47	0.75		
<i>Overall accuracy</i>										0.94
<i>Kappa</i>										0.72

The dominant land cover was low producing grassland for all sites and years. Analysis at the pixel level showed that most pixels remained as low producing grassland between each time step (62.5 – 97.0%) (Table S4.4). The largest change in pixel classification was between 2008 and 2021 for all sites (Figure 4.3). However, the transitions between pixel classifications were site specific. At Tekapō, there was an ~2% ($\pm$ 0.3%) increase in pines at each time step, with successful management indicated by 2.6% of pixels changing from pine to low producing grassland between 2008 and 2021. At Irishman Creek, there were only small increases in pixels classified as pine up to 2008, but an increase in both live pine (5.5%) and dead pine (24.9%) between 2008 and 2021. At Pūkaki, there were initially small increases in pixels classified as pine, with a 0.5% increase by 1999 and 2.7% by 2008. However, this increased by 8.3% in 2021 and an additional 1.3% increase in pixels were classified as dead pine. At Maryburn, the most notable change was a 3.0% increase in high producing grassland by 2021, indicating land use change. There was also change between bare and low producing grassland (in both directions) at all time steps. Quailburn had early spread of pines with a 6.1% increase between 1985 and 1999, however this slowed with only a 1.8% increase between 2008 and 2021. Some management had been undertaken by 2008, with 2.8% pixels changing from pine to other classes (bare, dead pine or grassland), and more widespread management by 2021 with a 4.7% increase in pixels classified as dead pine and a further 4.5% of pixels changing from pine to other classes. Quailburn also had an increase in high intensity farming with 12.4% of pixels changing to high producing grassland in 2021.

At the individual plot scale (100 m²), the dominant land cover type was low producing grassland for both image and plot-derived classifications (Figure 4.5). This aligns with the image classification within AOIs. The classification derived from the images and the plots were concordant in 86% of plots in 1984; however, a Kappa value of 0.19 showed that the image classification missed less common plant communities. Shrub coverage was generally patchy, and the low image resolution often meant that this was not distinguished from grassland. This result aligns with the accuracy assessments from the image classification, where shrubland was the least accurately classified land cover type. In addition, one high-producing grassland plot was image-classified as low-producing grassland, likely due to the difficulty in distinguishing these classes in a greyscale image. The classification was concordant in 77% plots in 2021, with a Kappa value of 0.51, indicating that variation in the plant community was captured moderately well. The main mis-alignment was between plots classified as grassland when the image derived classification was dead pine. This may be because either the threshold for assigning plots to dead pine (30% cover) was too high, or because the method for assigning percent cover of dead pine per plot was too conservative.

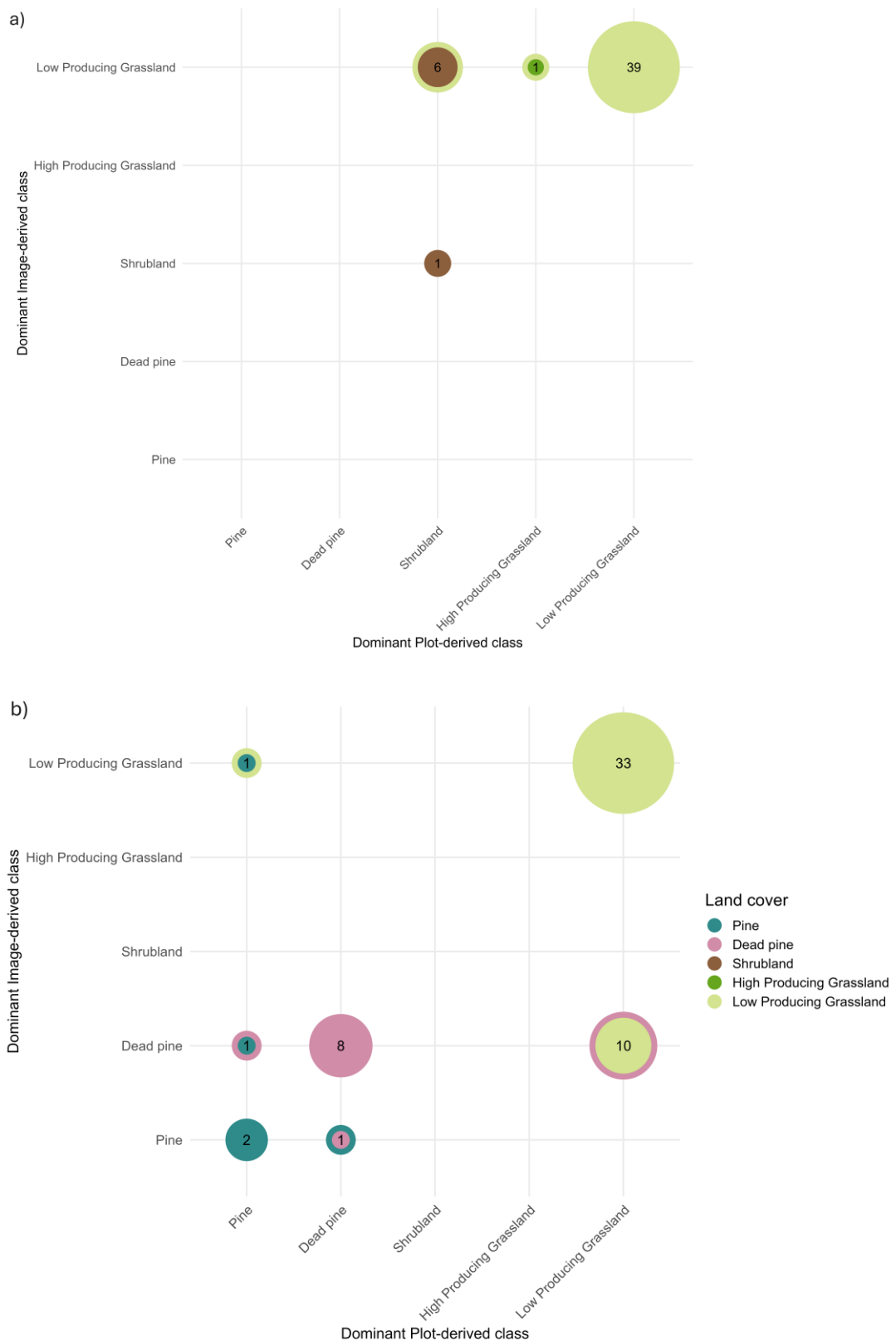


Figure 4.5 Comparison of image-derived and plot-derived land cover classifications for plant community plots measured in a) 1984 and b) 2022-23. The colour in filled circles is the plot-derived class, the colour of the border is the image-derived class.

4.4 Discussion

Our landscape-scale analysis of four decades of historical aerial imagery shows that land cover trajectories in tussock grassland ecosystems are strongly shaped by both the spread of invasive pines and the timing of management interventions. We demonstrate the extent and speed of the invasion of wilding pines and have shown how remote sensing can effectively track invasion trajectories to help visualise and understand the long-term consequences of management decisions.

Land cover transitions were primarily associated with pine invasion; an expansion of pine cover occurred at most sites from 2008 onwards, highlighting how rapidly invasion fronts can expand once seed sources are established (Ledgard, 2001). Management of these infestations had been undertaken by 2021, with outcomes dependent on the stage of invasion that the management was undertaken. Early intervention prevents large-scale shifts away from tussock grassland, limits the spatial extent of invasion, and avoids the persistent legacy effects associated with dense, mature stands. At sites where management was undertaken at early stages of invasion the more significant landscape change is a result of intensification of agriculture. In contrast, delayed management allows rapid expansion driven by propagule pressure. Sites where pines reached later stages of invasion prior to management being undertaken exhibited persistent legacies, with patches of both live and dead pines remaining visible and a failure to return to a pre-invasion grassland state. Our results from the Mackenzie Basin are consistent with global patterns of woody encroachment into grasslands (Fogarty et al., 2022; Sá et al., 2017), and specifically the patterns of pine invasions (Moyano et al., 2025; Pauchard et al., 2016). These patterns show that delayed management increases both the spatial extent of invasion and the cost and complexity of management, showing that as propagule pressure increases, invasion fronts accelerate and the effects become increasingly difficult to reverse (Ahmed et al., 2022; Simberloff, 2009; Yokomizo et al., 2009).

Remote sensing proved to be a powerful tool for reconstructing these long-term trajectories. However, such multi-decadal analyses are dependent on the availability of imagery. The expansion of pine was rapid and would have been captured better with shorter intervals between imagery, particularly between 2008 and 2021. The accuracy of the analysis is dependent on the resolution of the aerial imagery available and the complexity of the landscape. While classification accuracy was generally high, it declined in areas with high levels of variation in land cover types meaning that there was high spectral variation, this is a pattern commonly seen in complex landscapes (Lu & Weng, 2007). Sparse or early-stage invasions were often undetected because individuals were too small to be distinguished from the dominant land cover primarily due to the image resolution (Bradley, 2014). Previous studies using aerial imagery to quantify the density, age structure and spatial pattern of pine invasions into grasslands successfully detected trees with canopy diameters greater than 2.5 m (Sprague et al., 2019), but were also less successful for identifying smaller trees which matches our results. While there are limitations for identifying precise tree numbers in dense areas, this broadscale approach is sufficient for the purpose of identifying approximate invasion extent and timeframes (Bradley, 2014; Soubry & Guo, 2022).

The alignment between image-derived and plot-derived classifications indicates that aerial imagery provides an effective coarse-scale monitoring method, particularly when complemented by ground-based surveys for early detection and fine-scale monitoring of plant communities. The image classification shows that both live and dead pines dominate the invaded areas in terms of cover. However, even in the moderately invaded areas, although the species composition changes, the understory often remains as grassland, which means that at the scale of plant community plots these same areas were classified as grassland for ten plots (Figure 4.5). This matches the results from our plant community study where the understory is dominated by grasses in early and intermediate-stage invasions, and the ground cover becomes predominantly pine needles only at the later stages of invasion (Chapters 2 and 3).

Land tenure and land management practices also play a role in determining land cover trajectories. Dryland pastoral farming practices have had significant impacts on the landscape since the 1850s, with continual burning, sheep grazing and since the 1970s widespread over-sowing and topdressing, all contributing to a change from mixed tall and short tussock grasslands to short tussock with high abundance of non-native grasses and forbs (Day & Buckley, 2013; Treskonova, 1991). In more recent decades intensified agricultural practises, specifically irrigation have become increasingly prevalent, and is the dominant factor contributing to land use intensification (Brower et al., 2018). This shift accelerated following tenure review, a process which divided leasehold land into private agricultural or public conservation areas (Brower et al., 2018).

The influence of land tenure on both invasion history and management decisions is evident in our study. Areas that are private land often have multiple landowners, requiring a co-ordinated approach to successfully manage invasions. However, this can be an advantage if decisions are made and implemented quickly, this is evident at Quailburn where the invasion from shelterbelts started earlier than some other sites, but management was also undertaken sooner. Tekapō has a mix of land tenures with the privately owned land in the north still containing planted pines which is an ongoing source of seed for the southern areas which are public conservation land. However, this is a high value conservation site and regular management efforts have ensured pines have not established. Pūkaki also has mixed ownership with the southern half a conservation area, while the northern part has widespread invasion that has been inconsistently managed. This site also contains areas that have been used for pine herbicide trials (Rolando et al., 2025), which is evident in the patchiness of dead pines in the 2021 image classification (Figure 4.2). Maryburn has low propagule pressure with few shelterbelts or plantations in close proximity. (Figure 4.1; Chapter 1, Table 1.1). Irishman Creek was already invaded by pine prior to public ownership and substantive management has been undertaken since land tenure change. Importantly, our results show that proactive, consistent management can prevent pine establishment even under high propagule pressure, as demonstrated at sites actively managed for conservation, such as Tekapō Scientific Reserve.

Although low producing grassland remained the dominant land cover across all sites, its gradual decline reflects the cumulative influence of pine invasion, agricultural intensification, and site-specific

management histories. The reduction of native species cover has been widespread across areas used for pastoral farming and those that are managed for conservation purposes (Duncan et al., 2001). In New Zealand often conservation and agriculture are split into binary land types when making management decisions; given that these dryland landscapes are used for agriculture and support native biodiversity, the Mackenzie Basin is an area that would benefit from integrated land use planning (Abbott et al., 2019). Remote sensing can be used as a tool for land use planning enabling integration of different data types at a landscape scale and providing information about the current state, as well as monitoring change (Rogan & Chen, 2004). Recent climate adaptation modelling (Richards et al., 2023) and initiatives such as Te Manahuna Aoraki, a landscape scale project to eradicate mammalian predators (Foster et al., 2022), demonstrate how this can be implemented for areas such as the Mackenzie Basin.

The remote sensing approach used here offers a valuable tool for monitoring remote areas that are difficult to access, and for reconstructing historical invasion dynamics where ground data are limited across a range of spatiotemporal scales. While our focus was on pine invasion, this method has broader applicability to other grassland systems experiencing woody encroachment (Dovčiak et al., 2014).

By combining four decades of aerial imagery with field data, we demonstrate that remote sensing provides an effective tool for tracking invasion trajectories and evaluating management outcomes at landscape scales. Our results show that the timing of wilding pine management is the primary determinant of long-term land cover outcomes in tussock grasslands. Early intervention is the most effective and least costly strategy for managing woody invasions, preventing invasions from reaching self-sustaining stages and avoiding landscape-scale transformation (Moyano et al., 2025). The ecological and economic impacts of wilding pines have prompted substantial national investment in management programmes (Ministry for Primary Industries, 2014; Peck et al., 2022), yet the long-term outcomes of these efforts remain poorly quantified. By exploring how biological invasion and land-use change interact to shape dryland ecosystems, this research provides new insights to support management and long-term conservation planning in one of New Zealand's most vulnerable landscapes. These findings highlight the need for proactive management, coordinated across the landscape to maintain native grasslands and to reduce the ecological and economic costs of wilding pine invasion. Successful conservation outcomes will be aided by early detection and rapid response to invasions, and long-term monitoring frameworks that pair remote sensing with ground-based ecological data.

Chapter 5

General discussion

The aim of this thesis was to investigate the legacy effects of a dominant landscape invader on plant communities and ecosystem processes following its management. The results of this study revealed that legacies persist for at least 16 years and provide insights into direct and indirect mechanisms operating at two spatial scales. Specifically, the research addressed three broad questions: 1) Do pine legacies persist following management?; 2) What are the long-term drivers shaping native plant communities?; and 3) What are the landscape scale patterns of invasion and subsequent management?

To address these questions, I combined empirical field data, statistical modelling and spatial analyses for a space-for-time chronosequence of past wilding pine management that spans up to 16 years post-management in short tussock grasslands. Integrating field-based plot data measured at a local scale with remotely sensed landscape scale data provided a multi-disciplinary assessment of invasion legacies. The observational study showed that the legacies of pine invasions continue for at least a decade following management and are related to the stage of the invasion at the time of management. Plant communities are shaped both directly by invasion, as well as indirectly through changes to soil biogeochemical processing and competition from non-native grasses. At the landscape scale, invasion patterns reflect propagule pressure, whereas management outcomes are related to property-scale decisions, with legacies of dead pine on land cover still evident.

These findings have important implications for conservation management, informing decisions about the timing of invader removal and the need for additional management activities post-removal. Below I outline the key contributions of this research to long-term management of transformative invasions, discuss the main limitations of this study, and identify directions for future research.

5.1 Synthesis and novel contributions

5.1.1 Invasion legacies and drivers of plant community trajectories

Ecosystem trajectories following the management of a dominant plant invader are shaped by persistent legacy effects. This study provides unique insights into long-term outcomes by quantifying legacies that persisted for at least 16 years after management. Such long-term studies are rare; most research focuses on the period during invasion or shortly after management (Hulme, 2020). The persistence of altered ecosystem properties long after invader removal highlights the importance of understanding invasion legacies, which can alter ecosystem functioning. Invasive species can modify ecosystem processes and displace native species, creating legacies that may persist long after their removal (Corbin & D'Antonio, 2012; Ehrenfeld, 2010), yet the mechanisms and duration of these effects remain poorly understood. By examining ecosystem

change over more than a decade, this study enhances our understanding of the long-term consequences of invasion and its management.

Using a chronosequence approach that substitutes space for time, this study leveraged past management interventions to examine ecosystem trajectories at a scale larger than is possible for researcher-led experiments. I used complementary observational and modelling approaches to go beyond describing patterns by identifying the drivers of post-invasion outcomes. I quantified the magnitude and duration of legacies, showing how the effects of the invasion stage at the time of management, the length of time since management, and soil abiotic properties shape plant community responses. Modelling showed that legacies occur through both direct and indirect pathways. Direct effects include the displacement of native species and changes to soil biogeochemical processes; indirect effects include increased nutrient availability promoting the abundance of non-native grasses, which compete with native species reshaping the plant community. Late stage invasions in particular lead to less diverse, simpler plant communities dominated by a few non-native grasses. This indicates a trend towards ecosystem homogenisation, as seen in other ecosystems invaded by pines (García et al., 2018). Although there is some recovery of native plant communities over time, it is slower than reinvasion by pine or secondary invasions by other non-native species, resulting in novel or no-analogue communities rather than a return to pre-invasion communities (Urban et al., 2012). This is consistent with other research showing that dense invasions generate stronger ecosystem level modifications (Elgersma & Ehrenfeld, 2011; Vilà et al., 2011).

By utilising an existing chronosequence of management across the landscape, this study provides an assessment of post-invasion dynamics. However, the combination of historical invasion stage and time since management was not fully balanced, with late stage invasion sites predominantly managed within the last decade. The study was also limited to the age of the invasion, and the timing of when management was previously undertaken meaning that we could only assess legacies up to 16 years post management. However, as I have established a network of permanently marked plots these can be used to measure legacies into the future, and to quantify how long these changes persist. The analyses in this thesis were limited to comparisons between categorical invasion stages due to the lack of data prior to either invasion or management. The absence of pre-invasion data meant I was unable to fully assess ecosystem recovery or reconstruct successional trajectories to determine if communities were returning to pre-invasion states. Further, because soil biogeochemistry was measured at a single point in time, I was able to make comparisons between historical pine invasion stages; however, change is inferred rather than directly measured. Density-impact functions are widely used in ecological modelling of invasive species, but their development requires comprehensive datasets (Accolla et al., 2024; Norbury et al., 2015; Pereira-Ribeiro et al., 2026). I did not have quantitative data on the pine invasion prior to management, measures of tree size and stems per hectare would have allowed a more nuanced analysis and potentially a more precise assessment of impact or legacy thresholds. For future studies, having these data would enable a more robust assessment of baseline conditions and the drivers of change.

This research demonstrates how a single dominant invader can alter resource availability triggering facilitation of multiple non-native species (Ricciardi & Simberloff, 2025), and also shows that persistent legacy effects prolong this outcome long after the invader has been removed. By quantifying persistent legacy effects and determining the underlying drivers of plant community trajectories, I show the need for both a whole of system approach and long-term perspectives for managing and restoring invaded ecosystems.

5.1.2 Timing of invasion management

Early management maintained tussock grassland dominance and prevented landscape-scale transformation, whereas delayed management left enduring legacies of live and dead pines, even after management. This analysis of four decades of historical aerial imagery provides unique insight into these dynamics. Tussock grassland ecosystems are strongly shaped by both the spread of invasive pines and the timing of management interventions. Although management timing is widely recognised as a critical determinant of invasion outcomes (Ahmed et al., 2022), and managing invasions at early stages is effective, there is limited empirical evidence demonstrating how management timing shapes long-term trajectories at a landscape scale.

The relatively rapid progression of pine invasions highlights the importance of early management. Globally, pine invasions can progress from sparse establishment to dense, self-sustaining stands in as little as 10–20 years; this is particularly pronounced in New Zealand and is faster than in their native range (Ledgard, 2001; Taylor et al., 2016b). Early intervention is often the most effective and least costly strategy for managing pine invasions, reducing both the financial cost of management and the likelihood that invasions reach self-sustaining stages that are far more difficult to manage (Buckley et al., 2005; Moyano et al., 2025). Undertaking management before invasions become well advanced also limits the development of persistent biological legacies, which continue to shape plant community structure for at least a decade after management. However, early action is often constrained by detection ability, funding or political will, resulting in management being delayed until invasions reach advanced stages (Epanchin-Niell & Hastings, 2010; Hulme, 2020).

Early management of invasions also reduces the need for additional subsequent conservation action, such as secondary management of non-native grasses or active native restoration. These interventions become increasingly necessary once dense invasions alter soil biogeochemical processes and facilitate secondary invaders (Cuevas & Zalba, 2010; Franzese et al., 2017). This analysis shows that at the landscape level, early management is essential for preserving ecosystem types that are otherwise lost under advanced invasions. Together, the local and landscape scale outcomes reinforce that the timing of management shape ecological trajectories, determining whether invaded landscapes continue to support tussock grassland ecosystems or transition into novel states, dominated by invasion legacies.

5.1.3 The importance of scale

The widespread invasion by *P. contorta* has both local and landscape scale effects, that persist after management. Utilising a multi-disciplinary approach that combines local-scale plot measurements with landscape-scale remotely sensed data provides unique insights into the broader ecological consequences of invasion and management. While invasive pines exert strong local effects on soil biogeochemical processing and plant communities, their spread also drives landscape level transformations that cannot be captured through plot-based studies alone. This research shows that widespread pine invasion reshapes tussock grassland ecosystems at both scales, with altered plant communities at a local scale, and changing land cover at a landscape scale. This approach also highlights that while managing sparse invasions is the most efficient strategy, managing advanced invasions is necessary to limit further spread; while dense stands may have altered local ecosystem properties, reducing propagule pressure remains vital for protecting adjacent areas. The scale-dependent processes shown here are consistent with other studies in New Zealand grasslands (Buckley et al., 2005; Sapsford et al., 2022), and globally in other systems (Franzese et al., 2017; Steers et al., 2013; Wasowicz et al., 2025).

The interaction of multiple drivers of global change, namely pine invasion, land use change and land management, is demonstrated here at both local and landscape scales. The landscape scale analysis highlights the need for a coordinated management approach across landowners, as is being achieved through the national wilding conifer management programme (Ministry for Primary Industries, 2014), and as seen with other landscape scale invasions globally (Adoyo et al., 2022; Graham, 2019). In addition, the combination of plot-based and landscape scale analyses revealed that while pines have transformative effects on native plant communities, invaded areas retain some native biodiversity. In comparison, the expansion of irrigated, high producing grassland represents a far more severe landscape scale threat, effectively replacing native ecosystems altogether. To address this threat to native biodiversity would require a change in both policies and regulation relating to land use change, becoming an economic and social question rather than an ecological one.

The complementary approaches taken here emphasise the importance of long-term biodiversity monitoring, and high-quality remotely sensed data. The limited availability of plot-based plant community data at a landscape scale meant that we were only able to compare two time points. The investigation of data sources revealed the existence of data from the mid-twentieth century when landscape scale monitoring was more common than in recent decades, where it tends to be undertaken at a smaller scale. The lack of comprehensive monitoring since 1990 was notable and highlights an underinvestment in long-term biodiversity monitoring outside of the New Zealand Tier One broad scale monitoring programme (Bellingham et al., 2020). The analyses of remotely sensed data were constrained by the characteristics of the available of aerial imagery, including temporal coverage, spatial resolution, and RGB and spectral availability. Some fine-scale detail was lost because transitions between timesteps had to be assessed at the coarsest resolution. Distinguishing between land cover types was less reliable using greyscale imagery

compared with colour imagery, and the absence of a near infrared (NIR) band reduced the ability to differentiate visually similar colour vegetation. Despite these limitations, this research demonstrates a methodology that could be more broadly applied, showing that landscape-scale patterns can be quantified using freely available imagery, and that this approach could produce more precise results when applied to higher quality multi-spectral data.

5.1.4 Management implications post invader removal

The findings of this research provide quantitative evidence on how plant communities respond after pine management, offering a basis on which to decide if active management such as further weed management, to limit either reinvasion or secondary invasion, or if restoration of native species is necessary. Legacy effects, which can persist for years after removal, must be explicitly considered in management planning, particularly in systems facing multiple interacting threats (Corbin, 2025). Managing landscapes where pine invasion is followed by secondary invasions is inherently complex, requiring strategies that address both immediate impacts and longer-term ecological consequences (Suding et al., 2024). The persistence of legacy effects highlights that the timing of invasive species management is important for reducing the need to undertake further management action. Delaying management increases the strength of legacies and has long term consequences at both local and landscape scales increasing the likelihood that additional intervention will be required. By advancing our understanding of direct and indirect effects of invasion and management at local and landscape scales, this research shows that simply removing an invader is often insufficient to retain native-dominated plant communities.

Understanding ecosystem trajectories following the removal of a dominant invader is essential for determining whether additional management intervention is needed to conserve ecosystems (Zavaleta et al., 2001). The aim of conservation management is to enhance conservation values and develop a system which is sustainable in the long term (Hobbs & Norton, 1996; Ruiz-Jaen & Mitchell Aide, 2005). Conservation management can be active (direct intervention via planting and threat management) or passive (addressing the threats while relying on natural succession to retain habitat) (Holl & Aide, 2011; Rohr et al., 2018).

Decisions on how to deal with persistent invasion legacies depend on the management goals, ranging from simply managing the invasion, to restoring ecosystems to a previous state (Dickie et al., 2022). These short tussock grassland ecosystems have been managed as production landscapes for over 100 years, and while there is a recorded decline in biodiversity, these landscapes still preserve unique plant diversity (Day & Buckley, 2013; Duncan et al., 2001). There is currently no consensus on what a target ecosystem may be within these highly modified grassland ecosystems, and the goal is likely to vary based on landowner and the resources available. Although some areas are now being managed solely for conservation purposes, it is still useful to consider their management within the context of a matrix of productive land, noting that complex landscapes benefit from integrated land use planning (Abbott et al., 2019). Achieving successful conservation outcomes will depend on early detection and rapid response to new invasions, supported by

long-term monitoring frameworks that combine remote sensing with ground-based ecological data to track change.

5.2 Future directions

Future research could extend the approach taken here to other invasive species and a broader range of ecosystems. This study focused on a single invader, *Pinus contorta*, which is probably the most well studied of the invasive pine species in New Zealand. Emerging threats such as *Pseudotsuga menziesii* (Douglas fir) are comparatively understudied (Froude, 2011). Similar approaches could also be applied to other invaders known to modify ecosystem properties, including nitrogen-fixing species. Through structural equation modelling I show that pines are facilitating grasses but suppressing native plant species. Further research could more directly investigate the interactions between species, such as competition and facilitation between the dominant invader, secondary invaders and the native plant community. For example, if a decision was made to transition to a native woody system, then pines could be used as a nurse crop to facilitate regeneration, as has been shown in areas invaded by pine (Becerra & Montenegro, 2013; Wotton & McAlpine, 2013), and areas previously used for plantation forestry (Forbes et al., 2019; Pritchard et al., 2024).

Understanding changes at a landscape scale is particularly important for widespread invaders. The study sites were limited to a narrow set of environmental characteristics to limit confounding effects and understand specific drivers. However, pines invade across a wide range of ecosystems, and it would be beneficial to compare the legacy effects across a broader range of climate and environmental conditions, and across different ecosystems (Richardson & Rejmánek, 2004). Previous research has investigated the influences of climate and elevation on biotic interactions of pine within its native range (Gworek et al., 2007), but there is very little research investigating how interactions between these abiotic drivers and pine invasions shape biotic interactions or plant community outcomes.

By determining the drivers of successional trajectories, this research also highlights the likely need for active management to support native plant recovery. Future work could test interventions in sites that previously had late stage invasions, such as seed addition, planting native shrub species, or altering soil nutrients. Sheep grazing can be effective at limiting pine invasion in grasslands, although high stocking rates are required (Zamora-Nasca et al., 2020; Zamora Nasca et al., 2018). Grazing could be trialled to assess if it is a viable management approach to limit both the reinvasion of pine and the secondary invasions of non-native grasses in these post-invader systems. However, caution is needed as previous research in New Zealand's short tussock grassland ecosystems shows that the effects of grazing removal, and therefore the likely effects of reintroducing grazing, are context dependent (Ewans, 2004). For example, the exclusion of sheep may promote non-native grasses, accelerate native decline, or increase hawkweed abundance (Lord, 1990; Meurk et al., 2002; Rose et al., 1995); indicating that grazing may be beneficial. Conversely, other studies show benefits from excluding grazing, including recovery of tussock species and native woody cover

(Grove et al., 2002; Rose et al., 2004). Any use of grazing to manage non-native species should be carefully monitored to ensure it does not negatively affect native species.

5.3 Conclusions

This thesis presents a comprehensive assessment of how a dominant invasive species continues to shape ecosystems long after its removal, providing a quantitative analysis of the magnitude and persistence of legacy effects. By integrating plant community plot data, landscape scale remotely sensed data, and statistical modelling, this study moves beyond traditional short term or single scale approaches and reveals how invasion stage, management timing, and interacting drivers such as land use change collectively determine ecological trajectories. These complementary approaches provide an evidence base supporting a whole of system approach, which can be utilised as a basis for management decisions and to aid in achieving positive conservation outcomes.

References

- Abbott, M., Boyle, C., Lee, W., & Xuejing, L. (2019). Interweaving protected areas and productive landscapes in Aotearoa New Zealand: Using design to explore multifunctionality in the Mackenzie Basin. *Journal of Landscape Architecture*, 14(2), 6-19.
- Accolla, C., Schmolke, A., Vaugeois, M., & Galic, N. (2024). Density-dependent population regulation in freshwater fishes and small mammals: A literature review and insights for Ecological Risk Assessment. *Integrated Environmental Assessment and Management*, 20(5), 1225-1236.
- Adoyo, B., Schaffner, U., Mukhovi, S., Kiteme, B., Mbaabu, P. R., Eckert, S., Choge, S., & Ehrensperger, A. (2022). Spatiotemporal trajectories of invasive tree species reveal the importance of collective action for successful invasion management. *Journal of Land Use Science*, 17(1), 487-504.
- Ahmed, D. A., Hudgins, E. J., Cuthbert, R. N., Kourantidou, M., Diagne, C., Haubrock, P. J., Leung, B., Liu, C., Leroy, B., Petrovskii, S., Beidas, A., & Courchamp, F. (2022). Managing biological invasions: the cost of inaction. *Biological Invasions*, 24(7), 1927-1946.
- Aikio, S., Duncan, R. P., & Hulme, P. E. (2010). Lag-phases in alien plant invasions: separating the facts from the artefacts. *Oikos*, 119(2), 370-378.
- Al-Zubaidi, E. A., & Al Khafaji, R. (2024). Unsupervised Classification of Landsat-8 Satellite Imagery-Based on ISO Clustering. *Wasit Journal of Computer and Mathematics Science*, 3(1), 40-53.
- Allen, R., Wilson, J. B., & Mason, C. (1995). Vegetation change following exclusion of grazing animals in depleted grassland, Central Otago, New Zealand. *Journal of vegetation science*, 6(5), 615-626.
- Allen, R. B., Forsyth, D. M., MacKenzie, D. I., & Peltzer, D. A. (2022). Robustness of field studies evaluating biodiversity responses to invasive species management in New Zealand. *bioRxiv*, 2022.2003.2010.483864.
- Bai, Y., & Cotrufo, M. F. (2022). Grassland soil carbon sequestration: Current understanding, challenges, and solutions. *Science*, 377(6606), 603-608.
- Banks, P. B., Byrom, A. E., Pech, R. P., & Dickman, C. R. (2018). Reinvasion Is Not Invasion Again. *Bioscience*, 68(10), 792-804.
- Barrell, D. J. A., Andersen, B. G., & Denton, G. H. (2011). *Glacial geomorphology of the central South Island, New Zealand*. GNS Science.
- Becerra, P. I., & Montenegro, G. (2013). The widely invasive tree *Pinus radiata* facilitates regeneration of native woody species in a semi-arid ecosystem. *Applied Vegetation Science*, 16(2), 173-183.
- Bellingham, P. J., Richardson, S. J., Gormley, A. M., Allen, R. B., Cook, A., Crisp, P. N., Forsyth, D. M., McGlone, M. S., McKay, M., MacLeod, C. J., van Dam-Bates, P., & Wright, E. F. (2020). Implementing integrated measurements of Essential Biodiversity Variables at a national scale. *Ecological Solutions and Evidence*, 1(2), e12025.
- Belton, M., & Ledger, N. (1991). A study of the spread of exotic trees in the Canterbury high country. *J. Tussock Grassl. Mt. Lands Inst. Rev*, 48, 41-50.
- Boulant, N., Garnier, A., Curt, T., & Lepart, J. (2009). Disentangling the effects of land use, shrub cover and climate on the invasion speed of native and introduced pines in grasslands. *Diversity and distributions*, 15(6), 1047-1059.
- Bradley, B. A. (2014). Remote detection of invasive plants: a review of spectral, textural and phenological approaches. *Biological Invasions*, 16(7), 1411-1425.
- Brandt, A., Bellingham, P., Duncan, R., Etherington, T., Fridley, J., Howell, C., Hulme, P. E., Jo, I., McGlone, M., & Richardson, S. (2021). Naturalised plants transform the composition and function of the New Zealand flora. *Biological Invasions*, 23(2), 351-366.
- Brandt, A. J., Png, G. K., Jo, I., McGrannachan, C., Allen, K., Peltzer, D. A., D'Antonio, C., Dickie, I. A., French, K., & Leishman, M. R. (2023). Managing multi-species plant invasions when interactions influence their impact. *Frontiers in Ecology and the Environment*, 21(8), 370-379.
- Britton-Simmons, K. H., & Abbott, K. C. (2008). Short- and Long-Term Effects of Disturbance and Propagule Pressure on a Biological Invasion. *Journal of ecology*, 96(1), 68-77.
- Brower, A., & Page, J. (2017). Freeing the land beyond the shadow of the law: 20 years of the Crown Pastoral Land Act. *New Zealand Universities Law Review*, 27(4A), 975-995.

- Brower, A., Sprague, R., Vernotte, M., & McNair, H. (2018). Agricultural intensification, ownership, and landscape change in the Mackenzie Basin. *Journal of New Zealand Grasslands*, 47-54.
- Brown, N. D., Curtis, T., & Adams, E. C. (2015). Effects of clear-felling versus gradual removal of conifer trees on the survival of understorey plants during the restoration of ancient woodlands. *Forest Ecology and Management*, 348, 15-22.
- Buckley, D. S., Isebrands, J., & Sharik, T. L. (1999). Practical field methods of estimating canopy cover, PAR, and LAI in Michigan oak and pine stands. *Northern Journal of Applied Forestry*, 16(1), 25-32.
- Buckley, Y. M., Brockerhoff, E., Langer, L., Ledgard, N., North, H., & Rees, M. (2005). Slowing down a pine invasion despite uncertainty in demography and dispersal. *Journal of Applied Ecology*, 42(6), 1020-1030. (suf)
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. Springer-Verlag.
- Caplat, P., Coutts, S., & Buckley, Y. M. (2010). Gone with the wind: high-resolution analysis of pine dispersal in New Zealand mountains. Proceedings of the 17th Australian weeds conference,
- Caplat, P., Nathan, R., & Buckley, Y. M. (2012). Seed terminal velocity, wind turbulence, and demography drive the spread of an invasive tree in an analytical model. *Ecology*, 93(2), 368-377.
- Carlin, T. F., Roberts, T. P., Scott, M. B., Vorster, R. S., Rolando, C. A., & Paul, T. S. (2025a). Hiding in plain sight: Reinvasion risk from retained seed after dispersal events in introduced conifers. *Trees, Forests and People*, 20, 100852.
- Carlin, T. F., Scott, M. B., & Paul, T. S. (2025b). Reproductive trait shift in *Pinus contorta* helps explain invasion success in Aotearoa New Zealand. *New Zealand Journal of Ecology*, 49(1), 3584.
- Case, E. J., Harrison, S., & Cornell, H. V. (2016). After an invasion: understanding variation in grassland community recovery following removal of a high-impact invader. *Biological Invasions*, 18(2), 371-380.
- Catford, J. A., Jansson, R., & Nilsson, C. (2009). Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and distributions*, 15(1), 22-40.
- Catford, J. A., Wilson, J. R. U., Pyšek, P., Hulme, P. E., & Duncan, R. P. (2022). Addressing context dependence in ecology. *Trends in Ecology & Evolution*, 37(2), 158-170.
- Chang, C., & HilleRisLambers, J. (2016). Integrating succession and community assembly perspectives. *F1000Research*, 5.
- Chen, C., Condon, L., Davis, M., & Sherlock, R. (2000). Effects of afforestation on phosphorus dynamics and biological properties in a New Zealand grassland soil. *Plant and soil*, 220(1), 151-163.
- Cieraad, E., Burrows, L., Monks, A., & Walker, S. (2015). Woody native and exotic species respond differently to New Zealand dryland soil nutrient and moisture gradients. *New Zealand Journal of Ecology*, 39(2), 198-207.
- Congalton, R. G. (1991). A review of assessing the accuracy of classifications of remotely sensed data. *Remote Sensing of Environment*, 37(1), 35-46.
- Connor, H. E., & Vucetich, C. (1964). Tussock grassland communities in the Mackenzie country, south Canterbury, New Zealand. *New Zealand Journal of Botany*, 2(4), 325-351.
- Corbin, J. D. (2025). The influence of exotic species' legacies on pathways of restoration. *Restoration ecology*, 33(3), e14381.
- Corbin, J. D., & D'Antonio, C. M. (2012). Gone but not forgotten? Invasive plants' legacies on community and ecosystem properties. *Invasive Plant Science and Management*, 5(1), 117-124.
- Coulston, J., Zaccarelli, N., Riitters, K., Koch, F., & Zurlini, G. (2014). The spatial scan statistic: A new method for spatial aggregation of categorical raster maps. *arXiv preprint arXiv:1408.0164*.
- Cox, G. R., & Dickie, I. A. (2026). DNA metabarcoding reveals the loss of soil micro-eukaryote diversity associated with *Pinus* invasion into New Zealand's shrubland ecosystems. *Biological Invasions*, 28(4), 99.
- Craine, S. I., & Orians, C. M. (2004). Pitch pine (*Pinus rigida* Mill.) invasion of Cape Cod pond shores alters abiotic environment and inhibits indigenous herbaceous species. *Biological Conservation*, 116(2), 181-189.
- Crisfield, V. E., Guillaume Blanchet, F., Raudsepp-Hearne, C., & Gravel, D. (2024). How and why species are rare: towards an understanding of the ecological causes of rarity. *Ecography*, 2024(2), e07037.
- Crooks, J. A. (2002). Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos*, 97(2), 153-166.

- Crooks, J. A. (2005). Lag times and exotic species: The ecology and management of biological invasions in slow-motion 1. *Écoscience*, 12(3), 316-329.
- Cuddington, K. (2011). Legacy Effects: The Persistent Impact of Ecological Interactions. *Biological Theory*, 6(3), 203-210.
- Cuevas, Y. A., & Zalba, S. M. (2010). Recovery of native grasslands after removing invasive pines. *Restoration ecology*, 18(5), 711-719.
- Cui, X., Dickhaus, T., Ding, Y., & Hsu, J. C. (2021). *Handbook of multiple comparisons*. CRC Press.
- Culbert, P. D., Radeloff, V. C., St-Louis, V., Flather, C. H., Rittenhouse, C. D., Albright, T. P., & Pidgeon, A. M. (2012). Modeling broad-scale patterns of avian species richness across the Midwestern United States with measures of satellite image texture. *Remote Sensing of Environment*, 118, 140-150.
- D'Antonio, C. M., & Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual review of ecology and systematics*, 23(1), 63-87.
- Dale, M. R. T. (2000). *Spatial pattern analysis in plant ecology*. Cambridge University Press.
- Davis, M. A., Grime, J. P., & Thompson, K. (2000). Fluctuating resources in plant communities: a general theory of invasibility. *Journal of ecology*, 88(3), 528-534.
- Day, N. J., Barratt, B. I., Christensen, B., Curran, T. J., Dickinson, K. J., Lavorel, S., Norton, D. A., & Buckley, H. L. (2023). Predicting ecological change in tussock grasslands of Aotearoa New Zealand. *New Zealand Journal of Ecology*, 47(1), 3549.
- Day, N. J., & Buckley, H. L. (2013). Twenty-five years of plant community dynamics and invasion in New Zealand tussock grasslands. *Austral Ecology*, 38(6), 688-699.
- del Río-Mena, T., Willemen, L., Tesfamariam, G. T., Beukes, O., & Nelson, A. (2020). Remote sensing for mapping ecosystem services to support evaluation of ecological restoration interventions in an arid landscape. *Ecological indicators*, 113, 106182.
- Dickie, I. A., Sprague, R., Green, J., Peltzer, D. A., Orwin, K., & Sapsford, S. (2022). Applying ecological research to improve long-term outcomes of wilding conifer management. *New Zealand Journal of Ecology*, 46(2), 1-16.
- Dickie, I. A., St John, M. G., Yeates, G. W., Morse, C. W., Bonner, K. I., Orwin, K., & Peltzer, D. A. (2014). Belowground legacies of *Pinus contorta* invasion and removal result in multiple mechanisms of invasional meltdown. *AoB plants*, 6.
- Dickie, I. A., Yeates, G. W., St John, M. G., Stevenson, B. A., Scott, J. T., Rillig, M. C., Peltzer, D. A., Orwin, K. H., Kirschbaum, M. U. F., Hunt, J. E., Burrows, L. E., Barbour, M. M., & Aislabie, J. (2011). Ecosystem service and biodiversity trade-offs in two woody successions. *Journal of Applied Ecology*, 48(4), 926-934.
- Didham, R. K., Tylianakis, J. M., Gemmell, N. J., Rand, T. A., & Ewers, R. M. (2007). Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology & Evolution*, 22(9), 489-496.
- Dong, J., Zhang, J., Zhang, S., Yu, Z., Song, Z., & Meng, T. (2025). Vegetation extraction through UAV RGB imagery and efficient feature selection. *PLOS ONE*, 20(5), e0322180.
- Dovčiak, M., Hrivnák, R., Ujházy, K., & Gömöry, D. (2014). Patterns of grassland invasions by trees: insights from demographic and genetic spatial analyses. *Journal of Plant Ecology*, 8(5), 468-479.
- Driscoll, D. A., Banks, S. C., Barton, P. S., Lindenmayer, D. B., & Smith, A. L. (2013). Conceptual domain of the matrix in fragmented landscapes. *Trends in Ecology & Evolution*, 28(10), 605-613.
- Dudenhöffer, J. H., & Hulme, P. E. (2025a). Legacy of pine invasion disrupts plant–soil feedback of native and non-native grasses. *New phytologist*, 247(4), 1887-1896.
- Dudenhöffer, J. H., & Hulme, P. E. (2025b). Soil and litter legacy effects of pine invasion on subsequent reinvasion and secondary invasion. *Journal of ecology*, 113, 2559–2574.
- Dukes, J. S., & Mooney, H. A. (2004). Disruption of ecosystem processes in western North America by invasive species. *Revista chilena de historia natural*, 77(3), 411-437.
- Duncan, R. P., Webster, R. J., & Jensen, C. A. (2001). Declining plant species richness in the tussock grasslands of Canterbury and Otago, South Island, New Zealand. *New Zealand Journal of Ecology*, 35-47.
- Dunn, P. K., & Smyth, G. K. (2018). *Generalized linear models with examples in R* (Vol. 53). Springer.
- Dymond, J. R., Shepherd, J. D., Newsome, P. F., & Belliss, S. (2017). Estimating change in areas of indigenous vegetation cover in New Zealand from the New Zealand Land Cover Database (LCDB). *New Zealand Journal of Ecology*, 41(1), 56-64.

- Edwards, P., Stahlmann-Brown, P., & Thomas, S. (2020). Pernicious pests and public perceptions: Wilding conifers in Aotearoa New Zealand. *Land Use Policy*, 97, 104759.
- Ehrenfeld, J. G. (2003). Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, 6(6), 503-523.
- Ehrenfeld, J. G. (2010). Ecosystem consequences of biological invasions. *Annual review of ecology, evolution, and systematics*, 41, 59-80.
- Elgersma, K. J., & Ehrenfeld, J. G. (2011). Linear and non-linear impacts of a non-native plant invasion on soil microbial community structure and function. *Biological Invasions*, 13(3), 757-768.
- Elgersma, K. J., Ehrenfeld, J. G., Yu, S., & Vor, T. (2011). Legacy effects overwhelm the short-term effects of exotic plant invasion and restoration on soil microbial community structure, enzyme activities, and nitrogen cycling. *Oecologia*, 167(3), 733-745.
- Enders, M., Havemann, F., Ruland, F., Bernard-Verdier, M., Catford, J. A., Gómez-Aparicio, L., Haider, S., Heger, T., Kueffer, C., Kühn, I., Meyerson, L. A., Musseau, C., Novoa, A., Ricciardi, A., Sagouis, A., Schittko, C., Strayer, D. L., Vilà, M., Essl, F., Hulme, P. E., van Kleunen, M., Kumschick, S., Lockwood, J. L., Mabey, A. L., McGeoch, M. A., Palma, E., Pyšek, P., Saul, W. C., Yannelli, F. A., & Jeschke, J. M. (2020). A conceptual map of invasion biology: Integrating hypotheses into a consensus network. *Glob Ecol Biogeogr*, 29(6), 978-991.
- Engelmark, O., Sjöberg, K., Andersson, B., Rosvall, O., Ågren, G. I., Baker, W. L., Barklund, P., Björkman, C., Despain, D. G., Elfving, B., Ennos, R. A., Karlman, M., Knecht, M. F., Knight, D. H., Ledgard, N. J., Lindelöw, Å., Nilsson, C., Peterken, G. F., Sörlin, S., & Sykes, M. T. (2001). Ecological effects and management aspects of an exotic tree species: the case of lodgepole pine in Sweden. *Forest Ecology and Management*, 141(1), 3-13.
- Epanchin-Niell, R. S., & Hastings, A. (2010). Controlling established invaders: integrating economics and spread dynamics to determine optimal management. *Ecology letters*, 13(4), 528-541.
- Espie, P., Hunt, J., Butts, C., Cooper, P., & Harrington, W. (1984). Mackenzie ecological region, New Zealand protected natural areas programme. *Department of Lands and Survey, Wellington*, 88.
- ESRI. (2025). *ArcGIS Pro*. In (Version 3.6.0) ESRI. <https://www.esri.com/en-us/arcgis/products/arcgis-pro/>
- Ewans, R. (2004). *Effects of removing grazing from native grasslands in the eastern South Island of New Zealand: a literature review* (0478220928). (DOC science internal series). Department of Conservation.
- Fahrig, L., Baudry, J., Brotons, L., Burel, F. G., Crist, T. O., Fuller, R. J., Sirami, C., Siriwardena, G. M., & Martin, J.-L. (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology letters*, 14(2), 101-112.
- Fahrmeir, L., Kneib, T., Lang, S., & Marx, B. D. (2022). Regression models. In *Regression: Models, methods and applications* (pp. 23-84). Springer.
- Faith, D. P., Minchin, P. R., & Belbin, L. (1987). Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio*, 69(1), 57-68.
- Ferraina, A., Molina, C. D., Mazia, N., Piñeiro, G., Miranda, I., & Chaneton, E. J. (2021). Tree invasion in secondary grasslands diminishes herbaceous biomass and diversity: A study of mechanisms behind the process. *Journal of vegetation science*, 32(5), e13074.
- Flory, S. L., & Clay, K. (2010). Non-native grass invasion suppresses forest succession. *Oecologia*, 164(4), 1029-1038.
- Fogarty, D. T., Peterson, R. B., & Twidwell, D. (2022). Spatial patterns of woody plant encroachment in a temperate grassland. *Landscape ecology*, 37(11), 2835-2846.
- Foody, G. M. (2002). Status of land cover classification accuracy assessment. *Remote Sensing of Environment*, 80(1), 185-201.
- Foody, G. M., & Mathur, A. (2004). A relative evaluation of multiclass image classification by support vector machines. *IEEE Transactions on Geoscience and Remote Sensing*, 42(6), 1335-1343.
- Foody, G. M., Mathur, A., Sanchez-Hernandez, C., & Boyd, D. S. (2006). Training set size requirements for the classification of a specific class. *Remote Sensing of Environment*, 104(1), 1-14.
- Forbes, A. S., Norton, D. A., & Carswell, F. E. (2019). Opportunities and limitations of exotic *Pinus radiata* as a facilitative nurse for New Zealand indigenous forest restoration. *New Zealand Journal of Forestry Science*, 49.

- Foster, N. J., Maloney, R. F., Seddon, P. J., Rodríguez-Recio, M., & van Heezik, Y. (2022). High-elevation landforms limit the movement of invasive small mammal species. *Landscape ecology*, 37(10), 2651-2670.
- Francis, R. J., Kingsford, R. T., Moseby, K., Read, J., Pedler, R., Fisher, A., McCann, J., & West, R. (2024). Tracking landscape scale vegetation change in the arid zone by integrating ground, drone and satellite data. *Remote Sensing in Ecology and Conservation*, 10(3), 374-387.
- Franklin, J., Serra-Diaz, J. M., Syphard, A. D., & Regan, H. M. (2016). Global change and terrestrial plant community dynamics. *Proceedings of the National Academy of Sciences*, 113(14), 3725-3734.
- Franzese, J., Urrutia, J., García, R. A., Taylor, K., & Pauchard, A. (2017). Pine invasion impacts on plant diversity in Patagonia: invader size and invaded habitat matter. *Biological Invasions*, 19(3), 1015-1027.
- Froude, V. A. (2011). *Wilding conifers in New Zealand: status report* (Report prepared for the Ministry of Agriculture and Forestry). Pacific Eco-Logic.
- Fuentes-Lillo, E., García, R. A., Lembrechts, J. J., & Pauchard, A. (2026). Beyond Control: Short-Term Legacy Effects of Invasive Nonnative Trees May Halt Biodiversity Recovery. *Journal of vegetation science*, 37(1), e70110.
- Gabler, C. A., & Siemann, E. (2012). Environmental Variability and Ontogenetic Niche Shifts in Exotic Plants May Govern Reinvasion Pressure in Restorations of Invaded Ecosystems. *Restoration ecology*, 20(5), 545-550.
- García, R. A., Franzese, J., Policelli, N., Sasal, Y., Zenni, R. D., Nuñez, M. A., Taylor, K., & Pauchard, A. (2018). Non-native Pines Are Homogenizing the Ecosystems of South America. In R. Rozzi, R. H. May Jr, F. S. Chapin III, F. Massardo, M. C. Gavin, I. J. Klaver, A. Pauchard, M. A. Nuñez, & D. Simberloff (Eds.), *From Biocultural Homogenization to Biocultural Conservation* (pp. 245-263). Springer International Publishing.
- García, R. A., Fuentes-Lillo, E., Cavieres, L., Cobar-Carranza, A. J., Davis, K. T., Naour, M., Nuñez, M. A., Maxwell, B. D., Lembrechts, J. J., & Pauchard, A. (2023). *Pinus contorta* Alters Microenvironmental Conditions and Reduces Plant Diversity in Patagonian Ecosystems. *Diversity*, 15(3), 320.
- Gavier-Pizarro, G. I., Kuemmerle, T., Hoyos, L. E., Stewart, S. I., Huebner, C. D., Keuler, N. S., & Radeloff, V. C. (2012). Monitoring the invasion of an exotic tree (*Ligustrum lucidum*) from 1983 to 2006 with Landsat TM/ETM+ satellite data and Support Vector Machines in Córdoba, Argentina. *Remote Sensing of Environment*, 122, 134-145.
- González-Moreno, P., Pino, J., Carreras, D., Basnou, C., Fernández-Rebollar, I., & Vilà, M. (2013). Quantifying the landscape influence on plant invasions in Mediterranean coastal habitats. *Landscape ecology*, 28(5), 891-903.
- Grace, J. B., Anderson, T. M., Olff, H., & Scheiner, S. M. (2010). On the specification of structural equation models for ecological systems. *Ecological Monographs*, 80(1), 67-87.
- Grace, J. B., & Keeley, J. E. (2006). A structural equation model analysis of postfire plant diversity in California shrublands. *Ecological applications*, 16(2), 503-514.
- Graham, S. (2019). Coordinating invasive plant management among conservation and rural stakeholders. *Land Use Policy*, 81, 247-255.
- Grove, P. B., Mark, A. F., & Dickinson, K. J. M. (2002). Vegetation monitoring of recently protected tussock grasslands in the southern South Island, New Zealand. *Journal of the Royal Society of New Zealand*, 32(3), 379-414.
- Grove, S., Parker, I. M., & Haubensak, K. A. (2015). Persistence of a soil legacy following removal of a nitrogen-fixing invader. *Biological Invasions*, 17(9), 2621-2631.
- Gundale, M. J., Pauchard, A., Langdon, B., Peltzer, D. A., Maxwell, B. D., & Nunez, M. A. (2014). Can model species be used to advance the field of invasion ecology? *Biological Invasions*, 16(3), 591-607.
- Gworek, J. R., Vander Wall, S. B., & Brussard, P. F. (2007). Changes in biotic interactions and climate determine recruitment of Jeffrey pine along an elevation gradient. *Forest Ecology and Management*, 239(1), 57-68.
- Hejda, M., Pyšek, P., & Jarošík, V. (2009). Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of ecology*, 97(3), 393-403.

- Hellmann, C., Sutter, R., Rascher, K. G., Máguas, C., Correia, O., & Werner, C. (2011). Impact of an exotic N₂-fixing *Acacia* on composition and N status of a native Mediterranean community. *Acta Oecologica*, 37(1), 43-50.
- Hijmans, R. J., Bivand, R., Forner, K., Ooms, J., Pebesma, E., & Sumner, M. D. (2022). Package ‘terra’. *Maintainer: Vienna, Austria*, 384(10.32614).
- Hobbs, R. J., & Huenneke, L. F. (1992). Disturbance, Diversity, and Invasion: Implications for Conservation. *Conservation biology*, 6(3), 324-337.
- Hobbs, R. J., & Humphries, S. E. (1995). An integrated approach to the ecology and management of plant invasions. *Conservation biology*, 9(4), 761-770.
- Hobbs, R. J., & Norton, D. A. (1996). Towards a conceptual framework for restoration ecology. *Restoration ecology*, 4(2), 93-110.
- Holl, K. D., & Aide, T. M. (2011). When and where to actively restore ecosystems? *Forest Ecology and Management*, 261(10), 1558-1563.
- Hopkins, A., & Holz, B. (2006). Grassland for agriculture and nature conservation: production, quality and multi-functionality. *Agronomy research*, 4(1), 3-20.
- Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous Inference in General Parametric Models. *Biometrical Journal*, 50(3), 346-363.
- Hulme, P. E. (2006). Beyond control: wider implications for the management of biological invasions. *Journal of Applied Ecology*, 43(5), 835-847.
- Hulme, P. E. (2017). Climate change and biological invasions: evidence, expectations, and response options. *Biological Reviews*, 92(3), 1297-1313.
- Hulme, P. E. (2020). Plant invasions in New Zealand: global lessons in prevention, eradication and control. *Biological Invasions*, 22(5), 1539-1562.
- Hulme, P. E. (2021). Unwelcome exchange: International trade as a direct and indirect driver of biological invasions worldwide. *One Earth*, 4(5), 666-679.
- Hurst, J., & Allen, R. B. (2007). *The Recce method for describing New Zealand vegetation – field protocols*. Manaaki Whenua - Landcare Research.
- Iannone, R., & Roy, O. (2016). Package ‘DiagrammeR’. *R package version*, 1(1).
- IPBES. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. In S. Díaz, J. Settele, E. S. Brondízio, H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. Brauman, & S. H. Butchart (Eds.), *Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*.
- IPBES. (2023). *Thematic assessment report on invasive alien species and their control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services* (H. Roy, A. Pauchard, P. Stoett, & T. Renard Truong, Eds.).
- Jeschke, J. M., Bacher, S., Blackburn, T. M., Dick, J. T. A., Essl, F., Evans, T., Gaertner, M., Hulme, P. E., Kühn, I., Mrugała, A., Pergl, J., Pyšek, P., Rabitsch, W., Ricciardi, A., Richardson, D. M., Sendek, A., Vilà, M., Winter, M., & Kumschick, S. (2014). Defining the Impact of Non-Native Species. *Conservation biology*, 28(5), 1188-1194.
- Jo, I., Fridley, J. D., & Frank, D. A. (2017). Invasive plants accelerate nitrogen cycling: evidence from experimental woody monocultures. *Journal of ecology*, 105(4), 1105-1110.
- Jordan, N. R., Larson, D. L., & Huerd, S. C. (2008). Soil modification by invasive plants: effects on native and invasive species of mixed-grass prairies. *Biological Invasions*, 10(2), 177-190.
- Katul, G. G., Porporato, A., Nathan, R., Siqueira, M., Soons, M. B., Poggi, D., Horn, H. S., & Levin, S. A. (2005). Mechanistic Analytical Models for Long-Distance Seed Dispersal by Wind. *The American Naturalist*, 166(3), 368-381.
- Kettenring, K. M., & Adams, C. R. (2011). Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. *Journal of Applied Ecology*, 48(4), 970-979.
- Kotowska, D., Pärt, T., Skórka, P., Auffret, A. G., & Żmihorski, M. (2022). Scale dependence of landscape heterogeneity effects on plant invasions. *Journal of Applied Ecology*, 59(5), 1313-1323.
- Kremer, N. J., Halpern, C. B., & Antos, J. A. (2014). Conifer reinvasion of montane meadows following experimental tree removal and prescribed burning. *Forest Ecology and Management*, 319, 128-137.
- Kuhn, M. (2008). Building predictive models in R using the caret package. *Journal of statistical software*, 28, 1-26.

- Larkin, D. J. (2012). Lengths and correlates of lag phases in upper-Midwest plant invasions. *Biological Invasions*, 14(4), 827-838.
- Latham, A. D. M., Latham, M. C., Norbury, G. L., Forsyth, D. M., & Warburton, B. (2020). A review of the damage caused by invasive wild mammalian herbivores to primary production in New Zealand. *New Zealand Journal of Zoology*, 47(1), 20-52.
- Leathwick, J., Morgan, F., Wilson, G., Rutledge, D., McLeod, M., & Johnston, K. (2002). *Land environments of New Zealand: A technical guide*. Ministry for the Environment.
- Ledgard, N. (1988). The spread of introduced trees in New Zealand's rangelands-South Island high country experience. *Journal of the Tussock Grasslands and Mountain Lands Institute*, 44, 1-8.
- Ledgard, N. (2001). The spread of lodgepole pine (*Pinus contorta*, Dougl.) in New Zealand. *Forest Ecology and Management*, 141(1-2), 43-57.
- Ledgard, N., & Belton, M. (1985). Exotic trees in the Canterbury high country. *New Zealand Journal of Forestry Science*, 15(3), 298-323.
- Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7(5), 573-579.
- Lefcheck, J. S. (2021). *An Introduction to Structural Equation Modeling in R* https://jslefcche.github.io/sem_book/index.html
- Legendre, P., & Legendre, L. (2012). *Numerical ecology* (Vol. 24). Elsevier.
- Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecology letters*, 7(7), 601-613.
- Leidinger, J. L. G., Gossner, M. M., Weisser, W. W., Koch, C., Rosadio Cayllahua, Z. L., Podgaiski, L. R., Duarte, M. M., Araújo, A. S. F., Overbeck, G. E., Hermann, J.-M., Kollmann, J., & Meyer, S. T. (2017). Historical and recent land use affects ecosystem functions in subtropical grasslands in Brazil. *Ecosphere*, 8(12), e02032.
- Lenth, R. (2023). emmeans: Estimated Marginal Means, aka Least-Squares Means. *R package version 1.8. 5*.
- Levin, S. A. (1992). The Problem of Pattern and Scale in Ecology. *Ecology*, 73(6), 1943-1967.
- Levine, J. M., Adler, P. B., & Yelenik, S. G. (2004). A meta-analysis of biotic resistance to exotic plant invasions. *Ecology letters*, 7(10), 975-989.
- Li, D., Monahan, W. B., & Baiser, B. (2018). Species richness and phylogenetic diversity of native and non-native species respond differently to area and environmental factors. *Diversity and distributions*, 24(6), 853-864.
- Linders, T. E. W., Schaffner, U., Eschen, R., Abebe, A., Choge, S. K., Nigatu, L., Mbaabu, P. R., Shiferaw, H., & Allan, E. (2019). Direct and indirect effects of invasive species: Biodiversity loss is a major mechanism by which an invasive tree affects ecosystem functioning. *Journal of ecology*, 107(6), 2660-2672.
- LINZ. (2021). *Wilding Conifer Information System (WCIS)*. <http://data.linz.govt.nz/>
- LINZ. (2026). *Location of Crown pastoral land*. Retrieved 14/04/2026 from <https://www.linz.govt.nz/our-work/crown-property-management/pastoral-land/location-crown-pastoral-land/>
- Lloyd, K., Smith, D., Rate, S., Gillies, R., & Bawden, R. (2016). *Methods for the prioritisation of wilding conifer sites across New Zealand* (Prepared for New Zealand Ministry for Primary Industries). Wildlands Consultants LTD. <https://www.wildingconifers.org.nz/assets/Uploads/Methods-for-wilding-conifer-site-prioritisation-15-4-16.pdf>
- Lord, J. M. (1990). The maintenance of *Poa cita* grassland by grazing. *New Zealand Journal of Ecology*, 43-49.
- Lu, D., & Weng, Q. (2007). A survey of image classification methods and techniques for improving classification performance. *International Journal of Remote Sensing*, 28(5), 823-870.
- Macara, G. R. (2016). *The climate and weather of Canterbury* (NIWA SCIENCE AND TECHNOLOGY SERIES). NIWA.
- Mack, R. N., Simberloff, D., Mark Lonsdale, W., Evans, H., Clout, M., & Bazzaz, F. A. (2000). Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological applications*, 10(3), 689-710.
- Manaaki Whenua - Landcare Research. (2025a). *Land Cover Database version 6.0, Mainland, New Zealand* Version 6.0). <https://doi.org/https://doi.org/10.26060/WM99-RY32>

- Manaaki Whenua - Landcare Research. (2025b). *New Zealand National Vegetation Survey databank (NVS)* <https://nvs.landcareresearch.co.nz>
- Marchante, H., Marchante, E., Freitas, H., & Hoffmann, J. H. (2015). Temporal changes in the impacts on plant communities of an invasive alien tree, *Acacia longifolia*. *Plant Ecology*, 216(11), 1481-1498.
- Mark, A. F., Barratt, B. I., & Weeks, E. (2013). Ecosystem services in New Zealand's indigenous tussock grasslands: conditions and trends. In J. Dymond (Ed.), *Ecosystem services in New Zealand: conditions and trends*. (pp. 1-33). Manaaki Whenua Press.
- Mark, A. F., & McLennan, B. (2005). The conservation status of New Zealand's indigenous grasslands. *New Zealand Journal of Botany*, 43(1), 245-270.
- Martin-Gallego, P., Aplin, P., Marston, C., Altamirano, A., & Pauchard, A. (2020). Detecting and modelling alien tree presence using Sentinel-2 satellite imagery in Chile's temperate forests. *Forest Ecology and Management*, 474, 118353.
- Martin, M. R., Tipping, P. W., & Sickman, J. O. (2009). Invasion by an exotic tree alters above and belowground ecosystem components. *Biological Invasions*, 11(8), 1883-1894.
- Mast, J. N., Veblen, T. T., & Hodgson, M. E. (1997). Tree invasion within a pine/grassland ecotone: an approach with historic aerial photography and GIS modeling. *Forest Ecology and Management*, 93(3), 181-194.
- McConnachie, M. M., van Wilgen, B. W., Richardson, D. M., Ferraro, P. J., & Forsyth, A. T. (2015). Estimating the effect of plantations on pine invasions in protected areas: a case study from South Africa. *Journal of Applied Ecology*, 52(1), 110-118.
- McCune, B., & Grace, J. B. (2002). *Analysis of ecological communities*. Mjmm Software Design.
- McGlone, M., & Moar, N. (1998). Dryland Holocene vegetation history, Central Otago and the Mackenzie Basin, South Island, New Zealand. *New Zealand Journal of Botany*, 36(1), 91-111.
- McGlone, M. S. (2001). The origin of the indigenous grasslands of southeastern South Island in relation to pre-human woody ecosystems. *New Zealand Journal of Ecology*, 1-15.
- McGregor, K. F., Watt, M. S., Hulme, P. E., & Duncan, R. P. (2012). What determines pine naturalization: species traits, climate suitability or forestry use? *Diversity and distributions*, 18(10), 1013-1023.
- Melbourne, B. A., Cornell, H. V., Davies, K. F., Dugaw, C. J., Elmendorf, S., Freestone, A. L., Hall, R. J., Harrison, S., Hastings, A., Holland, M., Holyoak, M., Lambrinos, J., Moore, K., & Yokomizo, H. (2007). Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecology letters*, 10(1), 77-94.
- Melgani, F., & Bruzzone, L. (2004). Classification of hyperspectral remote sensing images with support vector machines. *IEEE Transactions on Geoscience and Remote Sensing*, 42(8), 1778-1790.
- Mesacasa, L., Macagnan, L. B., Fiaschi, P., & Dechoum, M. d. S. (2022). Effects of time since invasion and control actions on a coastal ecosystem invaded by non-native pine trees. *Ecological Solutions and Evidence*, 3(1), e12138.
- Meurk, C. D., Walker, S., Gibson, R. S., & Espie, P. (2002). Changes in vegetation states in grazed and ungrazed Mackenzie Basin grasslands, New Zealand, 1990–2000. *New Zealand Journal of Ecology*, 95-106.
- Ministry for Primary Industries. (2013). *Biosecurity Risk Management of Entry Pathways for Pasture Pests*. Ministry for Primary Industries.
- Ministry for Primary Industries. (2014). *The right tree in the right place: New Zealand Wilding Conifer Management Strategy 2015–2030*.
- Morgan, J. L., Gergel, S. E., & Coops, N. C. (2010). Aerial Photography: A Rapidly Evolving Tool for Ecological Management. *Bioscience*, 60(1), 47-59.
- Movia, A., Beinat, A., & Crosilla, F. (2016). Shadow detection and removal in RGB VHR images for land use unsupervised classification. *ISPRS Journal of Photogrammetry and Remote Sensing*, 119, 485-495.
- Moyano, J., García-Díaz, P., Langdon, B., Palmer, S. C. F., Caplat, P., Lambin, X., Pauchard, A., & Nuñez, M. A. (2025). Remove saplings early: Cost-effective strategies to contain tree invasions and prevent their impacts. *Journal of Applied Ecology*, 62(3), 661-676.
- Müllerová, J., Brundu, G., Große-Stoltenberg, A., Kattenborn, T., & Richardson, D. M. (2023). Pattern to process, research to practice: remote sensing of plant invasions. *Biological Invasions*, 25(12), 3651-3676.

- Musseau, C. L., Bernard-Verdier, M., Heger, T., Skopeteas, L. H., Strasiewsky, D., Mietchen, D., & Jeschke, J. M. (2024). A conceptual classification scheme of invasion science. *Bioscience*, 74(12), 840-850.
- Myers, J. H., Simberloff, D., Kuris, A. M., & Carey, J. R. (2000). Eradication revisited: dealing with exotic species. *Trends in Ecology & Evolution*, 15(8), 316-320.
- Nandasena, W. D. K. V., Brabyn, L., & Serrao-Neumann, S. (2023). Monitoring invasive pines using remote sensing: a case study from Sri Lanka. *Environmental Monitoring and Assessment*, 195(2), 347.
- National Wilding Conifer Control Programme, & Environment Canterbury. (2020). *Wilding pine control handbook*. National Wilding Conifer Control Programme.
<https://www.wildingpines.nz/assets/Documents/WildingPinecontrolhandbook-v2.pdf>
- Newbold, T., Hudson, L. N., Arnell, A. P., Contu, S., De Palma, A., Ferrier, S., Hill, S. L. L., Hoskins, A. J., Lysenko, I., Phillips, H. R. P., Burton, V. J., Chng, C. W. T., Emerson, S., Gao, D., Pask-Hale, G., Hutton, J., Jung, M., Sanchez-Ortiz, K., Simmons, B. I., Whitmee, S., Zhang, H., Scharlemann, J. P. W., & Purvis, A. (2016). Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science*, 353(6296), 288-291.
- Norbury, G. L., Pech, R. P., Byrom, A. E., & Innes, J. (2015). Density-impact functions for terrestrial vertebrate pests and indigenous biota: Guidelines for conservation managers. *Biological Conservation*, 191, 409-420.
- North, H., & Ledgard, N. (2005). *Modelling Wilding Conifer Spread and Control*. Landcare Research.
- Norton, D. A. (2009). Species invasions and the limits to restoration: learning from the New Zealand experience. *Science*, 325(5940), 569-571.
- Novoa, A., Richardson, D. M., Pyšek, P., Meyerson, L. A., Bacher, S., Canavan, S., Catford, J. A., Čuda, J., Essl, F., Foxcroft, L. C., Genovesi, P., Hirsch, H., Hui, C., Jackson, M. C., Kueffer, C., Le Roux, J. J., Measey, J., Mohanty, N. P., Moodley, D., Müller-Schärer, H., Packer, J. G., Pergl, J., Robinson, T. B., Saul, W.-C., Shackleton, R. T., Visser, V., Weyl, O. L. F., Yannelli, F. A., & Wilson, J. R. U. (2020). Invasion syndromes: a systematic approach for predicting biological invasions and facilitating effective management. *Biological Invasions*, 22(5), 1801-1820.
- Nsikani, M. M., van Wilgen, B. W., & Gaertner, M. (2018). Barriers to ecosystem restoration presented by soil legacy effects of invasive alien N₂-fixing woody species: implications for ecological restoration. *Restoration ecology*, 26(2), 235-244.
- Núñez, M. A., Chiuffo, M. C., Torres, A., Paul, T., Dimarco, R. D., Raal, P., Policelli, N., Moyano, J., García, R. A., & Van Wilgen, B. W. (2017). Ecology and management of invasive Pinaceae around the world: progress and challenges. *Biological Invasions*, 19(11), 3099-3120.
- Núñez, M. A., Davis, K. T., Dimarco, R. D., Peltzer, D. A., Paritsis, J., Maxwell, B. D., & Pauchard, A. (2021). Should tree invasions be used in treeless ecosystems to mitigate climate change? *Frontiers in Ecology and the Environment*, 19(6), 334-341.
- Núñez, M. A., & Dickie, I. A. (2014). Invasive belowground mutualists of woody plants. *Biological Invasions*, 16(3), 645-661.
- NZPCN. (2026). *New Zealand Plant Conservation Network*. <https://www.nzpcn.org.nz/>
- O'Loughlin, L. S., & Green, P. T. (2017). Secondary invasion: When invasion success is contingent on other invaders altering the properties of recipient ecosystems. *Ecology and evolution*, 7(19), 7628-7637.
- O'Connor, K. (1981). Changes in the tussock grasslands and mountain lands. *Tussock Grasslands and Mountain Lands Institute Review*, 40, 47-63.
- Ogden, J. A. E., & Rejmánek, M. (2005). Recovery of native plant communities after the control of a dominant invasive plant species, *Foeniculum vulgare*: implications for management. *Biological Conservation*, 125(4), 427-439.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R., Simpson, G. L., Solymos, P., Stevens, M. H. H., & Wagner, H. (2013). Package 'vegan'. *Community ecology package, version 2.9*, 1-295.
- Olden, J. D., Poff, N. L., Douglas, M. R., Douglas, M. E., & Fausch, K. D. (2004). Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology & Evolution*, 19(1), 18-24.
- Ovaskainen, O., & Abrego, N. (2020). *Joint species distribution modelling: With applications in R*. Cambridge University Press.
- Parliamentary Commissioner for the Environment. (2009). *Change in the high country: Environmental stewardship and tenure review*.

- Pauchard, A., Escudero, A., García, R. A., de la Cruz, M., Langdon, B., Cavieres, L. A., & Esquivel, J. (2016). Pine invasions in treeless environments: dispersal overruns microsite heterogeneity. *Ecology and evolution*, 6(2), 447-459.
- Pauchard, A., & Shea, K. (2006). Integrating the Study of Non-native Plant Invasions across Spatial Scales. *Biological Invasions*, 8(3), 399-413.
- Pearson, D. E., Ortega, Y. K., Runyon, J. B., & Butler, J. L. (2016). Secondary invasion: the bane of weed management. *Biological Conservation*, 197, 8-17.
- Peart, R., & Woodhouse, C. (2020). *Mackenzie Basin & Landscape Protection*. Environmental Defence Society.
- Peck, C., Williamson, M., & Rohani, M. (2022). *Benefits and costs of additional investment in wilding conifer control* (National Wilding Conifer Control Programme). Ministry for Primary Industries.
- Peltzer, D. A. (2018). Ecology and consequences of invasion by non-native (wilding) conifers in New Zealand. *Journal of New Zealand Grasslands*, 80, 39-46.
- Peralta, G., Dickie, I. A., Yeates, G. W., & Peltzer, D. A. (2020). Community-and trophic-level responses of soil nematodes to removal of a non-native tree at different stages of invasion. *PLOS ONE*, 15(1), e0227130.
- Pereira-Ribeiro, J., Vagmaker, N., Ferregueti, A. C., Bergallo, H. G., & Rocha, C. F. D. (2026). How an invasive tree reshapes the forest floor and alters amphibian occupancy through direct and indirect effects. *Biological Invasions*, 28(3), 62.
- Pickett, S. T., Pickett, S. T., & White, P. (1985). *The ecology of natural disturbance and patch dynamics*. Academic press.
- Prangel, E., Kasari-Toussaint, L., Neuenkamp, L., Noreika, N., Karise, R., Marja, R., Ingerpuu, N., Kupper, T., Keerberg, L., Oja, E., Meriste, M., Tiitsaar, A., Ivask, M., & Helm, A. (2023). Afforestation and abandonment of semi-natural grasslands lead to biodiversity loss and a decline in ecosystem services and functions. *Journal of Applied Ecology*, 60(5), 825-836.
- Prior, K. M., Adams, D. C., Klepzig, K. D., & Hulcr, J. (2018). When does invasive species removal lead to ecological recovery? Implications for management success. *Biological Invasions*, 20(2), 267-283.
- Pritchard, A. S. E., Larcombe, M. J., Steel, J. B., & Lord, J. M. (2024). Plant diversity under native and exotic forests: Implications for transitional forestry in Aotearoa New Zealand. *Forest Ecology and Management*, 572, 122314.
- Pyšek, P., & Richardson, D. M. (2007). Traits Associated with Invasiveness in Alien Plants: Where Do we Stand? In W. Nentwig (Ed.), *Biological Invasions* (pp. 97-125). Springer Berlin Heidelberg.
- Pyšek, P., & Richardson, D. M. (2010). Invasive species, environmental change and management, and health. *Annual review of environment and resources*, 35, 25-55.
- R Core Team. (2025). *R: A Language and Environment for Statistical Computing*. In R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rabinowitz, D., Rapp, J. K., & Dixon, P. M. (1984). Competitive abilities of sparse grass species: means of persistence or cause of abundance. *Ecology*, 65(4), 1144-1154.
- Radford, I. J., Dickinson, K. J. M., & Lord, J. M. (2010). Does disturbance, competition or resource limitation underlie *Hieracium lepidulum* invasion in New Zealand? Mechanisms of establishment and persistence, and functional differentiation among invasive and native species. *Austral Ecology*, 35(3), 282-293.
- Rejmanek, M. (2011). Invasiveness. In D. Simberloff & M. Rejmanek (Eds.), *Encyclopedia of biological invasions* (pp. 379-385). University of California Press.
- Rejmanek, M., & Richardson, D. M. (1996). What attributes make some plant species more invasive? *Ecology*, 77(6), 1655-1661.
- Rejmanek, M., Richardson, D. M., & Pysek, P. (2005). Plant invasions and invasibility of plant communities. In E. van der Maarel (Ed.), *Vegetation ecology* (pp. 332-355). Blackwell Publishing.
- Reynolds, P. L., Glanz, J., Yang, S., Hann, C., Couture, J., & Grosholz, E. (2017). Ghost of invasion past: legacy effects on community disassembly following eradication of an invasive ecosystem engineer. *Ecosphere*, 8(3), e01711.
- Ricciardi, A., & Simberloff, D. (2025). Revisiting invasional meltdown: mechanisms and consequences of positive non-native species interactions. *Biological Invasions*, 27(8), 183.

- Richards, D., Herzig, A., Abbott, M., Ausseil, A.-G., Guo, J., Sood, A., & Lavorel, S. (2023). Diverse contributions of nature to climate change adaptation in an upland landscape. *Ecosystems and People*, 19(1), 2225647.
- Richardson, D. M., & Bond, W. J. (1991). Determinants of Plant Distribution: Evidence from Pine Invasions. *The American Naturalist*, 137(5), 639-668.
- Richardson, D. M., Hui, C., Nuñez, M. A., & Pauchard, A. (2014). Tree invasions: patterns, processes, challenges and opportunities. *Biological Invasions*, 16(3), 473-481.
- Richardson, D. M., Pyšek, P., Rejmánek, M., Barbour, M. G., Panetta, F. D., & West, C. J. (2000). Naturalization and invasion of alien plants: concepts and definitions. *Diversity and distributions*, 6(2), 93-107.
- Richardson, D. M., & Rejmánek, M. (2004). Conifers as invasive aliens: a global survey and predictive framework. *Diversity and distributions*, 10(5-6), 321-331.
- Richardson, D. M., & Rejmánek, M. (2011). Trees and shrubs as invasive alien species—a global review. *Diversity and distributions*, 17(5), 788-809.
- Richardson, D. M., Williams, P., & Hobbs, R. J. (1994). Pine invasions in the Southern Hemisphere: determinants of spread and invadability. *Journal of biogeography*, 511-527.
- Rogan, J., & Chen, D. (2004). Remote sensing technology for mapping and monitoring land-cover and land-use change. *Progress in Planning*, 61(4), 301-325.
- Rohal, C. B., Cranney, C., & Kettenring, K. M. (2019). Abiotic and Landscape Factors Constrain Restoration Outcomes Across Spatial Scales of a Widespread Invasive Plant [Original Research]. *Frontiers in Plant Science*, 10(481).
- Rohr, J. R., Bernhardt, E. S., Cadotte, M. W., & Clements, W. H. (2018). The ecology and economics of restoration. *Ecology and Society*, 23(2).
- Rolando, C. A., Richardson, B., Schou, W., Somchit, C., Paul, T. S., & Scott, M. B. (2025). Optimising aerial herbicide treatment for control of dense conifer infestations: a New Zealand case study. *Pest Management Science*, 81(4), 2144-2154.
- Romero, G. Q., Gonçalves-Souza, T., Vieira, C., & Koricheva, J. (2015). Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis. *Biological Reviews*, 90(3), 877-890.
- Rose, A., Platt, K., & Frampton, C. (1995). Vegetation change over 25 years in a New Zealand short-tussock grassland: effects of sheep grazing and exotic invasions. *New Zealand Journal of Ecology*, 163-174.
- Rose, A. B., & Frampton, C. M. (2007). Rapid short-tussock grassland decline with and without grazing, Marlborough, New Zealand. *New Zealand Journal of Ecology*, 232-244.
- Rose, A. B., Suisted, P. A., & Frampton, C. M. (2004). Recovery, invasion, and decline over 37 years in a Marlborough short-tussock grassland, New Zealand. *New Zealand Journal of Botany*, 42(1), 77-87.
- Ruiz-Jaen, M. C., & Mitchell Aide, T. (2005). Restoration success: how is it being measured? *Restoration ecology*, 13(3), 569-577.
- Rundel, P. W., Dickie, I. A., & Richardson, D. M. (2014). Tree invasions into treeless areas: mechanisms and ecosystem processes. *Biological Invasions*, 16(3), 663-675.
- Sá, N. C. d., Carvalho, S., Castro, P., Marchante, E., & Marchante, H. (2017). Using Landsat Time Series to Understand How Management and Disturbances Influence the Expansion of an Invasive Tree. *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing*, 10(7), 3243-3253.
- Sala, O. E., Stuart Chapin, F., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., & Kinzig, A. (2000). Global biodiversity scenarios for the year 2100. *Science*, 287(5459), 1770-1774.
- Sapsford, S. J., Brandt, A. J., Davis, K. T., Peralta, G., Dickie, I. A., Gibson II, R. D., Green, J. L., Hulme, P. E., Nuñez, M. A., Orwin, K. H., Pauchard, A., Wardle, D. A., & Peltzer, D. A. (2020). Towards a framework for understanding the context dependence of impacts of non-native tree species. *Functional Ecology*, 34(5), 944-955.
- Sapsford, S. J., & Dickie, I. A. (2023). Slow soil enzyme recovery following invasive tree removal through gradual changes in bacterial and fungal communities. *Journal of ecology*, 111(12), 2614-2626.
- Sapsford, S. J., Wakelin, A., Peltzer, D. A., & Dickie, I. (2022). Pine invasion drives loss of soil fungal diversity. *Biological Invasions*, 24(2), 401-414.
- Schils, R. L. M., Buße, C., Rhymer, C. M., Francksen, R. M., Klaus, V. H., Abdalla, M., Milazzo, F., Lellei-Kovács, E., Berge, H. t., Bertora, C., Chodkiewicz, A., Dămăţircă, C., Feigenwinter, I., Fernández-Rebollo, P., Ghiasi, S., Hejduk, S., Hiron, M., Janicka, M., Pellaton, R., Smith, K. E., Thorman, R.,

- Vanwalleghe, T., Williams, J., Zavattaro, L., Kampen, J., Derkx, R., Smith, P., Whittingham, M. J., Buchmann, N., & Price, J. P. N. (2022). Permanent grasslands in Europe: Land use change and intensification decrease their multifunctionality. *Agriculture, Ecosystems & Environment*, 330, 107891.
- Seabloom, E. W., Borer, E. T., Buckley, Y. M., Cleland, E. E., Davies, K. F., Firn, J., Harpole, W. S., Hautier, Y., Lind, E. M., MacDougall, A. S., Orrock, J. L., Prober, S. M., Adler, P. B., Anderson, T. M., Bakker, J. D., Biederman, L. A., Blumenthal, D. M., Brown, C. S., Brudvig, L. A., Cadotte, M., Chu, C., Cottingham, K. L., Crawley, M. J., Damschen, E. I., Dantonio, C. M., DeCrappeo, N. M., Du, G., Fay, P. A., Frater, P., Gruner, D. S., Hagenah, N., Hector, A., Hillebrand, H., Hofmockel, K. S., Humphries, H. C., Jin, V. L., Kay, A., Kirkman, K. P., Klein, J. A., Knops, J. M. H., La Pierre, K. J., Ladwig, L., Lambrinos, J. G., Li, Q., Li, W., Marushia, R., McCulley, R. L., Melbourne, B. A., Mitchell, C. E., Moore, J. L., Morgan, J., Mortensen, B., O'Halloran, L. R., Pyke, D. A., Risch, A. C., Sankaran, M., Schuetz, M., Simonsen, A., Smith, M. D., Stevens, C. J., Sullivan, L., Wolkovich, E., Wragg, P. D., Wright, J., & Yang, L. (2015). Plant species' origin predicts dominance and response to nutrient enrichment and herbivores in global grasslands. *Nature Communications*, 6(1), 7710.
- Sharma, A., Kaur, A., Kaur, S., Kohli, R. K., & Batish, D. R. (2023). Plant Invasion and Climate Change: A Global Overview. In S. Tripathi, R. Bhadouria, P. Srivastava, R. Singh, & D. R. Batish (Eds.), *Plant Invasions and Global Climate Change* (pp. 3-30). Springer Nature Singapore.
- Signorelli, S., Casaretto, E., Etchemendy-Gamundi, M., Bentancor, M., & Harvey Millar, A. (2025). The Green Index: A Widely Accessible Method to Quantify the Degree of Greenness of Photosynthetic Organisms. *Plant, Cell & Environment*, 48(11), 8027-8043.
- Simberloff, D. (2003). Eradication—preventing invasions at the outset. *Weed Science*, 51(2), 247-253.
- Simberloff, D. (2009). The Role of Propagule Pressure in Biological Invasions. *Annual review of ecology, evolution, and systematics*, 40(Volume 40, 2009), 81-102.
- Simberloff, D. (2011). How common are invasion-induced ecosystem impacts? *Biological Invasions*, 13(5), 1255-1268.
- Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., & Vilà, M. (2013). Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution*, 28(1), 58-66.
- Simberloff, D., & Von Holle, B. (1999). Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, 1(1), 21-32.
- Soubry, I., & Guo, X. (2022). Quantifying Woody Plant Encroachment in Grasslands: A Review on Remote Sensing Approaches. *Canadian journal of remote sensing*, 48(3), 337-378.
- Sprague, R., Godsoe, W., & Hulme, P. E. (2019). Assessing the utility of aerial imagery to quantify the density, age structure and spatial pattern of alien conifer invasions. *Biological Invasions*, 21(6), 2095-2106.
- Sprague, R., Hulme, P. E., Nuñez, M. A., & Peltzer, D. A. (2022). How to link people, government, and science in effective large-scale management of invasive trees [Policy and Practice Reviews]. *Frontiers in Environmental Science, Volume 10 - 2022*.
- Steers, R. J., Fritzke, S. L., Rogers, J. J., Cartan, J., & Hacker, K. (2013). Invasive pine tree effects on northern coastal scrub structure and composition. *Invasive Plant Science and Management*, 6(2), 231-242.
- Stephens, A. E., Krannitz, P. G., & Myers, J. H. (2009). Plant community changes after the reduction of an invasive rangeland weed, diffuse knapweed, *Centaurea diffusa*. *Biological control*, 51(1), 140-146.
- Stevens, N., Lehmann, C. E. R., Murphy, B. P., & Durigan, G. (2017). Savanna woody encroachment is widespread across three continents. *Global Change Biology*, 23(1), 235-244.
- Stinson, K. A., Campbell, S. A., Powell, J. R., Wolfe, B. E., Callaway, R. M., Thelen, G. C., Hallett, S. G., Prati, D., & Klironomos, J. N. (2006). Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. *PLoS biology*, 4(5), e140.
- Stotz, G. C., Gianoli, E., & Cahill Jr, J. F. (2019). Biotic homogenization within and across eight widely distributed grasslands following invasion by *Bromus inermis*. *Ecology*, 100(7), e02717.
- Straffellini, E., Luo, J., & Tarolli, P. (2024). Climate change is threatening mountain grasslands and their cultural ecosystem services. *CATENA*, 237, 107802.

- Strayer, D. L., Eviner, V. T., Jeschke, J. M., & Pace, M. L. (2006). Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution*, 21(11), 645-651.
- Suding, K. N., Collins, C. G., Hallett, L. M., Larios, L., Brigham, L. M., Dudley, J., Farrer, E. C., Larson, J. E., Shackelford, N., & Spasojevic, M. J. (2024). Biodiversity in changing environments: An external-driver internal-topology framework to guide intervention. *Ecology*, 105(8), e4322.
- Suding, K. N., Gross, K. L., & Houseman, G. R. (2004). Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution*, 19(1), 46-53.
- Szantoi, Z., Escobedo, F., Abd-Elrahman, A., Smith, S., & Pearlstine, L. (2013). Analyzing fine-scale wetland composition using high resolution imagery and texture features. *International Journal of Applied Earth Observation and Geoinformation*, 23, 204-212.
- Taylor, K. T., Maxwell, B. D., Pauchard, A., Nuñez, M. A., & Rew, L. J. (2016a). Native versus non-native invasions: similarities and differences in the biodiversity impacts of *Pinus contorta* in introduced and native ranges. *Diversity and distributions*, 22(5), 578-588.
- Taylor, K. T., Maxwell, B. D., Pauchard, A., Nuñez, M. A., Peltzer, D. A., Terwei, A., & Rew, L. J. (2016b). Drivers of plant invasion vary globally: evidence from pine invasions within six ecoregions. *Global Ecology and Biogeography*, 25(1), 96-106.
- ter Braak, C. J., & Looman, C. W. (1986). Weighted averaging, logistic regression and the Gaussian response model. *Vegetatio*, 65(1), 3-11.
- ter Steege, H. (2018). *Hemiphot.R: Free R scripts to analyse hemispherical photographs for canopy openness, leaf area index and photosynthetic active radiation under forest canopies*. Naturalis Biodiversity Center. <https://github.com/Hans-ter-Steege/Hemiphot>
- Theoharides, K. A., & Dukes, J. S. (2007). Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New phytologist*, 176(2), 256-273.
- Thompson, S., & Katul, G. (2008). Plant Propagation Fronts and Wind Dispersal: An Analytical Model to Upscale from Seconds to Decades Using Superstatistics. *The American Naturalist*, 171(4), 468-479.
- Tikhonov, G., Opedal, Ø. H., Abrego, N., Lehtikoinen, A., de Jonge, M. M., Oksanen, J., & Ovaskainen, O. (2020). Joint species distribution modelling with the R-package HMSC. *Methods in Ecology and Evolution*, 11(3), 442-447.
- Treskonova, M. (1991). Changes in the structure of tall tussock grasslands and infestation by species of *Hieracium* in the Mackenzie Country, New Zealand. *New Zealand Journal of Ecology*, 65-78.
- Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology letters*, 11(12), 1351-1363.
- Upadhyay, P., Mahadik, S., & Kamble, A. (2016). Image classification using visible RGB bands. *2016 3rd International Conference on Computing for Sustainable Global Development (INDIACom)*, 2660-2663.
- Urban, M. C., Tewksbury, J. J., & Sheldon, K. S. (2012). On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proceedings of the Royal Society B: Biological Sciences*, 279(1735), 2072-2080.
- Van Auken, O. W. (2009). Causes and consequences of woody plant encroachment into western North American grasslands. *Journal of Environmental Management*, 90(10), 2931-2942.
- Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., Pergl, J., Schaffner, U., Sun, Y., & Pyšek, P. (2011). Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology letters*, 14(7), 702-708.
- Vilà, M., & Ibáñez, I. (2011). Plant invasions in the landscape. *Landscape ecology*, 26(4), 461-472.
- Vitousek, P. M., D'antonio, C. M., Loope, L. L., Rejmanek, M., & Westbrooks, R. (1997). Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology*, 21(1), 1-16.
- Vitousek, P. M., & Walker, L. R. (1989). Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs*, 59(3), 247-265.
- Wainwright, C. E., Wolkovich, E. M., & Cleland, E. E. (2012). Seasonal priority effects: implications for invasion and restoration in a semi-arid system. *Journal of Applied Ecology*, 49(1), 234-241.
- Walker, B., & Steffen, W. (1997). An overview of the implications of global change for natural and managed terrestrial ecosystems. *Conservation ecology*, 1(2).

- Walker, S., Comrie, J., Head, N., Ladley, K. J., & Clarke, D. (2016). Hawkweed invasion does not prevent indigenous non-forest vegetation recovery following grazing removal. *New Zealand Journal of Ecology*, 40(1), 137-149.
- Walker, S., Lee, W. G., & Rogers, G. M. (2003). *The woody vegetation of Central Otago, New Zealand: its present and past distribution and future restoration needs*. (Science for Conservation). Department of Conservation.
- Wardle, D. A., & Peltzer, D. A. (2017). Impacts of invasive biota in forest ecosystems in an aboveground–belowground context. *Biological Invasions*, 19(11), 3301-3316.
- Wardle, P. (1985). Environmental influences on the vegetation of New Zealand. *New Zealand Journal of Botany*, 23(4), 773-788.
- Wardle, P. (1991). *Vegetation of New Zealand*. Blackburn Press.
- Wasowicz, P., Óskarsdóttir, G., & Þórhallsdóttir, Þ. E. (2025). Lodgepole pine (*Pinus contorta* Douglas ex Loudon) invasion in subarctic Iceland: evidence from a long-term study. *NeoBiota*, 97, 47-66.
- Weidlich, E. W., Flórido, F. G., Sorrini, T. B., & Brancalion, P. H. (2020). Controlling invasive plant species in ecological restoration: A global review. *Journal of Applied Ecology*, 57(9), 1806-1817.
- Wickham, H., François, R., Henry, L., Müller, K., & Wickham, M. H. (2019). Package ‘plyr’. *A Grammar of Data Manipulation. R package version*, 8.
- Wieczorkowski, J. D., & Lehmann, C. E. R. (2022). Encroachment diminishes herbaceous plant diversity in grassy ecosystems worldwide. *Global Change Biology*, 28(18), 5532-5546.
- Wiens, J. A., Nils Chr, S., Van Horne, B., & Ims, R. A. (1993). Ecological Mechanisms and Landscape Ecology. *Oikos*, 66(3), 369-380.
- Wiser, S. K., & Buxton, R. P. (2008). Context matters: Matrix vegetation influences native and exotic species composition on habitat islands. *Ecology*, 89(2), 380-391.
- With, K. A. (2002). The Landscape Ecology of Invasive Spread. *Conservation biology*, 16(5), 1192-1203.
- Wood, E. M., Pidgeon, A. M., Radeloff, V. C., & Keuler, N. S. (2012). Image texture as a remotely sensed measure of vegetation structure. *Remote Sensing of Environment*, 121, 516-526.
- Wotton, D. M., & McAlpine, K. G. (2013). *Predicting native plant succession through woody weeds in New Zealand*. Publishing Team, Department of Conservation.
- Wyse, S. V., & Hulme, P. E. (2021a). Dispersal potential rather than risk assessment scores predict the spread rate of non-native pines across New Zealand. *Journal of Applied Ecology*, 58(9), 1981-1992.
- Wyse, S. V., & Hulme, P. E. (2021b). Limited evidence for a consistent seed mass-dispersal trade-off in wind-dispersed pines. *Journal of ecology*, 109(1), 284-293.
- Yelenik, S., Stock, W., & Richardson, D. (2004). Ecosystem level impacts of invasive *Acacia saligna* in the South African fynbos. *Restoration ecology*, 12(1), 44-51.
- Yokomizo, H., Possingham, H. P., Thomas, M. B., & Buckley, Y. M. (2009). Managing the impact of invasive species: the value of knowing the density–impact curve. *Ecological applications*, 19(2), 376-386.
- Young, R. (2016). *Mackenzie wilding conifer strategy 2016-2030*. Te Manahuna Consulting.
- Young, R. (2023). *Post Harvest Wilding Conifer Management – Mackenzie District Plan*. Te Manahuna Consulting.
- Zamora-Nasca, L. B., Dimarco, R. D., Nassini, D., Alvear, P. A., Mayoral, A., Nuñez, M. A., & Relva, M. A. (2020). Sheep feeding preference as a tool to control pine invasion in Patagonia: influence of foliar toughness, terpenoids and resin content. *Scientific Reports*, 10(1), 12113.
- Zamora Nasca, L. B., Relva, M. A., & Núñez, M. A. (2018). Ungulates can control tree invasions: experimental evidence from nonnative conifers and sheep herbivory. *Biological Invasions*, 20(3), 583-591.
- Zavaleta, E. S., Hobbs, R. J., & Mooney, H. A. (2001). Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology & Evolution*, 16(8), 454-459.
- Zhang, W., Brandt, M., Wang, Q., Prishchepov, A. V., Tucker, C. J., Li, Y., Lyu, H., & Fensholt, R. (2019). From woody cover to woody canopies: How Sentinel-1 and Sentinel-2 data advance the mapping of woody plants in savannas. *Remote Sensing of Environment*, 234, 111465.
- Zhu, A.-X. (2017). Resampling, Raster. In *International Encyclopedia of Geography* (pp. 1-5). Wiley Blackwell.

Appendix A

Additional information for Chapter 2

A.1 Supporting Information

S2.1 Description of HMSC methods and parameters

Hierarchical modelling of species communities (HMSC) explains the distribution of species in the environment. This is achieved by first determining which explanatory variables may be acting as environmental filters. The residuals from this analysis are then assessed to determine if species interactions can explain the remaining variation that was not explained by the environment or by species traits.

We estimated model parameters using Markov chain Monte Carlo (MCMC) sampling implemented in the R package ‘HMSC’ (Tikhonov et al., 2020). We modelled environmental effects by using the plot scores from the first three principal components of the environmental variable PCA. We used growth form as a trait in the model, to test if these different groups of species responded differently to historical pine invasion stages and to, therefore, capture structural changes in the plant community. We included a phylogenetic tree to family level in the model to account for the evolutionary non-independence of species. We used plot as a random effect term. The model was fitted using a probit function.

We ran four parallel MCMC chains, retaining 4,000 posterior samples per chain after discarding the first 1,000 iterations as burn-in and applying a thinning interval of 10. This resulted in a total of 16,000 posterior samples per model. Convergence was assessed using the effective sample size (ESS; considered satisfactory when $ESS > 200$ for all parameters) and the Gelman-Rubin diagnostic (Potential Scale Reduction Factor; satisfactory when $PSRF < 1.05$) (Ovaskainen & Abrego, 2020). Model predictive performance was assessed using Tjur’s R^2 , Area Under the Curve (AUC) and Root Mean Squared Error (Ovaskainen & Abrego, 2020).

We used Bayesian posterior inference to assess species-specific responses to the environment, represented by principal components, examining whether regression coefficients (β) differed credibly from zero at a 0.95 support level. We assessed how species grouped by growth form responded to the environmental gradient represented by principal components, using posterior predictions from the HMSC model. We evaluated trait–environment relationships using posterior support values from the estimated gamma parameters (Γ). A relationship was considered credible if at least 95% of the posterior distribution lay above or below zero (Ovaskainen & Abrego, 2020).

A.2 Supplementary Tables

Table S2.1 Distribution of plots across historical pine invasion stages, and the length of time between when control was undertaken and plant community plots were measured.

<i>Time since control (years)</i>	<i>Early</i>	<i>Intermediate</i>	<i>Late</i>
2	0	3	7
3	0	1	4
4	0	2	3
5	8	1	0
6	0	0	2
10	0	4	1
11	1	1	0
12	0	3	0
13	0	4	0
14	4	0	1
16	4	0	0

Table S2.2 Results of a Principal Components Analysis (PCA) conducted to explain the relationships among key environmental variables. These statistics relate to Figure 2.3.

- a) Variance explained by each Principal Component (PC), representing the variation in environmental conditions between plots.

	<i>Component Standard deviation</i>	<i>Variance</i>	<i>Proportion of variance</i>	<i>Cumulative proportion</i>
<i>PC 1</i>	1.65	2.73	0.46	0.46
<i>PC 2</i>	1.35	1.82	0.30	0.76
<i>PC 3</i>	0.87	0.76	0.13	0.88
<i>PC 4</i>	0.63	0.39	0.07	0.95

- b) PCA loadings for each environmental variables on the three Principal Components that each explain more than 10% of variance. Loadings are coefficients that indicate the strength and direction of the relationship between each environmental variable and a Principal Component.

	<i>PC 1</i>	<i>PC 2</i>	<i>PC 3</i>
<i>Soil moisture</i>	0.525	0.119	0.184
<i>Olsen phosphorus</i>	0.426	-0.340	0.372
<i>Available nitrogen</i>	0.166	0.667	0.219
<i>Total carbon</i>	0.235	0.572	-0.439
<i>pH</i>	-0.372	0.299	0.750
<i>Canopy openness</i>	-0.567	0.091	-0.160

- c) Correlation of the Principal Components with time since control using Pearson's correlation coefficient.

	<i>Pearson correlation coefficient</i>	<i>p value</i>
<i>PC 1</i>	-0.456	0.001
<i>PC 2</i>	-0.042	0.763
<i>PC 3</i>	-0.411	0.002

- d) ANOVA results that show whether each Principal Component varies with historical pine invasion stage.

	<i>Component</i>	<i>df</i>	<i>Sum sq</i>	<i>Mean sq</i>	<i>F value</i>	<i>p value</i>
<i>PC 1</i>	Pine invasion stage	2	56.30	28.15	15.71	0.000
	Residuals	51	91.35	1.79		
<i>PC 2</i>	Pine invasion stage	2	6.50	3.25	1.81	0.174
	Residuals	51	91.57	1.80		
<i>PC 3</i>	Pine invasion stage	2	0.15	0.08	0.10	0.910
	Residuals	51	40.66	0.80		

Table S2.3 Plant species frequency (proportion of plots present) and mean cover when present (%) for species that are not rare (i.e. occur in >10% of plots, or have at least one occurrence with >1% cover). Species are sorted in descending order of frequency.

<i>Species</i>	<i>Family</i>	<i>Bio-status</i>	<i>Growth form</i>	<i>Frequency</i>	<i>Mean cover (%)</i>
<i>Anthoxanthum odoratum</i> L.	Gramineae	Non-native	Graminoid	0.98	27.2
<i>Agrostis capillaris</i> L.	Gramineae	Non-native	Graminoid	0.98	17.2
<i>Rumex acetosella</i> L.	Polygonaceae	Non-native	Forb	0.81	1.4
<i>Pilosella officinarum</i> Vaill.	Compositae	Non-native	Forb	0.69	34.5
<i>Pinus contorta</i> Douglas ex Loudon	Pinaceae	Non-native	Tree	0.57	4.5
<i>Festuca novae-zelandiae</i> (Hack.) Cockayne	Gramineae	Native	Graminoid	0.48	2.7
<i>Aira caryophyllea</i> L.	Gramineae	Non-native	Graminoid	0.39	1.0
<i>Festuca rubra</i> L.	Gramineae	Non-native	Graminoid	0.31	6.1
<i>Carex breviculmis</i> R.Br.	Cyperaceae	Native	Graminoid	0.31	1.0
<i>Microtis unifolia</i> (G.Forst.) Rchb.f.	Orchidaceae	Native	Orchid	0.31	1.0
<i>Thelymitra longifolia</i> J.R.Forst. & G.Forst.	Orchidaceae	Native	Orchid	0.31	1.0
<i>Poa colensoi</i> Hook.f.	Gramineae	Native	Graminoid	0.3	1.2
<i>Rosa rubiginosa</i> L.	Rosaceae	Non-native	Shrub	0.28	2.9
<i>Wahlenbergia albomarginata</i> Hook.	Campanulaceae	Native	Forb	0.28	1.0
<i>Pilosella piloselloides</i> subsp <i>praealta</i> (Gochnat) S.Bräut. & Greuter	Compositae	Non-native	Forb	0.26	1.0
<i>Pimelea oreophila</i> C.J.Burrows	Thymelaeaceae	Native	Shrub	0.22	1.0
<i>Prasophyllum colensoi</i> Hook.f.	Orchidaceae	Native	Orchid	0.20	1.0
<i>Hypericum perforatum</i> L.	Hypericaceae	Non-native	Forb	0.19	1.3
<i>Cerastium fontanum</i> Baumg.	Caryophyllaceae	Non-native	Forb	0.19	1.1
<i>Rytidosperma setifolium</i> (Hook.f.) Connor & Edgar	Gramineae	Native	Graminoid	0.19	1.0
<i>Trifolium arvense</i> L.	Leguminosae	Non-native	Forb	0.19	1.0
<i>Veronica arvensis</i> L.	Plantaginaceae	Non-native	Forb	0.17	1.0
<i>Styphelia nesophila</i> (DC.) Sleumer	Ericaceae	Native	Shrub	0.15	1.0
<i>Coprosma petriei</i> Cheeseman	Rubiaceae	Native	Shrub	0.13	1.7
<i>Celmisia gracilentia</i> Hook.f.	Compositae	Native	Forb	0.13	1.0
<i>Rytidosperma exiguum</i> (Kirk) H.P.Linder	Gramineae	Native	Graminoid	0.11	1.3
<i>Rytidosperma pumilum</i> (Kirk) Connor & Edgar	Gramineae	Native	Graminoid	0.11	1.2
<i>Anthosachne solandri</i> (Steud.) Barkworth & S.W.L.Jacobs	Gramineae	Native	Graminoid	0.11	1.0
<i>Rytidosperma</i> Steud.	Gramineae	Native	Graminoid	0.11	1.0

<i>Species</i>	<i>Family</i>	<i>Bio-status</i>	<i>Growth form</i>	<i>Frequency</i>	<i>Mean cover (%)</i>
<i>Verbascum thapsus</i> L.	Scrophulariaceae	Non-native	Forb	0.11	1.0
<i>Muehlenbeckia axillaris</i> (Hook.f.) Endl.	Polygonaceae	Native	Vine	0.09	5.4
<i>Styphelia nana</i> (M.I.Dawson & Heenan) Hislop, Crayn & Puente-Lel.	Ericaceae	Native	Shrub	0.09	2.0
<i>Cirsium arvense</i> (L.) Scop.	Compositae	Non-native	Forb	0.07	1.8
<i>Achillea millefolium</i> L.	Compositae	Non-native	Forb	0.07	1.5
<i>Trifolium repens</i> L.	Leguminosae	Non-native	Forb	0.07	1.3
<i>Muehlenbeckia complexa</i> (A.Cunn.) Meisn.	Polygonaceae	Non-native	Vine	0.06	2.0
<i>Anthosachne falcis</i> (Connor) Barkworth & S.W.L.Jacobs	Gramineae	Native	Graminoid	0.06	1.3
<i>Carmichaelia monroi</i> Hook.f.	Leguminosae	Native	Shrub	0.04	1.5
<i>Hypolepis ambigua</i> (A. Rich.) Brownsey et Chinnock	Dennstaedtiaceae	Native	Fern	0.02	3.0
<i>Carmichaelia vexillata</i> Heenan	Leguminosae	Native	Shrub	0.02	2.0
<i>Chionochloa rubra</i> Zotov	Gramineae	Native	Graminoid	0.02	2.0
<i>Melicytus alpinus</i> (Kirk) Garn.-Jones	Violaceae	Native	Shrub	0.02	2.0
<i>Pseudotsuga menziesii</i> (Mirb.) Franco	Pinaceae	Non-native	Tree	0.18	5.0
<i>Pinus sylvestris</i> L.	Pinaceae	Non-native	Tree	0.18	2.0
<i>Solanum dulcamara</i> L.	Solanaceae	Non-native	Forb	0.02	2.0

Table S2.4 Results of pairwise comparisons between non-native and native species cover and richness between historical pine invasion stages. Stars show significance * $p < 0.05$, ** $p < 0.01$, * $p < 0.001$.**

- a) Generalised linear model comparisons showing differences in percent cover between different historical pine invasion stages for non-native and native plant species.

<i>Bio status</i>	<i>Historical pine invasion stage comparison</i>	<i>Coefficient</i>	<i>Standard error</i>	<i>z value</i>	<i>p value</i>	<i>Significance</i>
<i>Non-native</i>	Early - Intermediate	-0.001	0.186	-0.005	1.000	
	Intermediate - Late	-0.334	0.184	-1.821	0.449	
	Early - Late	-0.335	0.189	-1.776	0.478	
<i>Native</i>	Early - Intermediate	-0.837	0.218	-3.849	0.002	**
	Intermediate - Late	-0.539	0.243	-2.221	0.226	
	Early - Late	-1.377	0.236	-5.823	< 0.001	***

- b) Generalised linear model comparisons showing differences in species richness between different historical pine invasion stages for non-native and native plant species.

<i>Bio status</i>	<i>Historical pine invasion stage comparison</i>	<i>Estimate</i>	<i>Standard error</i>	<i>z value</i>	<i>p value</i>	<i>Significance</i>
<i>Non-native</i>	Early - Intermediate	0.239	0.121	1.977	0.347	
	Intermediate - Late	-0.279	0.120	-2.321	0.179	
	Early - Late	-0.040	0.130	-0.309	1.000	
<i>Native</i>	Early - Intermediate	-0.680	0.132	-5.157	< 0.001	***
	Intermediate - Late	-0.757	0.190	-3.983	0.001	***
	Early - Late	-1.437	0.177	-8.125	< 0.001	***

Table S2.5 Hierarchical Modelling of Species Communities (HMSC) model statistics for the native and non-native plant species models.

- a) HMSC model convergence. ESS = Effective Sample Size, values > 200 indicate satisfactory sampling efficiency and convergence. β represents species-specific regression coefficients describing the effects of environmental covariates on species occurrences. Γ represents trait-based regression coefficients that describe how species traits mediate species responses to environmental covariates. PSRF = Potential Scale Reduction Factor, a Gelman-Rubin diagnostic, values < 1.05 indicate that multiple Markov chains have satisfactory convergence.

	<i>ESS (β) – Minimum</i>	<i>ESS (β)– Median</i>	<i>ESS (Γ) – Minimum</i>	<i>ESS (Γ)– Median</i>	<i>PSRF - maximum point estimate</i>	<i>PSRF - maximum upper 95% CI</i>
<i>Native</i>	2,003	8,641	3,418	13,215	1.006	1.019
<i>Non-native</i>	2,756	12,779	14,796	15,839	1.006	1.011

- b) Hierarchical Modelling of Species Communities (HMSC) model fit statistics. Root Mean Square Error (RMSE) measures the difference between predicted and actual values; values $\leq 20\%$ of the observed range indicate satisfactory performance. Turj R^2 assesses the separation between presences and absences; values > 0.10 indicate satisfactory class discrimination. Area under the Curve (AUC) assesses the model's discriminative ability, values > 0.65 indicate satisfactory performance.

	<i>RMSE Mean</i>	<i>RMSE Range</i>	<i>Tjur R^2 Mean (sd)</i>	<i>AUC Mean (sd)</i>
<i>Native</i>	0.27	0.12 - 0.41	0.23 (0.17)	0.84 (0.14)
<i>Non-native</i>	0.30	0.13 - 0.46	0.15 (0.12)	0.84 (0.09)

Table S2.6 Generalised linear model comparisons showing differences in proportional cover between historical pine invasion stages for different plant growth forms. Comparisons were calculated separately for non-native and native plant species.

<i>Bio status</i>	<i>Growth form</i>	<i>Historical pine invasion stage comparison</i>	<i>Estimate</i>	<i>Standard Error</i>	<i>z Value</i>	<i>p Value</i>
<i>Non-native</i>	Graminoid	Early - Intermediate	-1.3	0.2	-5.5	< 0.001
		Intermediate - Late	-1.2	0.3	-4.3	< 0.001
		Early - Late	-2.5	0.3	-8.6	< 0.001
	Forb	Early - Intermediate	0.9	0.2	3.8	0.001
		Intermediate - Late	1.6	0.3	5.0	< 0.001
		Early - Late	2.5	0.3	8.0	< 0.001
	Fern	Early - Intermediate	NA	NA	NA	NA
		Intermediate - Late	NA	NA	NA	NA
		Early - Late	NA	NA	NA	NA
	Shrub	Early - Intermediate	0.2	0.5	0.3	0.936
		Intermediate - Late	0.2	0.7	0.2	0.973
		Early - Late	0.3	0.8	0.4	0.898
	Tree	Early - Intermediate	-0.7	0.5	-1.2	0.457
		Intermediate - Late	0.2	0.4	0.7	0.788
		Early - Late	-0.4	0.6	-0.7	0.764
<i>Native</i>	Graminoid	Early - Intermediate	0.3	0.3	1.0	0.598
		Intermediate - Late	-0.1	0.4	-0.4	0.934
		Early - Late	0.2	0.4	0.5	0.877
	Forb	Early - Intermediate	0.2	0.5	0.3	0.942
		Intermediate - Late	-0.1	0.6	-0.1	0.992
		Early - Late	0.1	0.5	0.2	0.983
	Orchid	Early - Intermediate	0.0	0.4	0.0	0.999
		Intermediate - Late	0.3	0.9	0.3	0.944
		Early - Late	0.3	0.9	0.3	0.950
	Fern	Early - Intermediate	NA	NA	NA	NA
		Intermediate - Late	0.4	0.8	0.5	0.601
		Early - Late	NA	NA	NA	NA
	Sub shrub	Early - Intermediate	0.0	0.7	0.1	0.948
		Intermediate - Late	NA	NA	NA	NA
		Early - Late	NA	NA	NA	NA
	Shrub	Early - Intermediate	0.4	0.4	0.9	0.663
		Intermediate - Late	0.1	0.7	0.1	0.994
		Early - Late	0.4	0.7	0.6	0.804
	Vine	Early - Intermediate	0.2	0.6	0.4	0.706
		Intermediate - Late	NA	NA	NA	NA
		Early - Late	NA	NA	NA	NA

A.3 Supplementary Figures

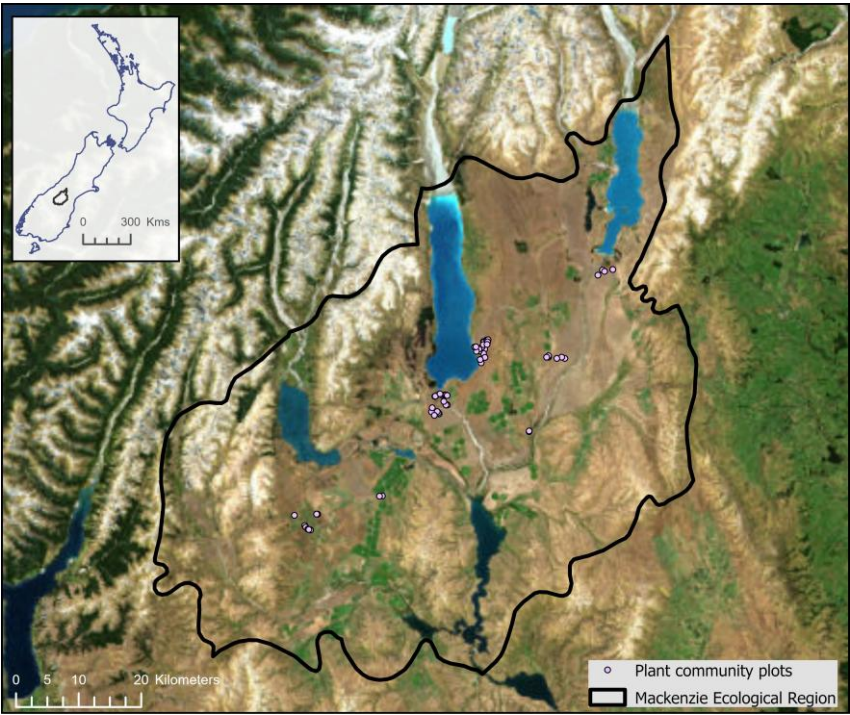


Figure S2.1 Location of study sites within the Mackenzie Ecological Region. Basemap sourced from ESRI/LINZ.

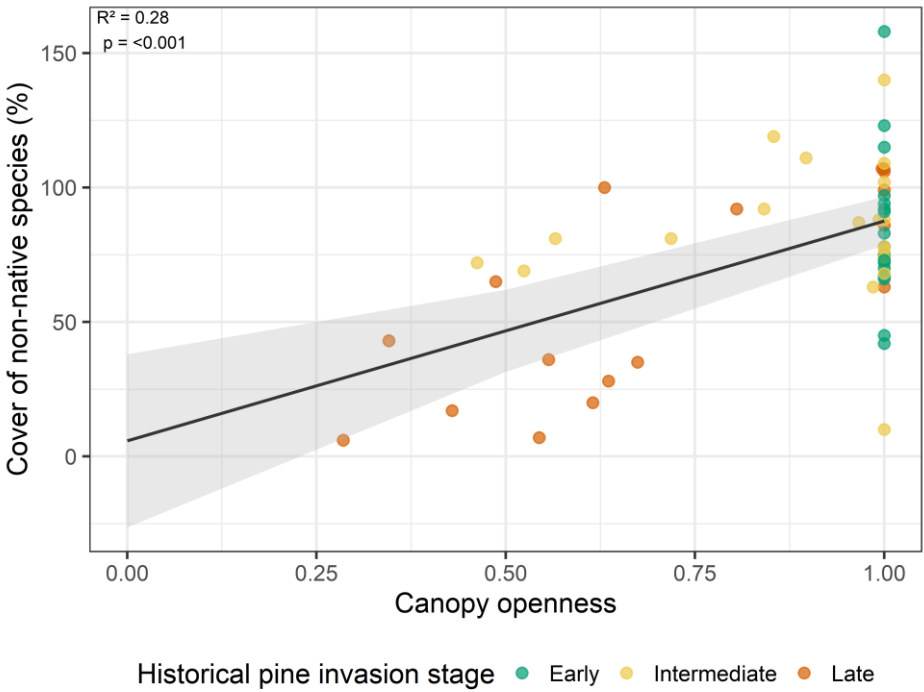


Figure S2.2 Total cover of non-native species in each plot compared to canopy openness (a measure of light availability). Lower light levels indicate standing dead trees or survival/reinvasion of live trees. Point colours show the historical pine invasion stage.

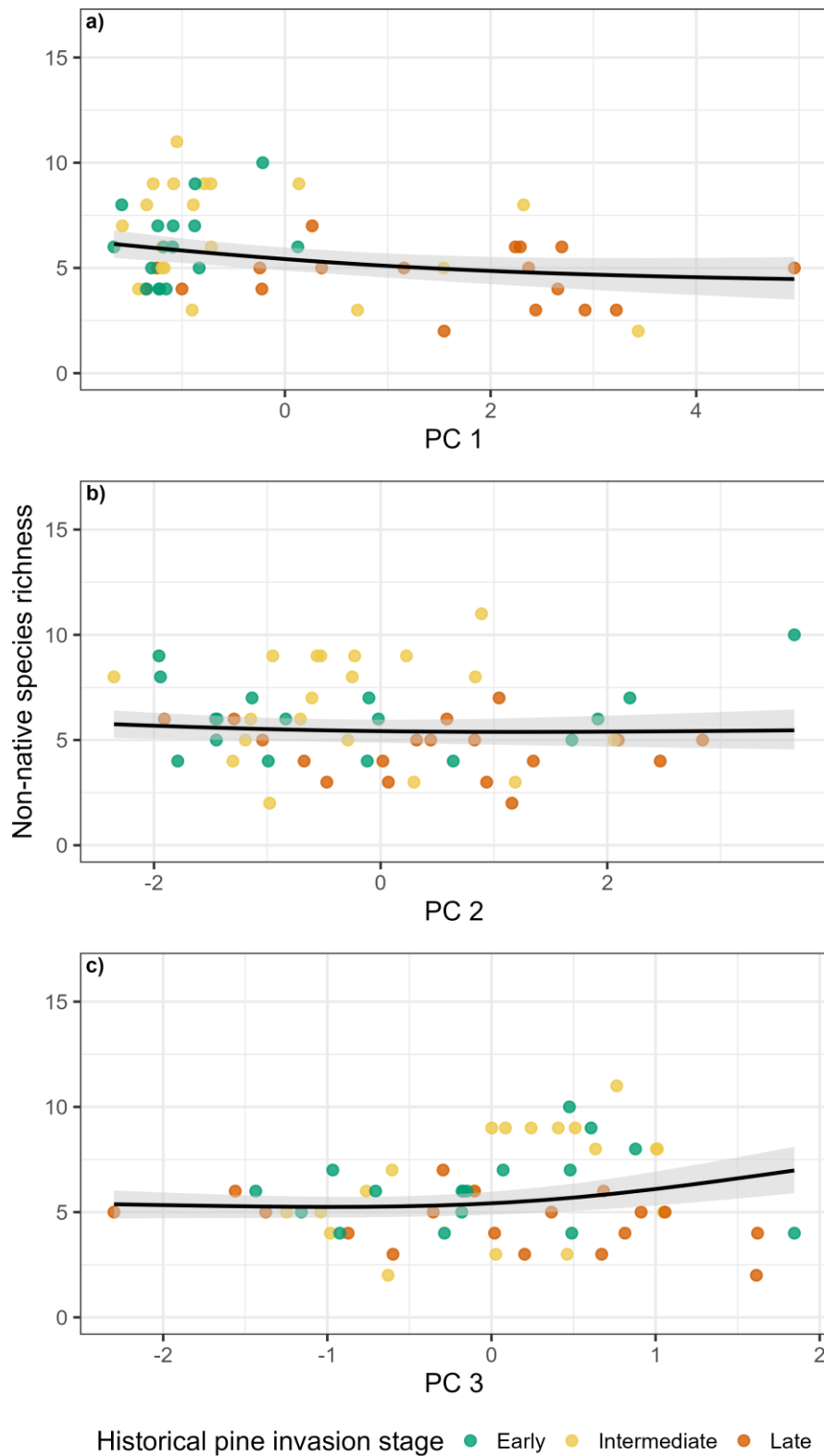


Figure S2.3 Hierarchical modelling of plant species communities (HMSC) comparing the relationship between predicted non-native species richness and plot principal component scores (black line) with 90% Confidence Interval (grey shading). The measured plot values are shown as points colour coded based on historical pine invasion stage. Plot a) shows the relationship with PC 1; b) PC 2; and c) PC 3.

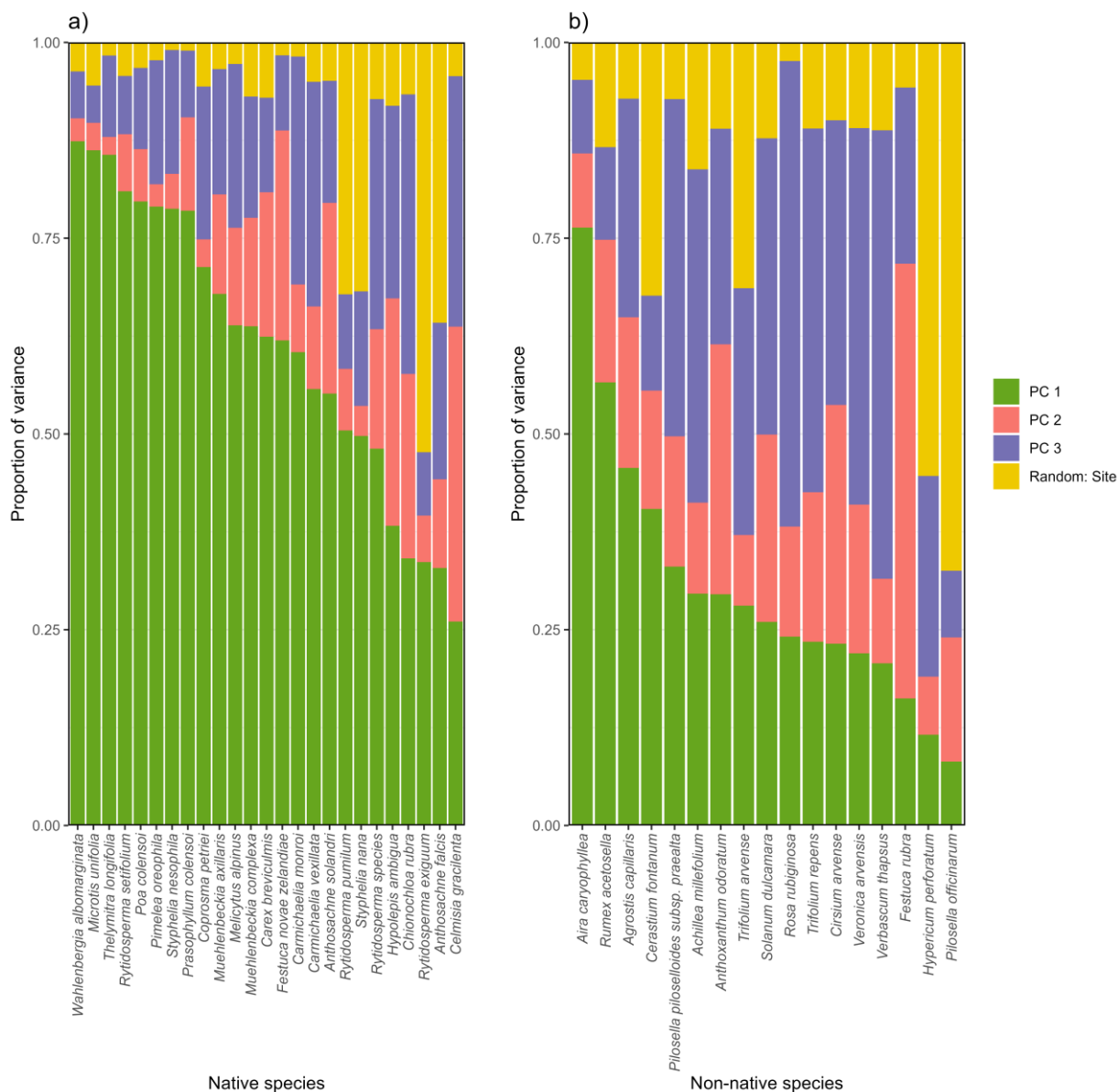


Figure S2.4 Hierarchical modelling of species communities (HMSC) variance partitioning showing the proportion of variation in plant species occurrence explained by each principal component and by the site-level random effect for a) native species; and b) non-native species.

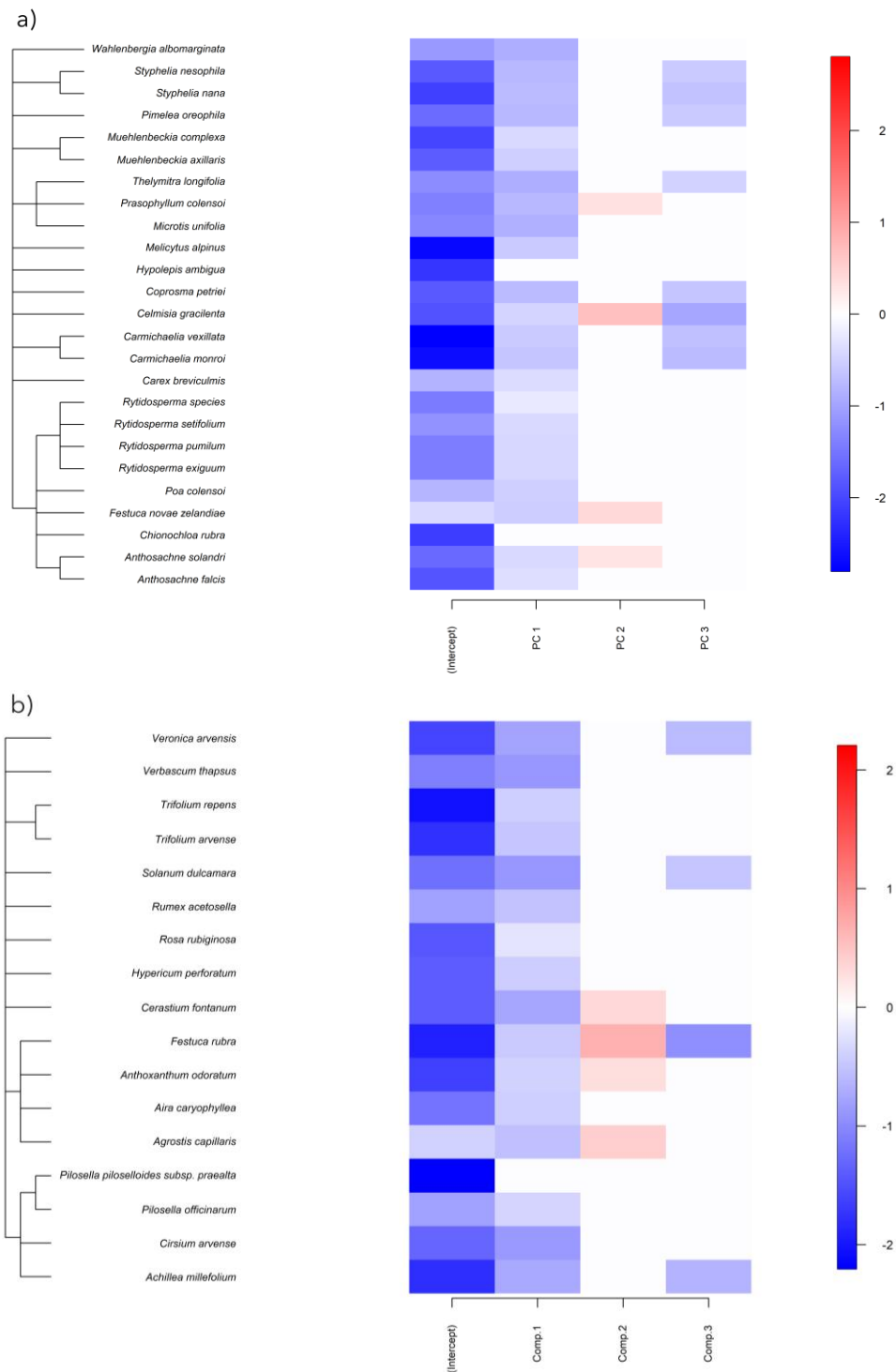


Figure S2.5 Plant species responses to principal components, modelled using Hierarchical modelling of species communities (HMSC). Plot of beta parameters showing how species responded to environmental covariates represented by principal components for a) native species; and b) non-native species. Only coefficients where 95% of posterior samples were either > 0 or < 0 are considered supported. The heat map shows the magnitude (mean effect sizes) and direction (positive or negative) of each species' responses. The phylogeny indicates the relationship of plant species to family level.

Appendix B

Additional information for Chapter 3

B.1 Supplementary Figures

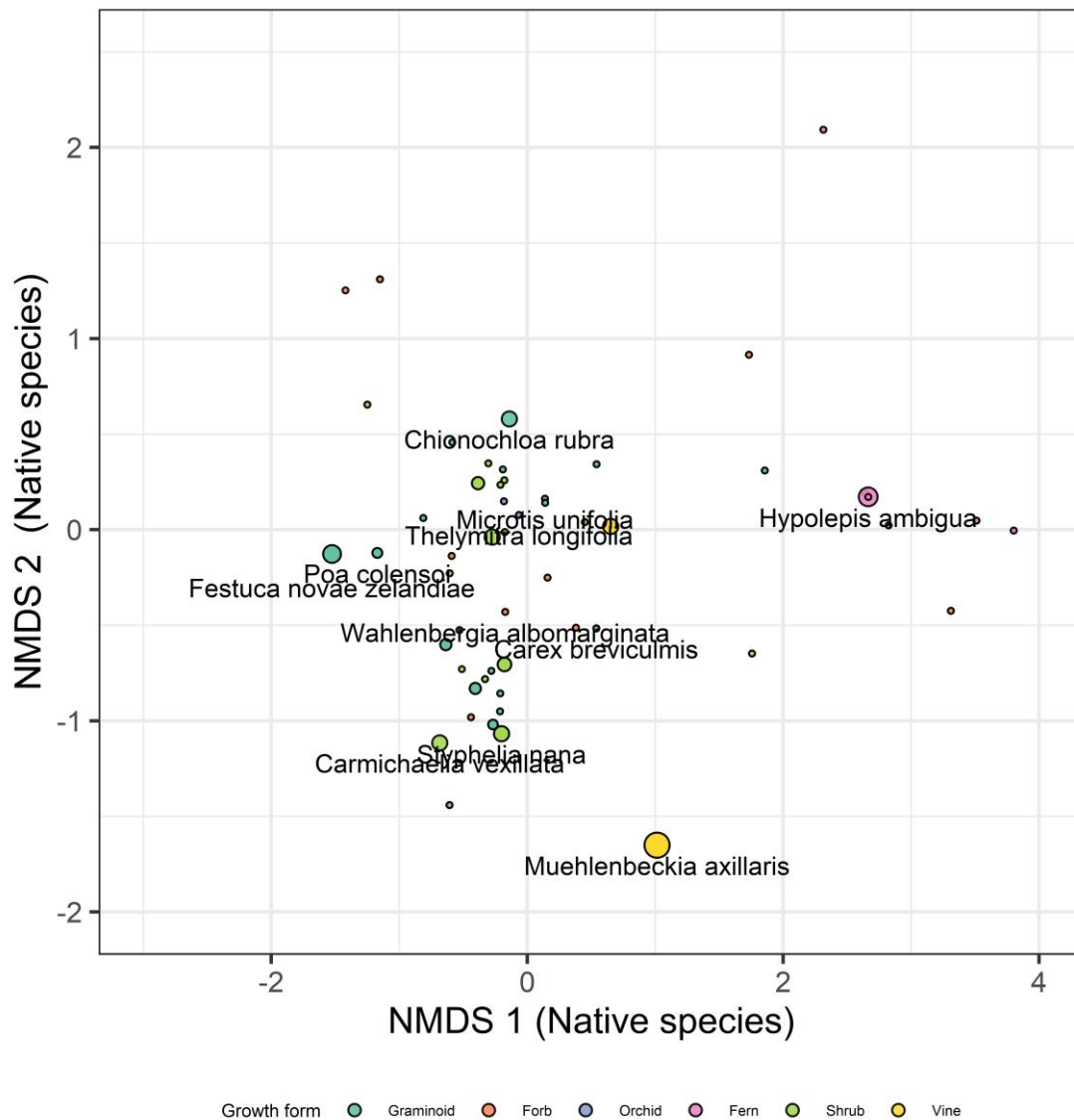


Figure S3. 1 Non-metric Multidimensional scaling (NMDS) of native plant communities. Points are proportional to cover when present. The six most frequent and six most abundant species are labelled (*Festuca novae zelandiae* is the only species in the top six of both groups). This plot compares the relationship between NMDS axes 1 and 2.

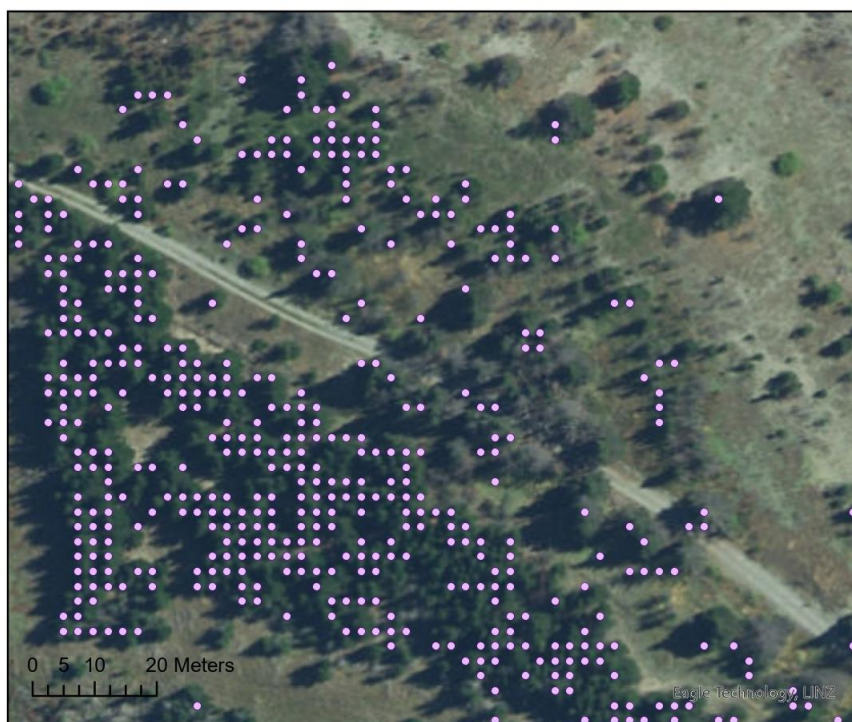


Figure S3.2 Example of point locations identified as pine trees derived from pixel-based image classification. Basemap sourced from ESRI/LINZ.

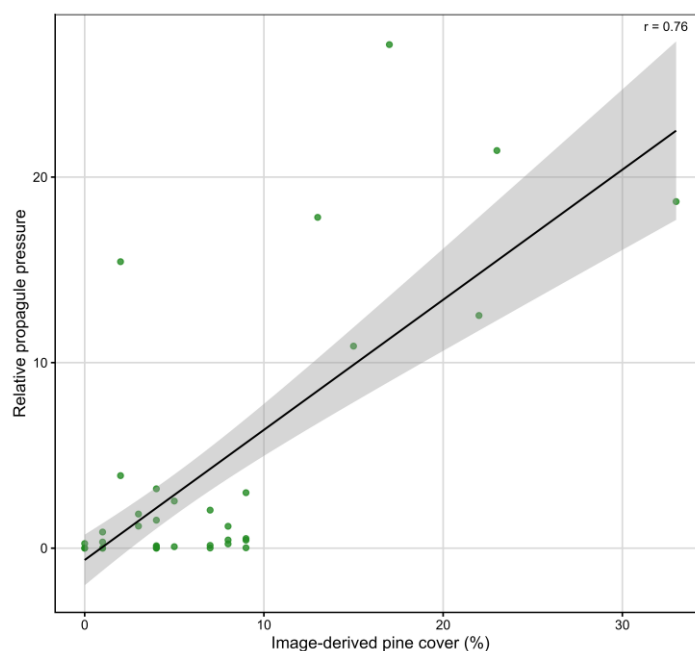


Figure S3.3 Comparison of percent cover of pine derived from supervised pixel-based classification with the propagule pressure metric calculated using a WALD dispersal kernel. Both metrics were derived using a 1 km radius buffer around the centre of the plant community plots.

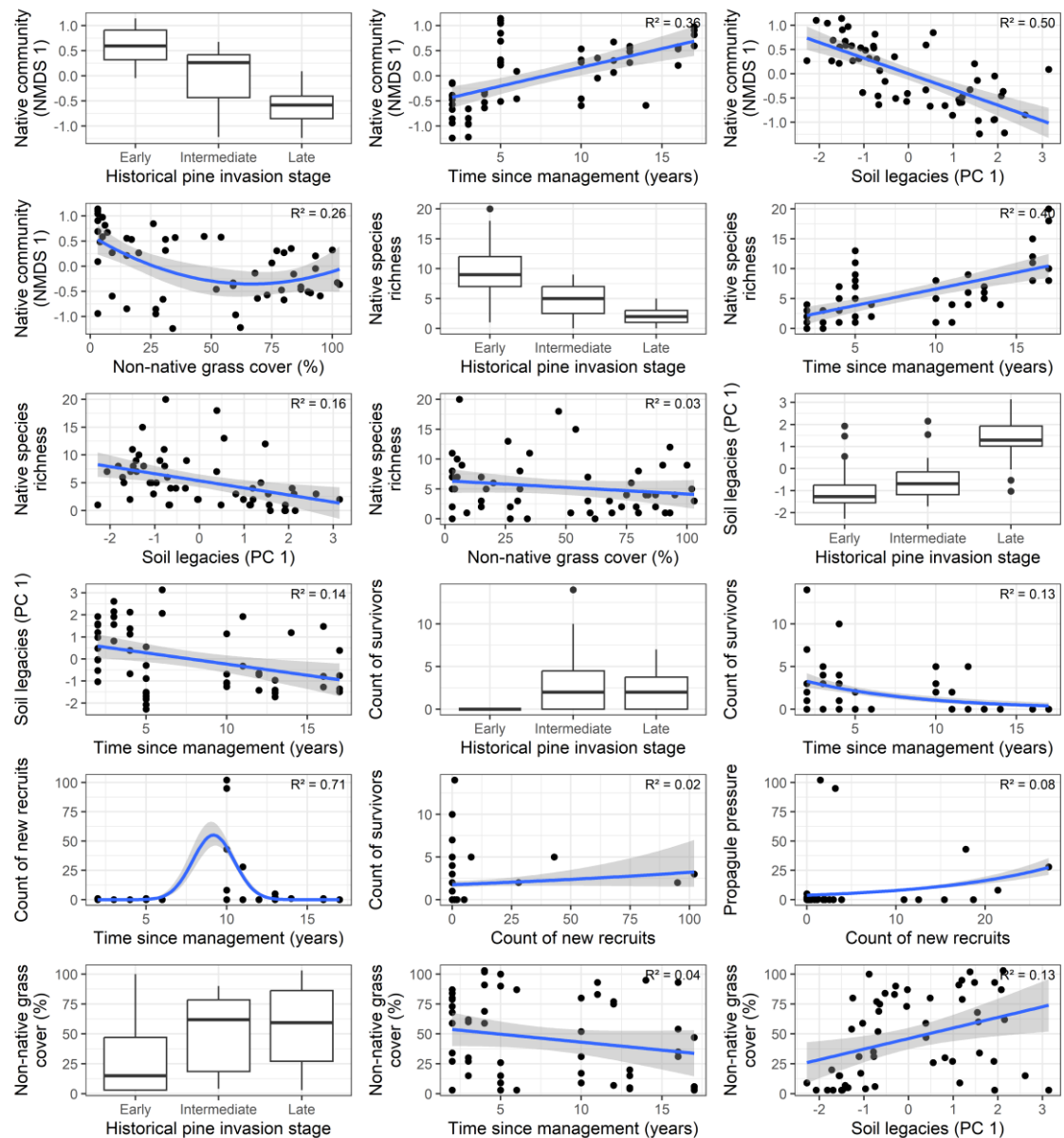


Figure S3.4 Pairwise relationships between variables included in the Structural Equation Modelling (SEM). The blue line shows the relationship predicted by the general linear model, and the grey shading shows the 95% Confidence Interval.

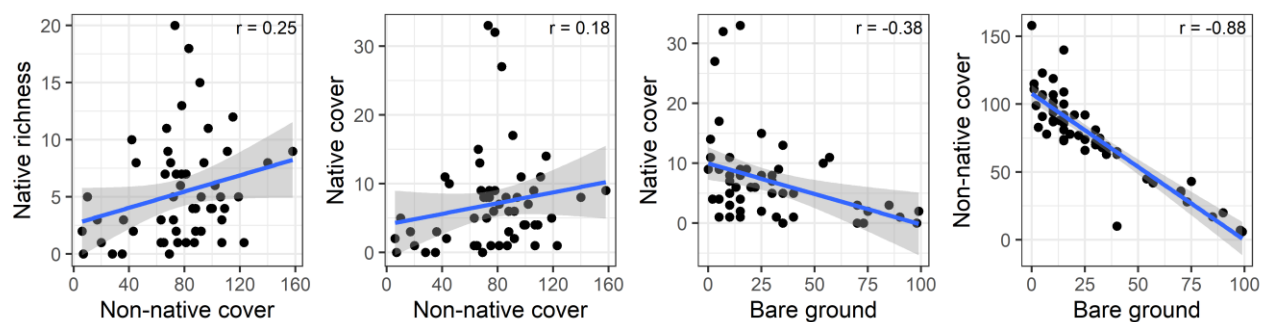


Figure S3.5 Pairwise correlations among plant community metrics, including cover and richness, and bare ground. Points are the observed values, the blue line shows the fitted linear relationship, and grey shading shows the 95% Confidence Interval.

Appendix C

Additional information for Chapter 4

C.1 Supplementary Tables

Table S4.1 Details of aerial imagery used for the land cover classification

<i>Image year</i>	<i>Image source</i>	<i>Colour type</i>	<i>Resolution (Pixel size)</i>
1983-86	Canterbury maps	Greyscale	16.5 m
1999	Canterbury maps	Greyscale	17.6 m
2008	LINZ	Colour	0.75 m
2021	LINZ	Colour	0.30 m

Table S4.2 Assignment of species to merged land cover classes; based on growth form, bio status, and habitat preference

- a) Assignment of species groups to merged land cover classes, primarily based on the combination of growth form and bio status.

<i>Growth form</i>	<i>Bio status</i>	<i>Additional classifier</i>	<i>Land cover class</i>
<i>Tree</i>	Non-native	Dead pine	Dead pine
<i>Tree</i>	Non-native	Pine	Pine
<i>Tree</i>	Non-native	Deciduous species	Deciduous hardwood
<i>Tree</i>	Native	See exceptions in Table S4.2 b)	Indigenous forest
<i>Shrub or Vine</i>	All	-	Shrubland
<i>Graminoid</i>	Native	-	Low producing grassland
<i>Graminoid</i>	Non-native	See exceptions in Table S4.2 b)	Low producing grassland
<i>Forb, orchid or subshrub</i>	All	-	Low producing grassland

- b) Assignment of individual species to merged land cover classes based on habitat preferences where the combination of growth form and bio status could not be used to infer land cover.

<i>Species Name</i>	<i>Habitat</i>	<i>Land cover class</i>
<i>Paesia scaberula</i>	Disturbed sites	Shrubland
<i>Histiopteris incisa</i>	Disturbed sites	Shrubland
<i>Hypolepis millefolium</i>	Disturbed sites	Shrubland
<i>Asplenium</i> species	Forest	Dead pine
<i>Cystopteris tasmanica</i>	Forest	Dead pine
<i>Dryopteris filix-mas</i>	Forest	Dead pine
<i>Polystichum vestitum</i>	Forest	Dead pine
<i>Hypolepis rufobarbata</i>	Forest margin	Shrubland
<i>Pteridium esculentum</i>	Grassland/shrubland	Shrubland
<i>Lycopodium fastigiatum</i>	Grassland/shrubland	Shrubland
<i>Blechnum penna-marina</i>	Open/forest	Shrubland
<i>Hypolepis ambigua</i>	Open forest/shrubland	Shrubland
<i>Dactylis glomerata</i>	Pasture	High producing grassland
<i>Phleum pratense</i>	Pasture	High producing grassland
<i>Trifolium repens</i>	Pasture	High producing grassland
<i>Trifolium pratense</i>	Pasture	High producing grassland
<i>Ophioglossum coriaceum</i>	Open areas	Low producing grassland
<i>Polystichum</i> species	Open/shrubland/forest	Shrubland
<i>Discaria toumatou</i>	Shrubland	Shrubland
<i>Coprosma propinqua</i>	Shrubland	Shrubland

Table S4.3 Overall image classification accuracy for each Area of Interest (AOI) and year of aerial imagery

<i>AOI</i>	<i>1983-86</i>	<i>1999</i>	<i>2008</i>	<i>2021</i>
<i>Tekapō</i>	0.94	0.98	0.90	0.95
<i>Irishman Creek</i>	0.97	0.98	0.92	0.91
<i>Maryburn</i>	0.99	0.95	0.96	0.97
<i>Pūkaki</i>	0.96	0.93	0.90	0.94
<i>Quailburn</i>	0.94	0.93	0.86	0.84

Table S4.4 Transition tables showing the pixels level change in land cover type (as a percentage of the total number of pixels) between each time step of aerial photography for each of the five Areas of Interest (AOIs).

<i>Area of interest</i>	<i>Transition years</i>	<i>Initial land cover class</i>	<i>New land cover class</i>	<i>Percentage of pixels</i>
Tekapō	1986 → 1999	Pine	Pine	2.2
		Low producing grassland	Pine	1.7
		Bare	Pine	0.1
		Pine	Low producing grassland	1.7
		Low producing grassland	Low producing grassland	92.4
		Bare	Low producing grassland	1.2
	1999 → 2008	Low producing grassland	Bare	0.6
		Pine	Pine	2.9
		Low producing grassland	Pine	2.0
		Bare	Pine	0.1
		Low producing grassland	Shrubland	0.4
		Pine	Low producing grassland	1.1
		Low producing grassland	Low producing grassland	91.3
		Bare	Low producing grassland	0.6
		Pine	Bare	0.1
		Low producing grassland	Bare	1.3
		Bare	Bare	0.1
	2008 → 2021	Pine	Pine	2.2
		Shrubland	Pine	0.2
		Low producing grassland	Pine	1.9
		Bare	Pine	0.1
		Low producing grassland	Deciduous hardwoods	0.1
		Pine	Shrubland	0.2
		Shrubland	Shrubland	0.1
		Low producing grassland	Shrubland	0.4
		Low producing grassland	High producing grassland	0.7
		Pine	Low producing grassland	2.6
		Shrubland	Low producing grassland	0.2
		Low producing grassland	Low producing grassland	89.0
		Bare	Low producing grassland	1.1
		Pine	Bare	0.1
		Low producing grassland	Bare	0.7
		Bare	Bare	0.5
Irishman Creek	1986 → 1999	Low producing grassland	Pine	0.1
		Low producing grassland	Shrubland	1.6
		Shrubland	Low producing grassland	0.8
		Low producing grassland	Low producing grassland	97.0
	1999 → 2008	Bare	Low producing grassland	0.4
		Low producing grassland	Bare	0.1
		Shrubland	Pine	0.3
		Low producing grassland	Pine	1.6
		Shrubland	Shrubland	0.1
		Low producing grassland	Shrubland	0.9
		Pine	Low producing grassland	0.1
		Shrubland	Low producing grassland	1.0
		Low producing grassland	Low producing grassland	94.1
		Shrubland	Bare	0.1

<i>Area of interest</i>	<i>Transition years</i>	<i>Initial land cover class</i>	<i>New land cover class</i>	<i>Percentage of pixels</i>
Irishman Creek	2008 → 2021	Low producing grassland	Bare	1.5
		Shrubland	Shadow	0.1
		Pine	Pine	0.6
		Shrubland	Pine	0.1
		Low producing grassland	Pine	5.4
		Pine	Dead pine	0.8
		Shrubland	Dead pine	0.2
		Low producing grassland	Dead pine	23.9
		Shrubland	Shrubland	0.4
		Low producing grassland	Shrubland	2.9
		Pine	Low producing grassland	0.4
		Shrubland	Low producing grassland	0.4
		Low producing grassland	Low producing grassland	62.5
		Bare	Low producing grassland	1.0
		Low producing grassland	Bare	0.3
		Bare	Bare	0.9
		Shadow	Shadow	0.1
		Low producing grassland	Pine	0.6
		Bare	Pine	0.1
		Low producing grassland	Shrubland	0.7
Pūkaki	1986 → 1999	Pine	Low producing grassland	0.1
		Shrubland	Low producing grassland	0.4
		Low producing grassland	Low producing grassland	92.5
		Bare	Low producing grassland	3.3
		Low producing grassland	Bare	1.7
		Bare	Bare	0.6
		Pine	Pine	0.2
		Shrubland	Pine	0.2
		Low producing grassland	Pine	2.5
		Low producing grassland	Dead pine	0.1
	1999 → 2008	Low producing grassland	Shrubland	0.3
		Low producing grassland	High producing grassland	0.6
		Bare	High producing grassland	0.2
		Pine	Low producing grassland	0.2
		Shrubland	Low producing grassland	0.4
		Low producing grassland	Low producing grassland	91.8
		Bare	Low producing grassland	1.8
		Low producing grassland	Bare	0.6
		Bare	Bare	0.2
		Pine	Shadow	0.2
	2008 → 2021	Shrubland	Shadow	0.1
		Low producing grassland	Shadow	0.4
		Pine	Pine	1.9
		Shrubland	Pine	0.1
		Low producing grassland	Pine	7.9
		Shadow	Pine	0.3
		Pine	Dead pine	0.2
		Low producing grassland	Dead pine	1.2
		Shadow	Dead pine	0.1
		Pine	Shrubland	0.3
		Shrubland	Shrubland	0.1
		Low producing grassland	Shrubland	1.6

<i>Area of interest</i>	<i>Transition years</i>	<i>Initial land cover class</i>	<i>New land cover class</i>	<i>Percentage of pixels</i>
Pūkaki		Low producing grassland	High producing grassland	1.2
		Pine	Low producing grassland	0.4
		Dead pine	Low producing grassland	0.1
		Shrubland	Low producing grassland	0.1
		High producing grassland	Low producing grassland	0.7
		Low producing grassland	Low producing grassland	79.8
		Bare	Low producing grassland	0.4
		Shadow	Low producing grassland	0.1
		Low producing grassland	Bare	1.1
		Bare	Bare	0.8
		Pine	Shadow	0.2
		Low producing grassland	Shadow	1.1
		Shadow	Shadow	0.2
Maryburn	1986 → 1999	Low producing grassland	Low producing grassland	96.4
		Bare	Low producing grassland	0.3
		Low producing grassland	Bare	3.2
		Bare	Bare	0.1
	1999 → 2008	Low producing grassland	Low producing grassland	94.4
		Bare	Low producing grassland	3.1
		Low producing grassland	Bare	2.3
		Bare	Bare	0.2
	2008 → 2021	Low producing grassland	High producing grassland	2.7
		Bare	High producing grassland	0.3
		Low producing grassland	Low producing grassland	94.3
		Bare	Low producing grassland	1.9
		Low producing grassland	Bare	0.5
		Bare	Bare	0.3
Quailburn	1986 → 1999	Pine	Pine	0.4
		Low producing grassland	Pine	6.1
		Low producing grassland	Shrubland	0.7
		Pine	Low producing grassland	1.0
		Shrubland	Low producing grassland	0.3
		High producing grassland	Low producing grassland	1.0
		Low producing grassland	Low producing grassland	89.6
		Bare	Low producing grassland	0.6
		Low producing grassland	Shadow	0.1
	1999 → 2008	Pine	Pine	2.6
		Shrubland	Pine	0.2
		Low producing grassland	Pine	4.4
		Shadow	Pine	0.1
		Low producing grassland	Dead pine	0.1
		Low producing grassland	Deciduous hardwoods	0.2
		Low producing grassland	Shrubland	1.1
		Low producing grassland	High producing grassland	1.5
		Pine	Low producing grassland	2.2
		Shrubland	Low producing grassland	0.5
		Low producing grassland	Low producing grassland	83.5
		Shadow	Low producing grassland	0.1
		Pine	Bare	1.4
		Low producing grassland	Bare	1.0
		Pine	Shadow	0.3
		Low producing grassland	Shadow	0.8
		Pine	Pine	0.8

<i>Area of interest</i>	<i>Transition years</i>	<i>Initial land cover class</i>	<i>New land cover class</i>	<i>Percentage of pixels</i>
Quailburn	2008 → 2021	Shrubland	Pine	0.1
		Low producing grassland	Pine	0.8
		Shadow	Pine	0.1
		Pine	Dead pine	1.7
		Shrubland	Dead pine	0.1
		Low producing grassland	Dead pine	2.7
		Shadow	Dead pine	0.2
		Deciduous hardwoods	Deciduous hardwoods	0.1
		Low producing grassland	Deciduous hardwoods	0.2
		Pine	Shrubland	0.1
		Shrubland	Shrubland	0.3
		Low producing grassland	Shrubland	0.6
		Pine	High producing grassland	0.1
		Deciduous hardwoods	High producing grassland	0.1
		Shrubland	High producing grassland	0.1
		High producing grassland	High producing grassland	0.8
		Low producing grassland	High producing grassland	11.2
		Bare	High producing grassland	0.1
		Pine	Low producing grassland	4.3
		Dead pine	Low producing grassland	0.1
		Deciduous hardwoods	Low producing grassland	0.1
		Shrubland	Low producing grassland	0.6
		High producing grassland	Low producing grassland	0.6
		Low producing grassland	Low producing grassland	69.3
		Bare	Low producing grassland	2.1
		Shadow	Low producing grassland	0.6
		Low producing grassland	Bare	1.0
		Bare	Bare	0.2
		Low producing grassland	Shadow	0.3
		Shadow	Shadow	0.1

C.2 Supplementary Figures

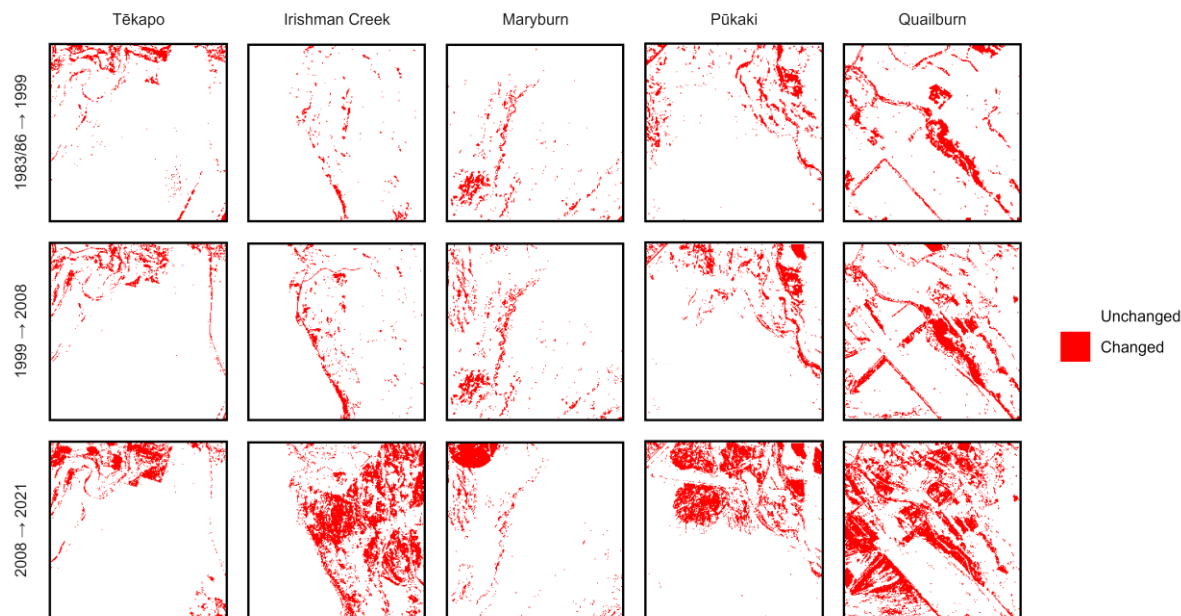


Figure S4.1 Binary depiction of whether there was a change in classification of individual pixels between each time step of aerial imagery for each of the five Areas of Interest (AOIs).