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Effects of flow regime on the distribution, richness and abundance of alien plants in braided rivers of New Zealand

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A thesis

submitted in partial fulfilment

of the requirements for the Degree of

Doctor of Philosophy

at

Lincoln University

by

Tyler Jacob Brummer

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Lincoln University

2016

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Braided river floodplains in the Canterbury Plains of New Zealand are classified as threatened ecosystems currently undergoing dramatic changes, including adjacent land-use intensification and increased water abstraction. In addition, both the regional environmental management authority and conservation NGOs are concerned by the invasion of these ecosystems by alien plants that can reduce biodiversity and alter ecosystem processes. However, whether these plant invasions are driven by flow regime has yet to be elucidated.

In this thesis I address how we study the effects of hydrological flows on the ecology of ecosystems by developing a framework for setting up flow-gradient analyses. I then evaluate the three aspects of invasion organised from most general to most specific. First, I address whether flow regime, land-cover, climate and floodplain factors are associated with alien versus native cover and richness. I then ask whether groups of alien species with the same regenerative and growth traits respond to floods and hydrologic drought similarly. Finally, I take a targeted approach to determine whether flow and other drivers are associated with three woody legume invaders in the system.

Using flow data from 19 river reaches, a regional multi-scale plant survey and data from the seed bank, I found that alien and native floras were driven by completely different drivers with aliens associated with flow variability and floodplain variation while natives were associated with climate and land-cover. The most prevalent species were woody and perennial herbaceous legumes, while annual and bienniel weeds had the greatest combined frequency across all the sampled rivers. Annual and biennial weeds increased in prevalence as winter flow variability increased, whereas perennial herbaceous species were more prevalent in rivers with a greater number of low flow days. Finally, flow regime played only a minor role in predicting the distribution and cover of the three most frequent woody legumes in the system. However, local patterns in the distribution of these

three species suggested that decreases in mean flows coupled with flow stabilisation could allow them to establish across more of the floodplain than they already occupy.

These results highlight a few key lessons. Flow-gradient studies can be used to study flow-ecology relationships if applied rigorously. Alien and native floras can be driven by completely different variables in the same ecosystem, thus management against aliens cannot presume management for natives. Finally, changes in river flows have the potential to influence aspects of alien invasion in the ecosystems and should be considered in the context of changing climate and resource use patterns in Canterbury. Future work on understanding invasion in the ecosystem could benefit from monitoring alien species responses to flow events through time and addressing whether invasive legumes drive invasional meltdown of the ecosystem.

Acknowledgements

I would like to express my most heartfelt gratitude to my mother Lori and father Joe. Without their encouragement, understanding, willing ears and adventurous spirit to come visit me in New Zealand, this thesis would not have been possible. My friend Katie Reese for always cheering me on and helping me understand I was doing more than a PhD. I would also like to thank my loving and supportive partner Sam. He stuck with me despite the emotional anguish that is a PhD. I think they will all be happy this is finished!

I want to acknowledge my supervisor Philip Hulme. He challenged me to be a better scientist. My advisor Andrea Byrom for her intellect, applied perspective, support and friendship. And Jon Sullivan for his botanical and ecological knowledge, approachability and contributions to my thinking. My supervisory team was diverse and this diversity has given me a cross-section of the discipline to draw from as I continue to grow professionally.

The Weed Wing at Lincoln was full of stimulating ideas and incredible minds. Maud Bernard-Verdier was always up for a chat about statistics, ecology, and science philosophy and helped shape my thinking and research in a profound way. Maki, Jennifer, Ian and Will were always friendly and challenged my thinking on all things ecological. And last but not least all my fellow PhD compatriots were allies in the roller coaster of the academic proving ritual we were all moving through, especially Jennifer Pannell. Her help in the last hurdles was invaluable.

I would like to thank Carmel Johnston for randomly showing up in New Zealand from Montana and enthusiastically helping me collect data. She brought memories of the USA, wonderful company and gave Sophie a well-deserved rest in the midst of an intense field season. I would also like to thank all the skilled botanists on NatureWatch. Without their help, I would never have been able to identify the hundreds of plants in my survey. Dean Anderson was a huge help with modelling techniques and taught me how to super compute.

A final and special thanks to Sophie Horstmann who helped me collect a massive dataset no one thought we could. Sophie was more than a field assistant. Sophie was integral to my coming to understand who I am and how to relate to the world around. A priceless gift.

Table of Contents

List of Tables

List of Figures

Chapter 1 – Riparian ecosystems, invasive plants and river flows: an overview

1.1 Introduction

My thesis addresses the effects of river flow regime on the level invasion in riparian ecosystems and the invasion success of vascular plant species in gravel floodplains. The four studies detailed in Chapters 2-5 address: (1) the methods of how we study the ecology of river ecosystems; (2) how alien and native floras respond to flow regimes and other environmental gradients; (3) whether plant functional groups respond to river flows; and (4) an improvement in our understanding of woody legume invasion though a demographic approach to distribution modelling. These are specific pieces of research that fit within the broader context of how river flow regimes affect plant invasions. In this introduction, I begin by contextualising the work within applied ecology generally and work through each of the concepts addressed in the four studies that follow.

1.2 Human impacts on the biosphere

Our planet is becoming continually more defined by human impacts on all facets of the natural world, with some arguing this constitutes a new geological epoch (Smil 2015; Waters *et al.* 2016). Humans are driving species to extinction at rates that rival other mass extinction events, wildlands free of human influence have become rare, climate patterns are changing, agriculture is already extensive and is becoming more intensive and species are overcoming biogeographic barriers to invade new regions faster than ever before (Williams *et al.* 2015). Meanwhile, scientists are scrambling to understand the environmental effects of these changes (Shaver *et al.* 2000; Hooper *et al.* 2012; Morse *et al.* 2014), to come up with strategies to protect what biodiversity remains (Tscharntke *et al.* 2012), and predict how human activities may affect ecosystems in the future (Tilman *et al.* 2001; Walther 2010; Bellard *et al.* 2012). The answers to these problems must be pragmatic given the need to provide adequate food and natural resources to support a growing human population (Tilman *et al.* 2001; Tscharntke *et al.* 2012). Thus, a critical and universal question in applied ecology is: what effects do human actions have on ecosystems and ecosystem services? Moreover, can we use knowledge of these effects to preserve ecosystem function and biodiversity while meeting human consumption needs? My studies address these questions in freshwater ecosystems. They speak to the current and potential impacts of increasing water consumption for

agriculture, and of climate change on riparian floodplain ecosystem invasion and biodiversity, by understanding how plant invasion relates to flow regimes.

1.3 Riparian ecosystems: definition, global context, research imperatives

Freshwater and riparian ecosystems provide critical ecosystem services to humans whether it be for drinking, irrigating crops and aquaculture, hydroelectricity, recreation, water filtration, pollution management, wildlife habitat, fisheries or flood control (Aylward, Bandyopadhyay & Belausteguigotia 2005; Arthington *et al.* 2010). Freshwater and riparian ecosystems are already some of the most human-altered ecosystems on a global scale, with at least two-thirds of all freshwater being directly obstructed by dams, and multiple other human features such as dikes, diversions, and ground water abstraction affecting water flow (Nilsson & Berggren 2000). Thus, 'natural' flow regimes are rare, but are thought beneficial to the maintenance and restoration of native biodiversity and ecosystem processes (Poff *et al.* 1997; Lytle & Poff 2004). The realisation that natural flow regimes are important has driven a rise in the desire to conserve unobstructed rivers and restore (at least in part) the natural character of flow regimes to support native biodiversity and natural ecosystem functioning (Dudgeon *et al.* 2006; Vörösmarty *et al.* 2010; Webb *et al.* 2015). However, because of the complexity and natural dynamism of these systems, our knowledge of how flow regimes affect the ecology of riparian ecosystems still lacks robust generalisations (Poff & Zimmerman 2010). This makes it difficult to generate evidence-based decisions that balance the biodiversity, economic and social interests involved in freshwater and riparian zone management.

In response to the inability of current scientific knowledge to provide general guidance on how flow alterations are likely to affect ecosystems, a global ecohydrology working group proposed a framework to facilitate a coordinated effort to drive ecological research in freshwater and riparian ecosystems (Poff *et al.* 2010). Their framework – Ecological Limits of Hydrological Alteration (ELOHA) – stresses the importance of general flow-ecology relationships in order to avoid always defaulting to system-specific research. This allows environmental flows or flow regimes (Arthington *et al.* 2006; Webb *et al.* 2015) to be designed that maintain or restore desirable attributes of freshwater and riparian ecosystems. However, cost and time efficient methods for ecohydrology studies to establish general relationships between river flows and river ecology are still in their developmental stages.

The effects of flow regimes on freshwater and riparian ecosystems have been studied with several methods. These include experiments where flows are manipulated using dams (e.g. Konrad *et al.* 2011), studies that correlate flow parameters to ecological response variables over time (e.g. Monk *et al.* 2006), and gradient analyses that substitute space for time to correlate ecological

responses to hydrological variables across multiple catchments (e.g. Riis *et al.* 2008; Catford *et al.* 2014). Experimental and time-series studies benefit from controlling for multiple sources of variability, but require heavy investment in time and resources and can be very river specific. Spatial gradient analyses (i.e. natural experiments) have the potential to quantify functional relationships at potentially lower cost and have shown real value in fields such as climate change research (Fukami & Wardle 2005). However, flow-gradient studies require certain assumptions and have potential limitations that must be considered. Thus, Chapter 2 asks: how do we perform robust flow-gradient analyses in ecohydrology as a basis for better understanding ecological relationships?

1.4   Species invasions: general concepts, questions and approaches to study

Chapters 3-5 address three aspects of plant invasions in riverbed ecosystems. Invasion is the result of human-aided migration, establishment and spread of species into new environments (Catford, Jansson & Nilsson 2009; Blackburn *et al.* 2011). Alien species' impacts are considered a major agent of global environmental change (Vitousek *et al.* 1997; Tylianakis *et al.* 2008) and one of the factors pushing Earth passed the biodiversity extinction planetary boundary (Rockström *et al.* 2009). Alien plants have measurable impacts on many aspects of ecosystems including nutrient cycling, community composition, productivity, and soil properties (Vilà *et al.* 2011). Regardless of whether their impacts are 'good' or 'bad' (e.g. for ecosystem services; Vilà *et al.* 2010), there is a global desire to predict where and when species will invade, with the goal to prevent and reduce the extent and abundance of the most impactful alien plant species. However, our current knowledge still fails to generate predictions that apply across species, ecosystems and geographic areas. Thus, we need continuing research on the causes of observed invasion patterns within systems, to feed back into our understanding of biological invasions more broadly (Bradley *et al.* 2010; González-Moreno *et al.* 2014).

Although our current knowledge cannot accurately predict the exact progression of ecosystem invasion, we have learned much about factors that may be important for explaining and predicting invasions. Synthesis of invasion research suggests that there is no "silver bullet" to explain the invasion of alien species into ecosystems, rather it is the dynamic interplay between propagule pressure (the supply and frequency of propagule introduction), abiotic conditions of the recipient environment (invasibility), and the biotic characteristics of the invaders (invasiveness) and the recipient community (Simberloff 2009; Catford *et al.* 2009). At ecosystem scales, disturbance (human and natural), has been proposed as the primary abiotic driver of invasion, with the generality of this assertion being hotly debated (Hobbs & Huenneke 1992; Lozon & MacIsaac 1997; Jesson, Kelly & Sparrow 2000; Lake 2004; Moles *et al.* 2012; Catford *et al.* 2012a; González-Moreno

et al. 2014; Jauni, Gripenberg & Ramula 2015). Consequently, research paradigms for understanding invasions at ecosystem scales have shifted in the past decade to a multiple hypothesis approach, testing the relative importance of multiple factors including propagule pressure, climate (niche requirements), disturbance, and biotic interactions (recipient community composition/diversity) (Moore & Elmendorf 2006; Colautti, Grigorovich & MacIsaac 2006; Eschtruth & Battles 2009; Catford *et al.* 2009). In Chapters 3-5 I adopt this approach to ask: how does disturbance in the form of river flow regimes affect the level of invasion in the ecosystem, the distribution of alien plant traits, and the success of alien woody legumes? Furthermore, I ask: what is the relative importance of disturbance compared with other potential drivers of invasion in the system? The ultimate aim is to add fundamental information on plant invasions in riparian ecosystems, and tangible practical information to help managers decide whether disturbance is the most important factor to consider when making decisions about riparian ecosystem management.

1.5 Invasions into riparian systems: impacts, invasibility, invasive species traits and ecosystem engineers

Alien plants cause impacts on many aspects of the hydrological cycle, which have direct and indirect effects on river and riparian ecosystems (Catford *in press*; Charles & Dukes 2007). Alien mediated transitions in dominant vegetation types (e.g. grassland to woodland or vice versa) can change interception and evapotranspiration rates in catchments, as well as alter albedo and surface roughness, which can alter the volume of river flows (Calder & Dye 2001; Deo *et al.* 2009). More direct to riparian and floodplain ecosystems, alien plants can impact the geomorphology of rivers by encroaching into wetlands, narrowing channels and altering sedimentation patterns (Corenblit *et al.* 2007; Hicks *et al.* 2008; Pejchar & Mooney 2009). These alien mediated changes to the hydrology of riparian and floodplain ecosystems are similar to human modification of flows via dams and abstraction in that they disrupt the natural conditions the native biota coevolved with over evolutionary timescales (Poff *et al.* 1997; Lytle & Poff 2004). Thus, not only do alien plants directly and indirectly threaten the ecosystem services that humans rely on (e.g. agriculture and recreational) they also impact the species across trophic levels that rely on the abiotic conditions of an uninvaded river ecosystem, threatening native biodiversity.

The potential global consequences of invasions on riparian ecosystems is compounded by the fact that riparian ecosystems have been found to have exceedingly high levels of invasion (Planty-Tabacchi *et al.* 1996; Richardson *et al.* 2007) because they are dynamic and disturbance prone, provide corridors for the rapid spread of propagules (Pyšek & Prach 1994; Planty-Tabacchi *et al.* 1996), and are heavily influenced by human activities (Poff *et al.* 1997, 2010; Lytle & Poff 2004; Poff

& Zimmerman 2010). However, we see variation in the level of invasion globally. Hypotheses put forward to explain these differences include variation in the disturbance regimes among rivers and river types, deviation in the flow regime relative to the "natural" flow regime, and the characteristics of the invading species, especially relative to the native species in the ecosystem.

Functional traits have been proposed as a way forward to finding generality in community and invasion ecology (Lloret *et al.* 2004; McGill *et al.* 2006; Kühner & Kleyer 2008; Webb *et al.* 2010; Verberk, van Noordwijk & Hildrew 2013). Profiling the traits that make a species more impactful or successful in an ecosystem has been the focus of much research. The ideal invader has been described as a short-lived species that produces prolific seed, grows quickly and reproduces vegetatively (van Kleunen, Weber & Fischer 2010; Thompson & Davis 2011). Riparian ecosystems are also shaped by frequent disturbance suggesting these plant adaptations to disturbance should be important to predicting species responses to changing flow regimes. However, trait based studies in riparian systems are still relatively rare (but see Greet, Cousens & Webb 2013; Greet, Webb & Cousens 2015; Catford & Jansson 2014; Catford *et al.* 2014). Fewer still have considered whether traits and trait syndromes respond similarly to flow regimes which describe various aspects of the disturbance regimes within these ecosystems. This is addressed in Chapter 4.

One subset of species that have been identified by their disproportionate impact on ecosystem form and function are called ecosystem engineers (Jones, Lawton & Shachak 1994). Plants that are ecosystem engineers not only respond to fluvial processes such as river flows and sedimentation but they modify these processes (Gurnell 2014). If alien species are ecosystem engineers, they have the potential to dramatically transform an invaded ecosystem, disrupting the abiotic environment that all other species in the system are adapted to. Thus, there is a large effort to control these species. Chapter 5 takes a demographic distribution modelling approach to understand the environmental drivers of such species to better understand how their distribution and impact may change in the future and whether management efforts should be prioritised differentially based on how they are invading the ecosystem.

1.6   Invasions in New Zealand: natural historical context

Although invasions are global phenomena, the way they operate depends largely on context. Thus, an understanding of New Zealand's natural history is necessary to interpret how the invasion patterns studied in Chapters 3-5 relate to the rest of the globe. Alien species are dominant and competitive in New Zealand and this has largely been ascribed to a lack of native disturbance-adapted species combined with the massive habitat clearance and increased disturbance rates in

lowland New Zealand (Wilson & Lee 2012). The native New Zealand flora has low diversity of certain life forms, especially annuals, likely due to the land mass being dominated by evergreen forested ecosystems (dominant families: Nothofagaceae and Podocarpaceae) until human settlement began circa 1300 CE. Furthermore, the lack of frequent physical disturbances except in the steep rocky slopes of the mountains and braided riverbeds (Wardle 1991), coupled with New Zealand's geographic isolation, are suggested to have precluded the evolution of a high diversity of ruderal species.

Once human settlement began, Māori used fire as a tool to clear roughly one third of the forest which then became grassland (McWethy *et al.* 2009; Perry, Wilmshurst & McGlone 2014). European colonists from the early 19th century onward further removed the forest ecosystems, and began transforming the landscape into one of pastoralism and cropping that resembled the management practices of Europe and the United Kingdom (McWethy *et al.* 2009; Perry *et al.* 2014). Along with the landscape transformation, alien plants (and animals and fungi) were imported intentionally and unintentionally, many of which are short-lived, disturbance-adapted species suited to the land management of their origins (Gatehouse 2008). This has resulted in a current flora that is approximately half alien (2418 native and 2252 alien) and a landscape where lowlands are alien dominated while uplands are where native forest and native alpine ecosystems remain (although invaded upland systems and lowland refugia both also exist) (Atkinson & Cameron 1993). The transformed, alien-dominated landscape has created heavy alien propagule pressure into native ecosystems, especially in remnant native ecosystems in the lowlands of which braided riverbeds are perhaps the most iconic (Holdaway, Wiser & Williams 2012). Braided riverbed ecosystems have experienced a large influx of alien species where, at least based on post-colonial records, there was never extensive plant biomass or diversity to begin with (Cockayne & Foweraker 1916; Cockayne 1927; Calder 1961; Fisher 1969; Winterbourn *et al.* 2008). Thus, braided riverbeds in New Zealand not only represent a good system to explore fundamental questions about invasion, but also represent a heavily impacted ecosystem in need of applied science to guide restoration and conservation.

1.7 The system: New Zealand braided river floodplains and alien plants

Braided rivers are globally uncommon ecosystems that generally occur in regions with steep alpine catchments and heavy precipitation (Gray & Harding 2007). Most braided rivers have been heavily modified by humans (e.g. by dams or channelisation) with only few remaining examples of unmodified rivers in Canada, Alaska, the Himalaya and Italy (Tockner & Stanford 2002). New Zealand has one of the highest concentrations of relatively unmodified braided rivers, with over 60% of the

floodplain area located in the Canterbury province (Wilson 2001; Gray & Harding 2007). These systems are highly valued for a suite of endemic birds that nest on the open gravel floodplains (Maloney *et al.* 1997; Caruso 2006), as well as specialised lizards, invertebrates and plant-life that make up the ecosystem (Gray & Harding 2007). Within New Zealand, these systems are considered naturally rare (Williams *et al.* 2007), and the associated bird life has been found to be in decline. As such, they have become a conservation priority, with the invasion of alien plants of primary threat (Holdaway *et al.* 2012).

The impact of alien invasions is presumed to be especially large in New Zealand braided riverbed ecosystems because the presumed natural state of these ecosystems was one with relatively low plant biomass (Gray & Harding 2007). Pre-colonial (colonisation began in the 1840's) records of the vegetation of these systems are non-existent, though there were a number of published observations throughout the 20th century (e.g. Cockayne & Foweraker 1916; Cockayne 1927; Calder 1961; Fisher 1969). These historical accounts describe the primary riverbed as being barren and stony, populated only by a few species of the genus *Epilobium*. As areas of the floodplain became protected from frequent flooding, cushion forming *Raoulia* and creeping woody *Muehlenbeckia axillaris* established, and once terraces became fixed, tussock grasses and shrubs began to dominate (Cockayne & Foweraker 1916; Cockayne 1927; Calder 1961; Fisher 1969). These native riverbed species are also found in the mountain shingle fields that are frequently disturbed by heavy rainfall and in turn supply the substrate that becomes the riverbed floodplains (Fisher 1969; Wardle 1991). This suggests that the natural state of braided riverbeds is much like that of alpine shingle fields: relatively low vegetation cover, with a few species having specialised adaptations to survive extreme conditions (Wardle 1991). More recently, the view that these ecosystems help only low diversity has been called into question as Woolmore (2011) found ~260 native species in alpine braided river floodplain and riparian zones, including 18 threatened plant species. Even with this relatively high diversity, most of the species were exceedingly rare (Woolmore 2011) highlighting that while the native flora can survive, it is not adapted to dominate these heavily-disturbed ecosystems. Alien plant species on the other hand have been found to establish and dominate many parts of this ecosystem (Williams & Wiser 2004).

The extent of alien invasion was highlighted by a survey of four of New Zealand's largest braided river floodplains that found over 60% of 289 species were alien (Williams & Wiser 2004). The impacts of these species have been highlighted in studies of the direct impacts of alien species on river flow dynamics through sediment consolidation (Hicks *et al.* 2008; Caruso *et al.* 2012; Caruso, Edmondson & Pithie 2013). Alien species also obstruct endangered floodplain nesting bird habitat

(Balneaves & Hughey 1990), alter plant community succession and assembly (Bellingham, Peltzer & Walker 2005; Holdaway & Sparrow 2006), change various soil properties (Peltzer *et al.* 2009), and cause nutrient enrichment (Bellingham *et al.* 2005; Drake 2011). This has led to a desire to understand and reduce the abundance and cover of alien plant species on braided river floodplains.

The riverbed substrate in Canterbury is generally unconsolidated sedimentary rock (glacially influenced greywacke) eroded from the shingle fields of the steep upper catchments in the Southern Alps and their foothills. The substrate, steep topography and frequent heavy rainfall causes rivers with multiple mobile channels to form in a floodplain of frequently reworked river gravels. Intense bed transforming flows occur frequently, making disturbance a dominant characteristic of these ecosystems (Gray & Harding 2007; Hicks *et al.* 2008). Rivers around the region have been progressively instrumented with flow recording stations. Continuous time series of flows from 7 to 40 years before present provide a rich dataset with which to quantify disturbance, as characterised by flow regimes. Adjacent land cover varies throughout the region with low- and mid-altitudinal areas dominated by arable and pastoral agriculture, and less-modified native ecosystems present at higher altitudes (Atkinson & Cameron 1993).

The Canterbury region is currently undergoing a dramatic shift in land-use from predominantly dryland pastoral sheep and beef production to more intensive irrigated pasture dairy production systems (Burns 2014). With this conversion, new irrigation schemes have been built to draw water out of rivers; more groundwater is being pumped, lowering water tables; and direct diversion from rivers has increased (Young, Smart & Harding 2004). Furthermore, climate change is expected to alter precipitation patterns in this region, affecting river flow regimes (Mullan *et al.* 2008; Hirabayashi *et al.* 2013). Thus, now more than ever, research is needed to understand the potential impacts of flow alterations on biodiversity and plant invasions in the ecosystem.

1.8   Specific questions and objectives

My thesis addresses the effects of flow regime on the level of ecosystem invasion and the success of alien plant species in gravel floodplains. The four specific studies in Chapters 2-5 address the following questions:

1. Can a hydrologic gradient analysis be used as a framework to study flow-ecology relationships in New Zealand gravel floodplains? (Chapter 2)

2. Does alien and native species diversity and abundance respond to the hydrologic gradients derived from Question 1 in the context of climate, land-cover (propagule pressure) and local floodplain variation? (Chapter 3)

3. Do growth and regenerative traits explain the level of invasion of alien plant species across disturbance and drought gradients in floodplain ecosystems? (Chapter 4)

4. Finally, what are the primary ecological constraints on three woody nitrogen-fixing ecosystem engineers? (Chapter 5)

The answer to the first question lays the analytical foundation for the subsequent questions by quantifying the primary independent variables of interest for the ecological studies. These subsequent questions look at alien species in three distinct ways. First, I look at alien species as a flora in contrast to the native flora. Second, I examine how alien species with different sets of traits respond to various aspects of flow regime. Third, I end with a species-focused study that targets three woody legumes that are considered ecosystem engineers and thus impact multiple aspects of floodplain ecosystem function. Each formulation of the ecological response variables targets distinct ecological processes: level of invasion of the ecosystem by alien and level of native species persistence, success of groups of alien species (grouped by traits), and finally the level of invasion of key species of concern in these floodplain ecosystems.

1.9   Structural notes

Terminology note: throughout this thesis 'altitude' is used to refer to a geographic location's mean height above sea level and 'elevation' is used in reference to the local floodplain topography.

Data are archived on the New Zealand National Vegetation Survey database. This can be found at: https://nvs.landcareresearch.co.nz/Data/Search.

Chapters 2 – 3 were written as self-contained research articles so they contain some repetition in the introduction and methods sections. Chapters 4-5 were written with the intention of future submission for publication, but reference some methodological and study design information from previous chapters.

Chapter 2 has been published as: Brummer, T.J., Byrom, A.E., Sullivan, J.J., & Hulme, P.E. (2016) A quantitative framework to derive robust characterization of hydrological gradients. *River Research and Applications*, **32**, 1517-1529. DOI: 10.1002/rra.3001.

Chapter 3 has been published as: Brummer, T.J., Byrom, A.E., Sullivan, J.J., & Hulme, P.E. (2016) Alien and native diversity and richness respond to different environmental drivers across multiple gravel floodplain ecosystems. *Diversity and Distributions,* **22**, 823-835. DOI: 10.1111/ddi.12448.

Chapter 2 - A quantitative framework to derive robust characterisation of hydrological gradients

2.1 Abstract

If ecological management of river ecosystems is to keep pace with increasing pressure to abstract, divert and dam, we must develop general flow-ecology relationships to predict the impacts of these hydrologic alterations. Regional flow gradient analyses are a promising tool to quickly reveal these functional relationships, but there are considerable uncertainties in this method due to variability in the historical extent of flow data across different rivers, combined with multiple indices characterising the ecological attributes of flow regimes. In response, we outline an objective framework for analysing spatial hydrologic gradients that addresses three major sources of uncertainty: robust estimation of flow indices, the potential for temporal trends to confound spatial variation in flow regimes, and the statistical robustness to detect underlying hydrological gradients. The utility of our framework was examined in relation to flow regimes across multiple braided river catchments in Canterbury, New Zealand. We found that a subset of flow indices could be robustly estimated using only 10 years of flow data, although indices that captured flow 'timing' required longer time series. Temporal trends were unlikely to confound conclusions from a spatial hydrologic gradient analysis, and there were three statistically-supported hydrologic gradients related to flow magnitude, flow variability and low flow events. The widespread application of robust spatial flow gradient analyses has the potential to further our understanding of how altered flow regimes affect the ecology of freshwater and riparian ecosystems, thereby providing the evidence base to inform river management.

2.2 Introduction

A major challenge in ecohydrology is to establish how river flows affect ecosystem processes in order to predict how water abstraction, land-use and climate change will affect freshwater ecosystems both instream and the riparian zone. For example, land cover change affects interception and runoff (e.g. Thanapakpawin *et al.* 2007), water abstraction can decrease mean and minimum flows (Maheshwari, Walker & McMahon 1995), and climate change can either increase or decrease the frequency of floods and droughts (Hirabayashi *et al.* 2013). Altered flow regimes are known to have ecological consequences (e.g. Growns & Growns 2001; Catford *et al.* 2014; Pool & Olden 2015), but generalizations about how organisms and processes (e.g. alien plant invasion, eutrophication, erosion, riparian vegetation, macroinvertebrates and fish) are affected by such

changes remain elusive (Poff & Zimmerman 2010). In response, a general framework (Ecological Limits of Hydrological Alteration – ELOHA) was created that stresses the importance of establishing general flow-ecology relationships of regional relevance, to circumvent the need for detailed system specific research to develop environmental flow standards (Poff & Zimmerman 2010; Poff *et al.* 2010).

To study the effects of altered flow regimes on freshwater ecosystems, several methods have been used. These range from experimental manipulations of flows in regulated catchments (e.g. Konrad *et al.* 2011), longitudinal studies that correlate flow parameters to ecological response variables over time (e.g. Monk *et al.* 2006), and gradient analyses that substitute space for time to correlate ecological responses to hydrological variables across multiple catchments (e.g. Riis *et al.* 2008; Catford *et al.* 2014). Although experimental and longitudinal studies benefit from controlling for multiple sources of variability, they require heavy investment in time and resources. Spatial gradient analyses have the potential to quantify functional relationships between flow regimes and observed ecological responses without the extended time scale required in longitudinal studies and at potentially lower cost. However, flow-gradient studies come with a set of assumptions and limitations that must be addressed explicitly before generating flow-ecology relationships that can then inform ecosystem management.

Currently, spatial gradient analyses lack a structured defensible approach to the characterisation of hydrological regimes using ecologically relevant indicators. There are several key challenges to ensuring spatial flow gradients can inform flow-ecology relationships. First, estimating indices that describe ecologically-relevant aspects of flow regime such as its *magnitude*, *duration*, *frequency*, *timing* and *rate of change* of flow (following Richter *et al.* 1996; Poff *et al.* 1997; Kennard *et al.* 2010), require a substantial time series of flow records (Kennard *et al.* 2010). Second, these indices may have progressively changed over time as a result of human (e.g. abstraction) or environmental (e.g. climate change) pressures such that the long-term average is not representative of contemporary trends. Third, the multivariate structure of flow regime data with multiple, often correlated, indices, requires a reduction in dimensionality to statistically evaluate flow-ecology relationships in a parsimonious manner (e.g. regression analysis).

The current approach to characterising hydrologic gradients (Olden & Poff 2003; Monk *et al.* 2007) begins by identifying rivers within a region that span a range of flow regimes. Records from flow gauging stations are assembled, hydrologic indices are calculated from a period of common flow records (Kennard *et al.* 2010), indices are evaluated for multicollinearity (e.g. through a principal components analysis; Olden & Poff 2003) and ecological responses are regressed against a

subset of independent indices that describe flow regime (e.g. Monk *et al.* 2007). There are several limitations to this approach that do not directly address the challenges laid out above. First, indices must be selected that are most informative and robust to data addition to ensure transferability of the functional relationships (Kennard *et al.* 2010). Second, temporal trends that may confound spatial gradients in flow indices must be considered. Third, identification of, and statistical support for, underlying hydrologic gradients should be evaluated, rather than simply selecting uncorrelated indices that vary among rivers (Monk *et al.* 2007).

We propose a framework that can be used to characterise hydrologic gradients when the goal is to evaluate how flow regimes affect ecosystem processes regionally (Figure 2.1), and apply the framework to a set of rivers in New Zealand. We contend that a standardized approach to characterising hydrologic gradients will improve the ability of spatial gradient analyses to establish general flow-ecology relationships. At the same time we can quantify the limitations of a study system to address specific questions, and ensure inferences from different spatial flow gradient analyses are comparable.

2.3   Methods

2.3.1   Framework

Our framework (Figure 2.1) for robust characterisation of hydrologic gradients draws on the methods that determine ecological responses to flow metrics (Richter *et al.* 1996; Olden & Poff 2003). In Step 1, we suggest not proceeding unless there are at least 10 rivers within the region for which flow data are available (gradient analyses with fewer than 10 points are generally underpowered) and that at least half of the flow stations have records beyond 10 years so that the robustness of index estimation using the common period method can be assessed in Steps 2 & 3. Step 2 addresses the robustness of index estimation relative to the chosen common period, and Step 3 determines the evidence for temporal trends in these indices. Step 4 evaluates the statistical support for hydrologic gradients within the system and Step 5 then carries these into ecological analyses.
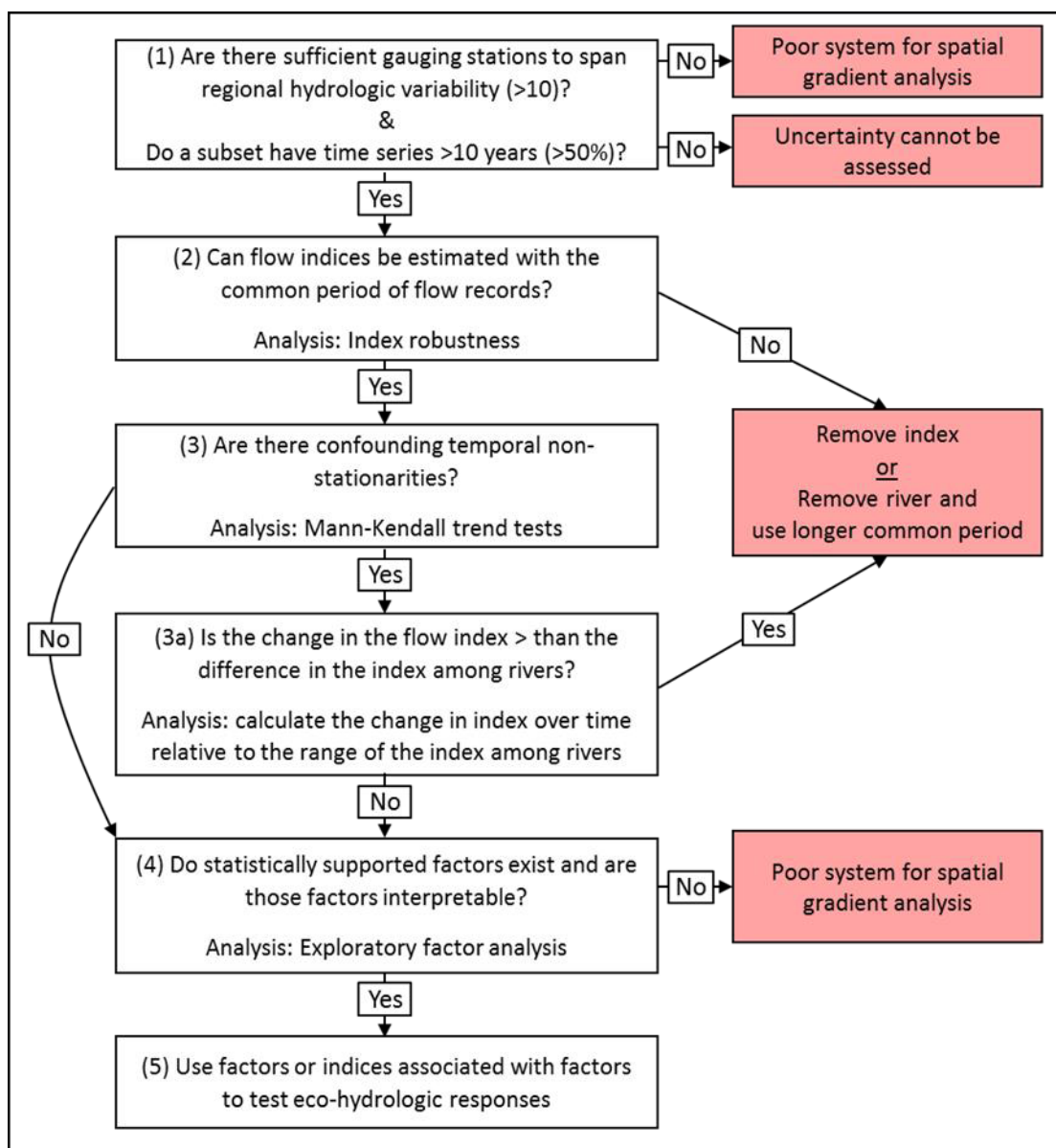
Figure 2.1. Framework for characterising hydrological gradients. The goal is to estimate and retain as many ecologically-relevant hydrologic indices as possible while filtering out those that are poorly estimated due to data limitations or to characteristics of river systems that prevent reliable estimation of indices. Each red box indicates a point at which rivers or indices should be excluded, and could be treated as a limitation of the study system. The final factor analysis is used to characterise hydrologic gradients based on flow indices that are estimated reliably with respect to data availability and an absence of confounding temporal trends.
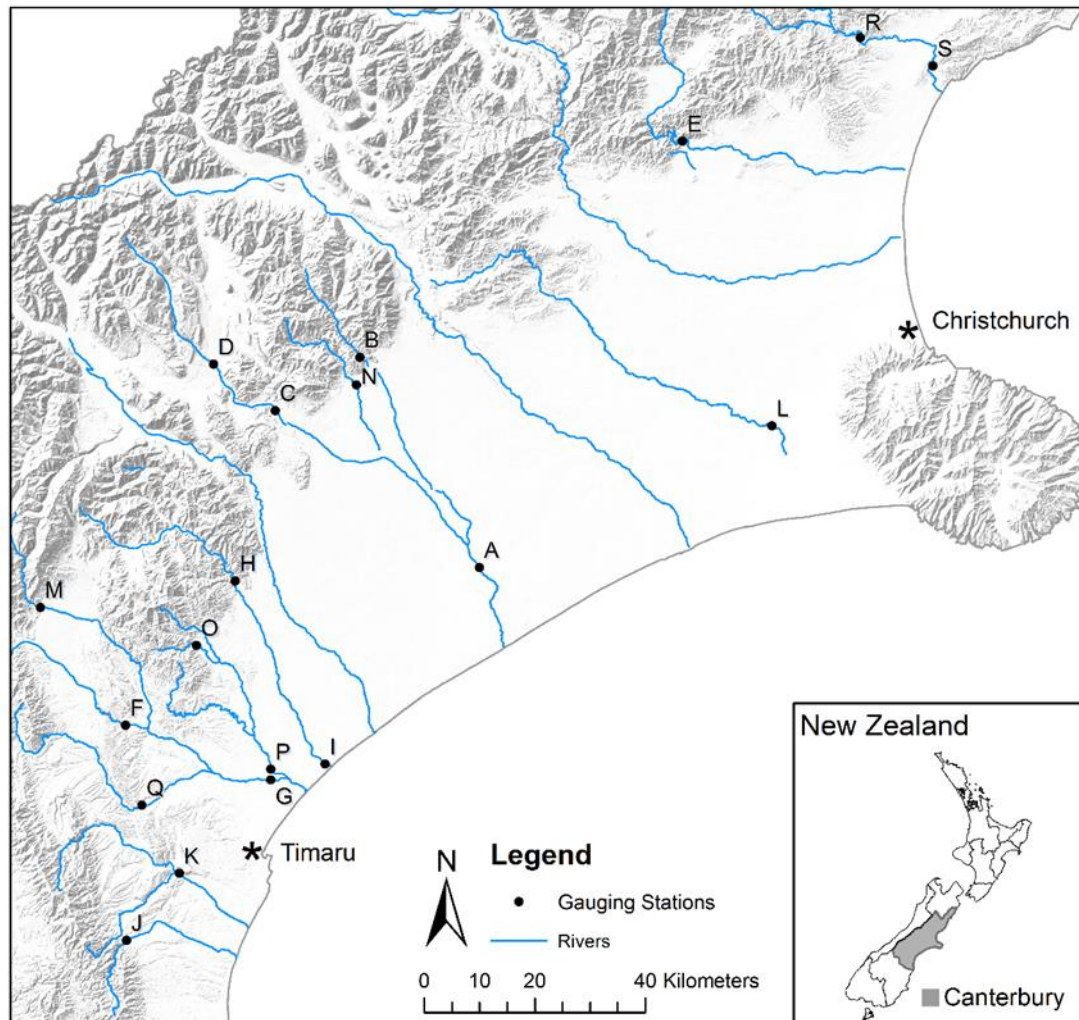
Figure 2.2. Sampling locations of 19 gauging stations used in the study. Letters correspond to Table 2.1 where river attributes are presented in detail. The inset map displays the location of the Canterbury region within New Zealand. Grey shaded relief depicts significant topography (hills and mountains) while flat topography is white (valleys and plains).

2.3.2 Study system

For our case study, we were interested in quantifying hydrologic gradients in New Zealand braided rivers that could then be used to develop flow-ecology relationships. Land conversion has driven increases in surface and ground water offtake, necessitating the development of environmental flow recommendations to meet biodiversity and ecosystem health targets of these ecosystems (Canterbury Water 2009). Flow data were available from the regional agency responsible for resource management (Environment Canterbury) and spanned latitudinal and land-use intensity gradients across the Canterbury Region of New Zealand (Figure 2.2).

The rivers were sourced in mountain, hill or plains catchments of varied topography, land-cover (Snelder, Biggs & Woods 2005) and size (Figure 2.2). Some catchments had multiple gauging stations throughout their network, or upland and lowland gauges (Figure 2.2). However, gauges that shared a common catchment were relatively independent as they were placed to account for major changes affecting flow regime. Although the rivers generally flow unimpeded from source to sea, two rivers were dammed, one in the 19th Century (Pareora River) prior to all gauging records and the other in 1998 (Opihi River). The dam that affects the Opihi River is on an upstream tributary and used for releases to maintain minimum flows. It is expected that this dam will have influenced the time series from the lower gauging station (Figure 2.2). Abstraction is heterogeneous across the region and detailed abstraction data were not readily available or reliable.

The three rivers sourced in the upper reaches of the Southern Alps (Waimakariri, Rakaia, Rangitata) were excluded from the study as a preliminary multivariate analysis suggested their flow regimes were significant outliers. The aim for the gradient analysis was to study rivers that fell along a continuum of flow regimes and were broadly comparable rather than include a few rivers that had substantially different flow dynamics.

2.3.3 Step 1: Data adequacy

Gauging stations with five or fewer years of flow data were removed immediately (n = 2) as this is the minimum flow record length that can practically be considered for estimating flow indices (Kennard *et al.* 2010). As a result, 19 gauging stations with a sufficient length of record were available (Table 2.1), which surpassed the minimum sample size required to explore the potential for spatial gradient analysis (Figure 2.1). Flow record lengths ranged from 7 to 45 years, 14 of which had flow records >10 years. These data met both of our initial criteria for the subsequent analyses (Figure 2.1). Years that were missing more than 30 days of data were evaluated for potential bias during index uncertainty analysis (*Step 2*, Figure 2.1). Flow records were generally only discontinuous

in the initial years of monitoring and thus did not unduly influence subsequent uncertainty and time series analyses.

Table 2.1. Attributes for 19 flow gauging stations on 13 braided river ecosystems in the Canterbury Region of New Zealand. The map code corresponds to the location of a station in Figure 2.1. 'Low data years' are defined as having less than 330 days (i.e. missing more than one month of records). Attributes relevant to variation in flow regimes (catchment area, source and land cover) are also reported. Abbreviations: Source – <u>H</u>ill, <u>M</u>ountain, <u>L</u>owland; Land Cover – <u>P</u>astoral, <u>T</u>ussock, <u>I</u>ndigenous <u>F</u>orest.

Map Code	Gauging Station	Year of First Record	Elev. (m)	Catchment Area (km^2)	Source	Land cover
A	Ashburton Main	1997	92	1579	H	P
B	Ashburton North Branch	1983	441	276	M	T
C	Ashburton South Branch L	2003	426	539	H	T
D	Ashburton South Branch U	1968	611	92	M	T
E	Ashley	1973	205	472	H	IF
F	Opihi Upper	1965	160	406	H	P
G	Opihi Lower	1999	27	1744	H	P
H	Orari Upper	1983	240	522	H	T
I	Orari Lower	2007	15	557	H	P
J	Otaio	2002	186	54	H	T
K	Pareora	1983	74	425	L	P
L	Selwyn	1985	42	762	L	P
M	South Opuha	2004	550	116	M	T
N	Taylors	2005	375	42.9	M	T
O	Te Moana	1984	205	67.8	H	T
P	Temuka	1984	17	577	L	P
Q	Tengawai	1983	132	486	H	P
R	Waipara Upper	1989	94	27.2	H	P
S	Waipara Lower	2001	33	716	L	P

2.3.4 Step 2: Index robustness

The first uncertainty analysis (*Step 2*, Figure 2.1) assesses the suitability of flow index estimates to be included in a gradient analysis. The main purpose of this analysis is to determine which indices should be removed because variability in estimation of the index is greater than differences in the indices across all gauging stations (i.e. 'robustness' to estimation with additional data). Following Kennard et al. (2010), we estimated 129 indices describing hydrologic variability (Table 2.2) using mean daily flow records summarised from 15-minute continuous data.

Indices were categorised as: *Magnitude*, *Frequency*, *Duration*, *Timing* and *Rate of Change* (Richter *et al.* 1996; Poff *et al.* 1997). Within each category, subgroups described average, low and high flow events. All hydrologic indices were calculated in R v3.1.0 (R Core Team 2014), using custom formulae and existing methods from packages 'lfstat' and 'hydrostats'. Other packages used for data manipulation were 'plyr', 'zoo', and 'lubridate' (Zeileis & Grothendieck 2005; Grolemund & Wickham 2011; Wickham 2011; Bond 2014; Koffler & Laaha 2014).

To assess the robustness of each flow index we evaluated how each index changed when additional data were added beyond either a 5- or 10-year common period (years of record were 2009–2013 and 2004–2013 for 5- and 10-year common periods respectively). Longer common periods can and should be assessed if this can be accommodated while maintaining a sufficiently high sample size. The 5-year common period was assessed to determine if two gauging stations with fewer than 10 years of data could be used in subsequent analyses, and to demonstrate the trade-off between maximising regional sample size while accounting for index uncertainty. For all flow time series longer than the common period, years of data were added sequentially (going back in time), and each index recalculated after each additional year, up to the full length of each station's record (Figure 2.3 - 1a, Figure 2.3 - 2a). To calculate the index change ($\Delta FlwInd_{ri}$), the index estimated from the common period (*FlwInd$_{CPr}$*) was subtracted from the index estimated with additional data (*FlwInd$_{ri}$* Figure 2.3 - 1b, Figure 2.3 - 2b; Eq. 2.1).

$$\Delta FlwInd_{ri} = FlwInd_{ri} - FlwInd_{CPr} \quad \text{Equation 2.1}$$

FlwInd – Flow Index

CP - common period

r – rivers

i – years of data before the common period
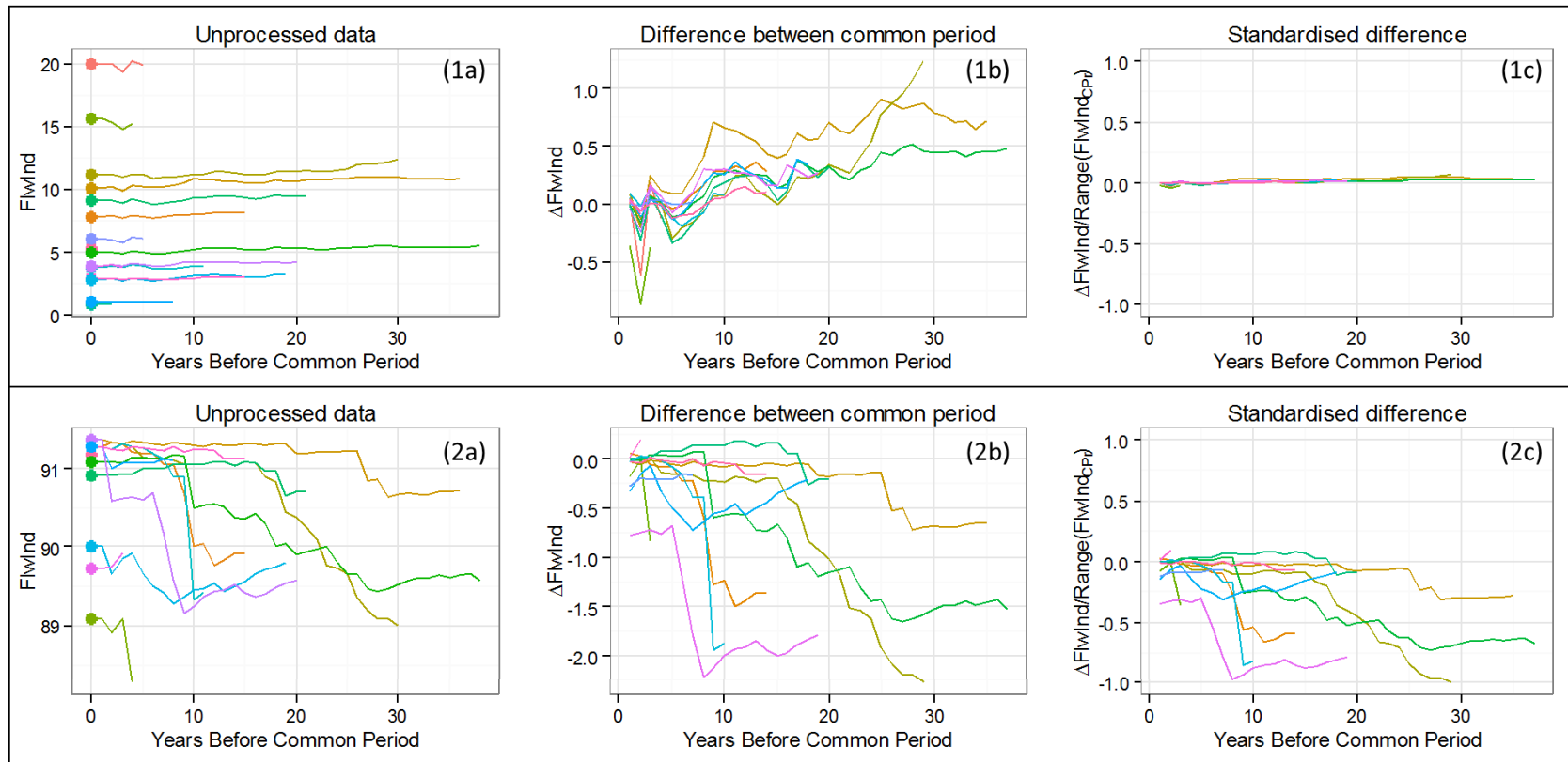
Figure 2.3. Graphical depiction of the calculations for the index robustness analysis. The top panel (1) demonstrate the process for an ideal index (mean daily flow) whereas the bottom panel (2) shows a non-robust index. Panels a plot the actual index estimate for the common period (points) and how the estimate changes when additional years of data are added. Each line indicates a different flow gauging station. Panels b apply Eq. 1 to calculate the difference in the index relative to the common period estimate (points in panels a). Panels c plot the differences standardised by the range of the index estimated for the common period (maximum – minimum of the points in panel a). In panel 1c we see that the differences in the index calculated with additional data are small relative to the range (2*SD = 0.03) suggesting the index is very robust to additional data and the differences are centred on 0 indicating it is unbiased (mean = 0.01). In panel 2c we see that the differences in the index are large relative to the common period range (2*SD = 0.59) suggesting the index is not robust to adding data and the points are on average below 0 suggesting the index is also biased (mean = -0.24). These two examples use a 10-year common period.

The change estimate was standardised by dividing it by the range of the index estimated for the common period across all rivers (Figure 2.3 - 1c, Figure 2.3 - 2c). This standardised the magnitude of difference between the common period estimate and the estimate with additional data. If this is small, then the index is considered robust to the addition of more data. The standardised measure can be interpreted as the proportional change of the index when estimated with additional data, relative to the variation among rivers as estimated from the common period. The utility of using the common period range to standardise the change in the index (and using the index in the gradient analysis) relies on good coverage across the range of the index (e.g. little clustering along its range). This can be assessed with a visual check of the distribution of values for each index (Figure 2.3 - 1a, Figure 2.3 - 2a), and indices with clustering should be removed from consideration. Two characteristics of the standardised change were considered: bias and robustness. Bias indicates whether the index was consistently over- or underestimated and defined as the mean of standardised changes in flow indices (Eq. 2.2). The robustness was defined as the spread of the standardised differences and defined as two standard deviations of the standardised index differences (Eq. 2.3). The smaller the spread the more robust the index.

$$Bias = Mean \left[\frac{\Delta FlwInd_{ri}}{Range(FlwInd_{CPr})} \right] \text{ Equation 2.2}$$

$$'Robustness' = 2 * SD \left[\frac{\Delta FlwInd_{ri}}{Range(FlwInd_{CPr})} \right] \text{ Equation 2.3}$$

2.3.5 Step 3: Time series analysis

Time series analysis is used to determine the potential for progressive temporal trends to confound spatial hydrologic gradients (*Step 3*, Figure 2.1). Such analyses should be undertaken on indices that are estimable on an annual basis rather than requiring integration over a time series (though these can be converted to annual indices). For indices that quantify a coefficient of variation, we used a three-year window to estimate the standard deviation of the particular measure of interest which resulted in two fewer observations per time series. In our study, this resulted in a subset of 48 flow indices estimated annually for the entire flow record of each gauging station (Table 2.2).

The non-parametric Mann-Kendall (MK) test for monotonic trend was used to estimate the direction and significance of trends for each index (Kendall 1938; Mann 1945). A trend-free pre-whitening procedure was use to adjust for lag 1 autocorrelation (Yue *et al.* 2002). This test is generally the most powerful when trends are non-normal or non-linear (Yue & Pilon 2004) and is more appropriate than traditional time series analysis that requires a longer time series to estimate

Table 2.2. Flow indices used to characterise hydrologic gradients. The D/M/A column indicates whether an index was calculated from Daily, Monthly or Annual series. A 'y' in the uncertain columns indicates the index was uncertain when estimated from a 5 or 10 year common period. Factor loadings are reported, bolded if they are greater than 0.6 and do not have other high loading indices (our criterion for determining if an index loaded strongly onto a factor). Rows without numbers indicate the index was removed from an analysis due to uncertainty, cross-loading, or high uniqueness. The index code indicates the category of each index. M – Magnitude, F – Frequency, D – Duration, T- Timing, R – Rate of change; a – average, h – high, l – low flow conditions. An '*' next to the code indicates the index was used in subsequent time series analysis.

Hydrologic Index			Uncertain?		Factor Loadings		
Code	Description (statistic)	D/M/A	5 Yr	10 Yr	F1	F2	F3
Ma1*	daily runoff (mean)	D			-	-	-
Ma2*	daily runoff (median)	D			-	-	-
Ma3*	daily flow (mean)	D			**0.99**	0.13	-0.05
Ma4*	daily flow (median)	D			**0.98**	-0.1	-0.02
Ma5*	daily flow (cv)	D			-	-	-
Ma6*	daily flow (skewness)	D	y	y	-	-	-
Ma7	jan flow (mean)	M			**0.97**	-0.09	0.11
Ma8	feb flow (mean)	M			**0.95**	0.06	0.21
Ma9	mar flow (mean)	M			**0.95**	0.09	0.18
Ma10	apr flow (mean)	M			**0.98**	0.05	0.12
Ma11	may flow (mean)	M			**0.96**	0.23	0.04
Ma12	june flow (mean)	M			**0.92**	0.34	-0.12
Ma13	jul flow (mean)	M			**0.87**	0.29	-0.26
Ma14	aug flow (mean)	M			**0.9**	0.4	-0.12
Ma15	sept flow (mean)	M			**0.95**	-0.01	-0.17
Ma16	oct flow (mean)	M			**0.94**	-0.02	-0.19
Ma17	nov flow (mean)	M			**0.96**	-0.16	-0.06
Ma18	dec flow (mean)	M			**0.99**	-0.05	0.11
Ma19	jan flow (cv)	M	y	y	-	-	-
Ma20	feb flow (cv)	M			-0.5	0.49	0.22
Ma21	mar flow (cv)	M	y	y	-	-	-
Ma22	apr flow (cv)	M			-	-	-
Ma23	may flow (cv)	M			-0.49	**0.67**	0.21
Ma24	june flow (cv)	M			-0.48	**0.59**	0.49
Ma25	jul flow (cv)	M			-0.53	**0.6**	0.44
Ma26	aug flow (cv)	M	y		-0.24	**0.83**	0.34
Ma27	sept flow (cv)	M	y	y	-	-	-
Ma28	oct flow (cv)	M			**-0.7**	0.45	0.26
Ma29	nov flow (cv)	M	y		-	-	-
Ma30	dec flow (cv)	M	y	y	-	-	-
Ma31	mean annual runoff (mean)	A			-	-	-
Ma32	mean annual flow (mean)	A			**0.99**	0.13	-0.05
Ma33	annual flow (cv)	A			-0.39	0.7	-0.28
Ma34	annual flow (skewness)	A	y	y	-	-	-

Code	Description	Type					
Ma35	annual runoff (median)	A			-	-	-
Ma36	annual flow (median)	A			0.98	0.11	-0.07
Ml1*	lowest annual flow (median)	A			-	-	-
Ml2*	ratio baseflow to total flow	A			0.53	**-0.78**	-0.02
Ml3	baseflow index (cv)	A			-0.42	**0.76**	-0.04
Ml4*	low flow discharge 99th (mean)	A			**0.89**	-0.37	0.05
Ml5*	low flow discharge 90th (mean)	A			**0.94**	-0.26	0.05
Ml6*	low flow discharge 75th (mean)	A			**0.97**	-0.16	0.05
Ml7	annual min (mean)	A			**-**	-	-
Mh1*	highest annual flow (median)	A	y		-0.61	0.43	0.46
Mh2*	high flow discharge 1st (mean)	A			-	-	-
Mh3*	high flow discharge 10th (mean)	A			**0.96**	0.16	-0.12
Mh4*	high flow discharge 25th (mean)	A			**0.98**	0.02	-0.07
Mh5	max runoff (spec. mean)	A			**-**	-	-
Mh6*	high flow vol. >1xMDF (mean)	A			**0.9**	0.39	-0.11
Mh7*	high flow vol. >3xMDF (mean)	A			**0.86**	0.45	0.06
Mh8*	high flow vol. >7xMDF (mean)	A			**0.8**	0.45	0.17
Mh9	magflood ARI1 (mean)	A			**0.74**	0.54	0.01
Mh10	magflood ARI2 (mean)	A	y		-	-	-
Mh11	magflood ARI5 (mean)	A			-	-	-
Mh12	max annual flow (skewness)	D	y	y	-	-	-
Fl1*	low flow days 75th (mean)	A	y	y	-	-	-
Fl2*	low flow days 90th (mean)	A	y	y	-	-	-
Fl3*	low flow days 99th (mean)	A	y	y	-	-	-
Fl4*	low flow days 75th (cv)	A	y		-	-	-
Fl5*	low flow days 90th (cv)	A	y	y	-	-	-
Fl6*	low flow days 99th (cv)	A	y	y	-	-	-
Fl7*	low flow days <MDF/3 (mean)	A			-0.41	0.46	**-0.7**
Fl8*	low flow days <MDF/7 (mean)	A			-	-	**-**
Fh1*	high flow days 1st (mean)	A	y	y	-	-	-
Fh2*	high flow days 10th (mean)	A	y	y	-	-	-
Fh3*	high flow days 25th (mean)	A	y	y	-	-	-
Fh4*	high flow days 1st (cv)	A	y	y	-	-	-
Fh5*	high flow days 10th (cv)	A	y	y	-	-	-
Fh6*	high flow days 25th (cv)	A	y	y	-	-	-
Fh7*	high flow days 3mdf (mean)	A			-0.44	**0.68**	-0.4
Fh8*	high flow days 7mdf (mean)	A			-	-	-
Dl1	1day means (min)	D			**0.88**	-0.37	0.05
Dl2*	3day means (min)	D			**0.9**	-0.35	0.05
Dl3*	7day means (min)	D			**0.91**	-0.32	0.05

Code	Description	Type			col1	col2	col3
Dl4*	30day means (min)	D			**0.95**	-0.25	0.05
Dl5*	90day means (min)	D			**0.98**	-0.14	0.05
Dl6	1day means (cv min)	D	y	y	**-**	-	-
Dl7	3day means (cv min)	D	y	y	**-**	-	-
Dl8	7day means (cv min)	D	y	y	-	-	-
Dl9	30day means (cv min)	D	y	y	-	-	-
Dl10	90day means (cv min)	D	y	y	-	-	-
Dl11*	duration lf 75th (mean)	A			-	-	-
Dl12*	duration lf 90th (mean)	A	y		-0.52	0.28	-0.32
Dl13*	duration lf 99th (mean)	A	y	y	-	-	-
Dl14	duration lf 75th (cv)	A	y	y	-	-	-
Dl15	duration lf 90th (cv)	A	y		-	-	-
Dl16	duration lf 99th (cv)	A	y	y	-	-	-
Dl17	duration lf <MDF/3 (mean)	A	y		-	-	-
Dl18	duration lf <MDF/7 (mean)	A	y		-0.44	0.38	**-0.74**
Dl19	cv duration lf <MDF/3 (cv)	A	y	y	-	-	-
Dl20	cv duration lf <MDF/7 (cv)	A			-	-	**-**
Dh1	1day means (max)	D			-	-	-
Dh2*	3day means (max)	D			-	-	-
Dh3*	7day means (max)	D			-	-	-
Dh4*	30day means (max)	D			**0.88**	0.44	-0.02
Dh5*	90day means (max)	D			**0.95**	0.29	-0.07
Dh6	1day means (cv max)	D	y	y	**-**	-	-
Dh7	3day means (cv max)	D	y		**-**	-	-
Dh8	7day means (cv max)	D			-0.26	**0.86**	0.11
Dh9	30day means (cv max)	D			-0.34	**0.84**	0.08
Dh10	90day means (cv max)	D			-0.41	**0.8**	-0.16
Dh11*	duration hf 1th (mean)	A	y	y	-	-	-
Dh12*	duration hf 10th (mean)	A			-	-	-
Dh13*	duration hf 25th (mean)	A			-	-	-
Dh14	duration hf 1th (cv)	A	y	y	-	-	-
Dh15	duration hf 10th (cv)	A	y	y	-	-	-
Dh16	duration hf 25th (cv)	A	y	y	-	-	-
Dh17	duration hf 3MDF (mean)	A			-	-	-
Dh18	duration hf 7MDF (mean)	A			-	-	-
Dh19	duration hf 3MDF (cv)	A	y		-	-	-
Dh20	duration hf 7MDF (cv)	A	y	y	-	-	-
Ta1	predictability MDF	D	y	y	-	-	-
Ta2	constancy MDF	D	y	y	-	-	-
Ta3	Seasonality MDF	D	y	y	-	-	-
Ta4	Perenniality monthly flows	A			-	-	-
Tl1	date min flow	D	y	y	-	-	-
Tl2	cv date min flow	D	y	y	-	-	-
Tl3	predictability min flow	D	y	y	-	-	-
Tl4	seasonality min flow	D	y	y	-	-	-

Th1	date max flow	D	y	y	-	-	-
Th2	cv date max flow	D	y	y	-	-	-
Th3	predictability max flow	D	y	y	-	-	-
Th4	seasonality max flow	D	y	y	-	-	-
R1	Rise rate	D			**0.79**	0.49	0.05
R2	cv rise rate	D			-0.44	**0.79**	0.14
R3	fall rate	D			**-0.87**	-0.46	-0.01
R4	cv fall rate	D	y	y	-	-	-
R5	num reversal	D			-	-	-
R6	cv reversals	D	y	y	-	-	-

autocorrelation structure. Short-term trends were evaluated on 10 years of flow data (2004-2013) common to 17 gauging stations, and for the whole time series for 9 stations with more than 20 years of data. Although 10-year analyses can be underpowered (Yue & Pilon 2004), trends in the 10-year data are likely to be highly influential (i.e. significant statistically and ecologically) if they are detected. The error rate for determining significance was predefined at 0.05 and false discovery rate correction was used to correct for multiple comparisons (Benjamini & Hochberg 1995).

To determine if any of the detected temporal trends had large magnitudes of change relative to differences among rivers (*Step 3a*, Figure 2.1), change across the time series was divided by the range of the index across rivers (calculated from the common period). This provided a measure of the relative importance of temporal trends compared to spatial variation in flow indices, to determine whether temporal trends could confound or obscure spatial variability in flow indices. This approach was then used in the rejection/acceptance criteria. For these analyses to be most informative, there needs to be a subset of gauges with longer time series to understand potential non-stationarity across the study region.

2.3.6 Step 4: Factor analysis

The penultimate step of the framework (*Step 4*, Figure 2.1) uses exploratory factor analysis (EFA; Costello & Osborne 2005) to determine the statistically-supported hydrologic gradients (i.e. factors) across gauging stations (e.g. Belmar *et al.* 2013). We recommend that the number of statistically-supported factors be determined using parallel analysis (Velicer, Eaton & Fava 2000). This technique performs a factor analysis, substituting observed data with random values drawn from a standard normal distribution. This is replicated 1000 times to estimate the distribution of eigenvalues for factors achievable from random data. Factors with eigenvalues greater than 95th percentile of those generated randomly are considered significant.

A factor analysis was conducted (R package 'HDMD' (Costello & Osborne 2005; McFerrin 2013)) on flow indices estimated from the 10-year common period, and the number of statistically-supported factors identified in the parallel analysis were extracted. The oblique rotation 'simplimax' was specified as it is currently considered best practice (Kiers 1994; Costello & Osborne 2005). To maximise the interpretability of the factor analysis, indices were removed that had a uniqueness greater than 0.5 or loaded strongly on more than one factor (termed 'cross-loaded'; absolute loading of 0.6 on more than one factor). Cross-loaded indices were removed and the factor model refitted iteratively until no indices were cross-loaded. Unique and cross-loaded variables can be caused by multiple processes and may warrant further investigation (Costello & Osborne 2005) as they may be important ecologically even if they do not covary strongly with the extracted factors (e.g. Monk *et al.* 2007). Further, cross-loaded and unique variables may arise due to too few factors being extracted, which may be due to low sample size. Or, in the case of unstable indices, such variables may arise randomly.

2.4 Results

2.4.1 Index uncertainty analysis

Systematic under- or over-estimation ('bias') tended to be greater in indices estimated using the 5 versus 10 year common period (median absolute bias 0.067 for the 5-year common period versus 0.034 for the 10-year common period; Figure 2.4). The median 'robustness' in flow index estimation did not differ between different period lengths (Figure 2.4). Indices that were not robust when estimated using 5 years of data were not robust when estimated using 10 years of data, with few exceptions (Table 2.2). In general, bias improved more than the robustness between the two common periods (Figure 2.4), suggesting that, on average, the use of a 5-year common period would introduce too much uncertainty to carry forward into further gradient analyses. As a rule-of-thumb we found that indices with a robustness less than 0.1 were safe to include, those between 0.2 and 0.3 should be checked visually to determine the nature of the change with additional data and those greater than 0.3 should be excluded from further analyses.

In general, flow indices in the *magnitude* category had the highest proportion of robust indices (Figure 2.5). *Timing* and *frequency* indices were the least robust, with only one timing variable classified as robust and unbiased with the use of 10 years of data for estimation. *Frequency* indices that used the flow duration curve to delimit thresholds were not robust, while indices that used thresholds based on median flow were more robust (Table 2.2). When indices were classified as robust or not, those that measured dispersion (i.e. that measured variation in flow or flow events)
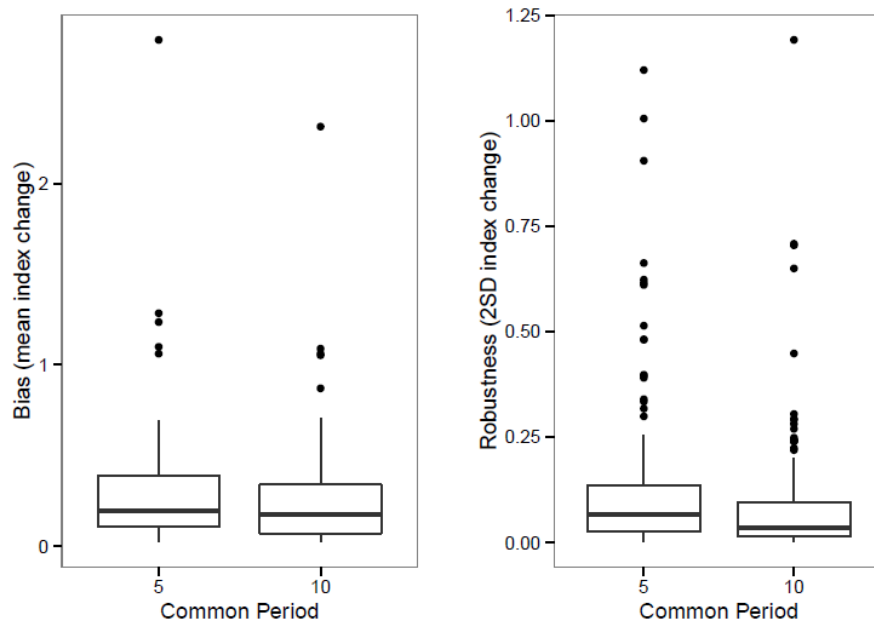
Figure 2.4. Change in bias (A) and robustness (B) between a 5- and 10-year common period used to estimate flow indices. Bias (over- or under-estimation of a flow index) tended to be reduced in the 10- compared to the 5-year common period while robustness (standard deviation of the change in index with added data) was slightly (but not significantly) lower using a 10 year common period (low values of 'robustness' are desirable)
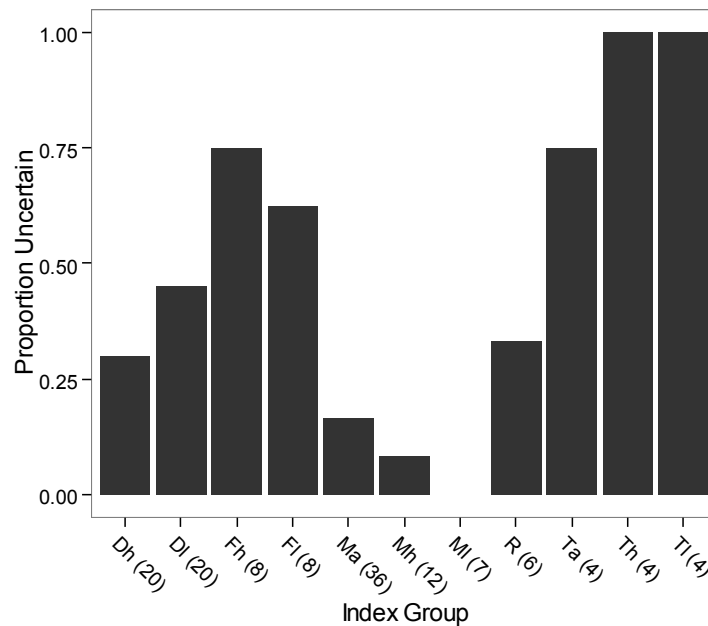
Figure 2.5. The proportion of indices that were not robust (uncertain) to adding data in each index group using a 10-year common period for estimation. The number of indices in each group are indicated parenthetically. Groups are abbreviated as: D – Duration, F – Frequency, M – magnitude, R – rate, and T – timing; with subgroups: h – high flow, l – low flow, a – average flow conditions.

were less robust (proportion not robust: 59% with a 95% CI of 44%-73%) than those that measured central tendency (21% with a 95% CI of 13%-32%). In general, there were indices from all categories of flow regime that were robust/unbiased; however, all of the timing of high and low flow events were not robust until at least 15 years of data were used for their estimation.

2.4.2 Time series analysis

After correcting for multiple tests using the false discovery rate criteria, there was only one statistically-supported trend in a flow series >20 years (decreasing variability in high flow events in the Tengawai River) and no statistically-supported trends in the 10-year flow series. Although we cannot conclude with certainty that there are no short-term temporal trends in flow indices among the gauging stations in our study, our findings suggest that the spatial gradient analyses would not be at significant risk of confounding by recent temporal variability. Further, a lack of observed long-term trends, in analyses with longer time series (greater statistical power), suggests that spatial flow gradients are not unduly influenced by temporal trends in our study rivers.

When we evaluated the potential for the one significant trend (in the Tengawai River) to confound a spatial analysis (*Step 3a*, Figure 2.1) we found that the coefficient of variation (CV) of the frequency of high flow events was estimated to decrease by 0.5 units (estimated from the Theil-Sen slope of the linear trend) over the 28-year period of record. The range of the average CV of the frequency of high flow events among rivers was only 0.35, suggesting that the magnitude of temporal change was greater than the spatial variability in this index. This represented an instance in which an index's temporal trend could confound the spatial gradient analysis, and was removed from subsequent factor analysis.

2.4.3 Factor analysis

Parallel analysis revealed three statistically-supported factors for robust flow indices estimated from a 10 year common period (Table 2.2). The first factor was correlated with indices that captured the magnitude of flow events, with indices from the *magnitude* and *duration* categories making up the majority of high loading indices. The second factor was explained by indices that captured variability in winter flows, base flow, the duration of maximum daily flows, and in the rise rate of flows. The third factor was explained by just two indices that captured the frequency and duration of low flow events.

2.5 Discussion

Developing general flow-ecology relationships in freshwater ecosystems is a global priority (ELOHA framework; Poff *et al.* 2010). Spatial hydrologic gradient analyses have the potential to address this need, however, studies that substitute space-for-time come with certain limitations. We have proposed and tested a framework (Figure 2.1) to address three limitations of using spatial gradient analysis in ecohydrology studies: (1) availability of flow data, (2) temporal trends confounding spatial gradients, and (3) statistical power to extract gradients amongst the many ecologically relevant flow indices. This framework supports Step 1 & 3 in the ELOHA framework of establishing the hydrologic data foundation and identifying flow gradients that can then feed into Step 4 that relates those gradients to ecological parameters of management interest. We applied this framework for a set of catchments and found that only a subset of flow indices were estimable given data constraints, that temporal trends were unlikely to heavily bias a spatial analysis, and that there were three primary hydrologic gradients.

2.5.1 Can flow indices be estimated robustly?

Spatial hydrologic gradient analyses are often constrained by sample size at a regional scale due to sparse placement of instrumentation or gauging stations with a short time period of data records. Our index uncertainty analysis confirmed that five years was too short a period to estimate indices robustly. This is consistent with the analysis that Kennard et al. (2010) conducted on six 75-year flow time series in Australia, and with other studies demonstrating better index estimation with longer time series (e.g. Richter *et al.* 1996; Cunderlik, Ouarda & Bobée 2004; Huh *et al.* 2005). Many indices that captured *dispersion*, *timing* and *frequency* of flow events were poorly estimated even with 10 years of flow data, supporting the view that indices capturing extreme events often require longer time series, perhaps as long as 15-30 years (Kennard *et al.* 2010).

We found representative indices from most flow categories were retained after robustness analysis in our system using the framework, demonstrating good coverage of potential ecologically-relevant aspects of flow regime. The one exception was *timing* indices which were poorly estimated, even with 10 or 15 years of data. Additionally, the frequency of high- and low-flow events calculated using the flow duration curve to define thresholds were uncertain using a 10-year time series, but when thresholds were defined using median flows as a reference (as in the commonly used FRE3 index; Clausen & Biggs 2000), indices were well estimated while still capturing the desired hydrologic processes (flood and drought events). Thus, our framework and subsequent analyses enabled us to

target indices that captured most of the ecologically-relevant aspects of flow regime, while also being robustly estimable.

Our findings suggest, for our system, that the 15 year minimum flow time series rule-of-thumb (Kennard *et al.* 2010) is true for some indices but not others. And, importantly, our framework allowed for the determination of an appropriate common period length on a system and index specific basis. This can be applied to any system with similar data. The decision points in the framework strategically balance which indices can be estimated with the available data and whether the non-robust indices can be ejected without compromising the goals of the study. Or in the case that indices of interest cannot be estimated, that a longer common period should be adopted, which decreases the regional sample size but improves the confidence in the gradient analysis study. While our specific dataset faced limitations regarding the estimation of especially timing variables, it highlighted the utility of our framework in assessing these limitations, and resulted in a set of defensible indices that captured flow processes that were in line with the goals of the follow on ecological studies.

2.5.2 Potential for temporal trends to confound spatial gradients

One of the primary limitations of gradient analysis is the potential for unmeasured processes (such as non-stationary indices) to confound spatial gradients (Fukami & Wardle 2005). Non-stationary flows can arise through direct human influence (such as progressive water abstraction), or indirect effects such as shifts in land-use that affect surface run off or climate change. The affected indices will show poor robustness and a common period estimate will fail to estimate a long term average; this temporal trend can confound inferences on spatial hydrologic variability driven by differences among catchments alone. Thus, it is critical to evaluate evidence for temporal trends where spatial gradient analyses are being considered.

Detection of temporal trends can be problematic, as the statistical tools can be underpowered if flow records are short. Our framework requires only a subset of representative gauging stations from the regional set to contain longer records, and then uses those periods of longer record to determine the likelihood of confounding temporal trends amongst all flow records. The time series analysis showed only one statistically-supported trend, suggesting that temporal trends will have a low probability of influencing inferences from a hydrologic gradient analysis in our system. Although we cannot conclude that flow regimes are not changing over time, we do provide evidence that inter-annual variability in flow metrics is greater than systematic temporal changes in flow regimes in our system, suggesting that any observed effects of flow patterns on the ecology of

the system will more likely be attributable to the spatial hydrologic gradient than to any temporal changes in flow.

The power of these tests will always be dependent on both sample size (Yue & Pilon 2004) and on how representative stations with longer flow records are of hydrological flow patterns in the region generally. The primary advance of our framework is that it enables quantification of trends across a whole system, by inferring the probability of non-stationarity from a subset of recorded flow characteristics from rivers in a region. We recognize that the proposed framework only captures monotonic trends, and could fail to capture step changes (e.g. due to engineering works or cyclical weather patterns). However, information on engineering works is generally more reliable and easily obtainable (in contrast to abstraction which in our system is not well monitored), and could be used to evaluate the range over which indices should be estimated.

2.5.3 Extracting hydrologic gradients

The many hydrologic indices that capture elements of flow regime increase the complexity of gradient analyses and thus require data reduction methods to derive statistically-supported hydrologic gradients. This enables clear inferences to emerge even when sample sizes are limited. Our use of factor analysis is not new in hydrologic studies (e.g. Belmar *et al.* 2013); however, it is not generally paired with parallel analysis that tests the statistical power of any underlying gradients. Our analysis strengthens the ability to define major hydrologic gradients, because the robustness of factor extraction is a function of regional sample size (de Winter, Dodou & Wieringa 2009).

We found three statistically-supported gradients, suggesting that even though regional sample size was relatively low, we can address questions related to flow magnitude (Poff & Zimmerman 2010), flow variability (Stewardson & Gippel 2003; Samuelson & Rood 2004), and the frequency and duration of low flow events (Rolls, Leigh & Sheldon 2012). That one of the extracted factors was related to low flow hydrology, which is most likely to be affected by future water abstraction, was promising because we can now address primary water management concerns. Indices that are highly correlated with the extracted factors, or the factor scores themselves, can be taken forward into ecological studies, with a high degree of confidence as they were derived from robustly estimated flow indices.

2.5.4 Conclusions

We believe this structured, defensible method for characterising flow gradients at a regional scale will lead to robust studies of ecological responses to flow regime that can inform general flow-

ecology relationships that fit within the broader Ecological Limits of Hydrologic Alteration Framework (Poff *et al.* 2010) and can be used for setting environmental flows (Davies *et al.* 2014). By addressing sources of uncertainty before the ecological studies are carried out, we can invest our time and resources into the most fruitful model systems for improving our fundamental understanding of river ecology.

2.6 Acknowledgements

Chapter 3 - Alien and native plant richness and abundance respond to different environmental drivers across multiple gravel floodplain ecosystems

3.1 Abstract

Aim: To assess whether native and alien plant cover and richness respond similarly to flow regime, propagule pressure, climate, and floodplain characteristics in highly-dynamic braided river ecosystems.

Location: Canterbury, New Zealand

Methods: A regional, multi-scale survey was conducted across 19 braided river floodplains in multiple catchments. We measured alien and native cover and richness across gradients of flow regime (flow magnitude, variability, and high/low-flow events), propagule pressure (inferred from land-cover), climate, and local-scale floodplain substrate and topography. Boosted regression trees were used to determine the relative and absolute importance of these variables on plant cover and richness.

Results: The floodplain ecosystems were highly invaded with 154 alien species and only 31 natives. Alien cover was higher in rivers with larger maximum flows, in plots with fine substrate texture, and at higher local riverbed elevations. Alien richness increased as the variability of winter flows increased, and followed a humped-shaped relationship with riverbed elevation. In contrast, native species richness and cover were both shaped primarily by climate and land-cover, higher in cooler and wetter areas with more adjacent native vegetation.

Main conclusions: Alien and native richness and cover were shaped by different variables, so managing the ecosystem (e.g. flow regime) to mitigate aliens would not necessarily promote natives. In contrast, promotion of natives will require considerations of propagule supply and whether extant native species are suited to low altitude climatic conditions. Aliens were associated with predictors that approximate disturbance processes while natives were restricted by predictors that approximate propagule pressure and climate. Increased flow variability in winter could lead to an increase in the number of aliens; conversely, flow stabilisation is likely to allow problematic invaders to increase in cover locally.

3.2 Introduction

Whether alien and native plant species typically respond similarly to environmental drivers such as climate, land-cover and disturbance remains an open question (Davis *et al.* 2011; Simberloff 2011;

Hulme *et al.* 2015; Thomas & Palmer 2015). On one hand, plant communities with high alien richness have often been found to also have high native richness (Stohlgren, Barnett & Kartesz 2003; Fridley *et al.* 2007) which suggests that similar environmental drivers shape the richness and abundance of alien and native species. Yet other studies have found that while alien and native richness are often driven by the same variables, the nature of the underlying relationships can differ (Marini *et al.* 2009, 2012; Polce *et al.* 2011; Greet *et al.* 2013; Tomasetto, Duncan & Hulme 2013; Pouteau, Hulme & Duncan 2015). These divergent perspectives have been attributed to differences in the spatial scale at which relationships were examined (Fridley *et al.* 2007) yet, to date, few studies have attempted to assess the drivers of native and alien plant richness or abundance at different spatial scales (Brooks, Lockwood & Jordan 2013). Depending on the spatial scale examined there are potentially three distinct scenarios by which the native and alien richness or abundance might respond to ecological drivers: they may 1) respond to the same drivers in the same direction, 2) respond to the same drivers in opposite directions, or 3) respond to completely different sets of drivers. Each of these scenarios has distinct implications for ecosystem management to mitigate the impacts of aliens and promote natives. Thus, comparative studies of the ecological drivers of native and alien plant species distribution and abundance assessed at different spatial scales remain critical to inform ecosystem management practices which aim to limit human-mediated invasion and promote native species (Catford *et al.* 2012b).

Riparian ecosystems provide an excellent opportunity to address how alien and native floras respond to underlying ecological gradients because they are disproportionately susceptible to invasion as a result of their disturbance and resource dynamics (Nilsson & Berggren 2000; Richardson *et al.* 2007; Pyšek *et al.* 2010). Disturbance is a dominant feature of riparian ecosystems in the form of flow regime variation (Lake 2000) and is central to hypotheses as to what promotes ecosystem invasibility (Catford *et al.* 2009; Jauni *et al.* 2015). Riparian ecosystems are of high biodiversity value globally, yet the flow regimes of these systems have been altered with uncertain impacts on alien and native species (Poff & Zimmerman 2010). Theoretical and empirical predictions suggest that any alteration of natural flow dynamics should, on average, negatively impact natives and promote aliens (Nilsson *et al.* 1991; Decamps, Planty-Tabacchi & Tabacchi 1995; Poff *et al.* 1997; Lite, Bagstad & Stromberg 2005; Catford *et al.* 2011). However, there has yet to be an evaluation of how native and alien floras simultaneously respond to flow regime and how this might be modified by differences in climate, land-cover, and substrate characteristics across multiple floodplains and catchments.

We carried out a multi-scale study of the ecological drivers of alien and native, richness and cover in New Zealand braided riverbeds, ecosystems of high global conservation value (Holdaway *et al.* 2012). A previous biogeographic scale study in similar systems suggested that aliens were associated with human land-cover and temperate climates whereas natives were more prevalent in

higher altitude, higher rainfall, less modified landscapes (Williams & Wiser 2004). Our study expands on their work by examining alien invasion and native persistence across gradients of flood disturbance and drought, and more explicitly includes the effects of local floodplain drivers at local scales. By examining the relationships between environmental variables and cover and richness at a local scale (1-m^2 plots) and regional scale (geographic extent >200 km^2) we aimed to disentangle the key drivers of native and alien communities across broad differences in landscape context and river flows. This not only provides the opportunity to assess whether species richness and cover are a function of native and alien status but also addresses the feasibility of interventions to limit plant invasions and promote or restore native plant diversity. At the local scale, we expected disturbance, inundation, and resource availability to be important predictors of where species occur (Table 3.1; Bertoldi, Drake & Gurnell 2011; Catford & Jansson 2014). At the regional scale, we expected that, compared to native species, alien species richness and abundance would be higher in, or adjacent to, human-modified landscapes, in low-altitude temperate climates, and/or in areas of high resource availability/disturbance (Table 3.1; Pearson & Dawson 2003; Chytrý *et al.* 2008; Polce *et al.* 2011; Marini *et al.* 2012; Pyšek & Chytrý 2013).

Table 3.1. Predictor variables of alien and native cover and richness and their scale of measurement, ecological rationale (hypothesised processes associated with measured predictors) and the hypothesised direction of the relationship between the predictor and alien cover (AC), alien richness (AR), native cover (NC) and native richness (NR). These represent simplified expectations as some predictors were expected to have non-linear relationships with the responses. All predictors were continuous except human disturbance which was presence/absence. Land-cover variables were continuous proportions ranging (0-1).

Predictor	Scale	Ecological Rationale	AC	AR	NC	NR
Land-use						
% Cropping (10 km)	Site	Propagule source for alien species	+	+	-	-
% Exotic Grassland (10 km)	Site	Propagule source for alien species	+	+	-	-
% Artificial Surfaces (10 km)	Site	Propagule source for alien species	+	+	-	-
% Native (10 km)	Site	Propagule source for native species	-	-	+	+
Climate						
Growing Degree Days (10°C)	Site	Plant phenological response; climate niche	+	+	-	-
Growing Season Precipitation	Site	Water availability in non-flood times	+	+	+	+
GS Cumulative Water Deficit	Site	Water stress in non-flood times	-	-	-	-
Flow Regime						
Median Daily Flow (Ma4)	Reach	Disturbance	+	+	+	+
CV August Flow (Ma26)	Reach	Disturbance variability (winter flow variability)	+	+	-	-
Low Flow Days <MDF/3 (Fl7)	Reach	Drought frequency	-	-	-	-
Duration LF <MDF/7 (Dl18)	Reach	Drought intensity	-	-	-	-
CV Max 7day Means (Dh8)	Reach	Disturbance variability	+	+	-	-
Maximum Annual Flow (Mh1)	Reach	Disturbance magnitude	-	-	-	-
Floodplain Variables						
Substrate Texture	Plot	Resource availability; Hydrologic disturbance intensity	-	-	-	-
Riverbed Elevation	Plot	Disturbance and drought gradients	+	+	+	+
Distance to Water	Plot	Disturbance and drought gradients	+	+	+	+
Human Disturbance (Binary)	Plot	Disturbance due to engineering or recreation	-	-	-	-
General						
Season (Sampling Day)	Day	Control for seasonal effects	+	+	+	+
Altitude	Site	Propagule pressure; Human population density; Climate	-	-	+	+

The header "Expectation" spans the AC, AR, NC, NR columns.

3.3 Methods

3.3.1 Study system

Braided riverbed ecosystems were studied in the Canterbury region of New Zealand. The riverbed substrate is generally unconsolidated sedimentary rock (glacially influenced greywacke) eroded from steep upper catchments in the Southern Alps and their foothills. The substrate, steep topography and frequent heavy rainfall causes rivers with multiple mobile channels to form in a floodplain of frequently reworked gravels. Intense bed transforming flows occur frequently, making disturbance a dominant characteristic of these ecosystems (Gray & Harding 2007; Hicks *et al.* 2008). Over 60% of the floodplain flora was found to be alien, introduced to New Zealand since the mid-19th century (Williams & Wiser 2004). Native species persist, especially at higher altitudes, dominated by cushion plants (e.g. *Raoulia hookeri* Allan), herbaceous perennials (e.g. *Epilobium melanocaulon* Hook.) and sub-shrubs (e.g *Muehlenbeckia axillaris* (Hook.f.) Endl.). Rivers around the region have been progressively instrumented with flow recording stations ("gauging stations"); 15-minute continuous time series of flows from 7 to 40 years before present provide a rich dataset with which to quantify disturbance as characterised by flow regimes (Brummer *et al.* 2016a). The region also varies in adjacent land-cover with low and mid-altitude areas dominated by arable and pastoral agriculture, and less-modified native ecosystems present at higher altitudes.

3.3.2 Sampling scheme

A spatially nested sampling scheme was used to capture regional climate and land-cover variation, river-specific flow gradients, and local floodplain characteristics (Figure 3.1). This allowed us to evaluate the relative importance of environmental gradients at two scales in shaping alien and native plant species richness and cover. Nineteen gauging stations were selected where sufficient flow data were available to describe flow regimes and spanned regional climate and land-cover gradients (Brummer *et al.* 2016a). For each gauging station, a single reach (river segment) was delimited by upstream and downstream tributaries to ensure that the flow metrics would be as applicable as possible to each reach. For each of the 19 reaches, three sample sites were established between 500 and 2,000 metres apart from one another to encompass both substrate and floristic variation. Each site was sampled in a single day but the different sites within a reach were sampled randomly at early, mid or late season to account for seasonal effects. Within each site, three transects were sampled, perpendicular to the floodplain corridor. Transects were spaced 125 m apart and spanned the entire floodplain, ending at either armoured banks or forested riparian corridors. A 1-m^2 plot was randomly located along each five metre section of the transect, resulting in a total of 2,930 plots.
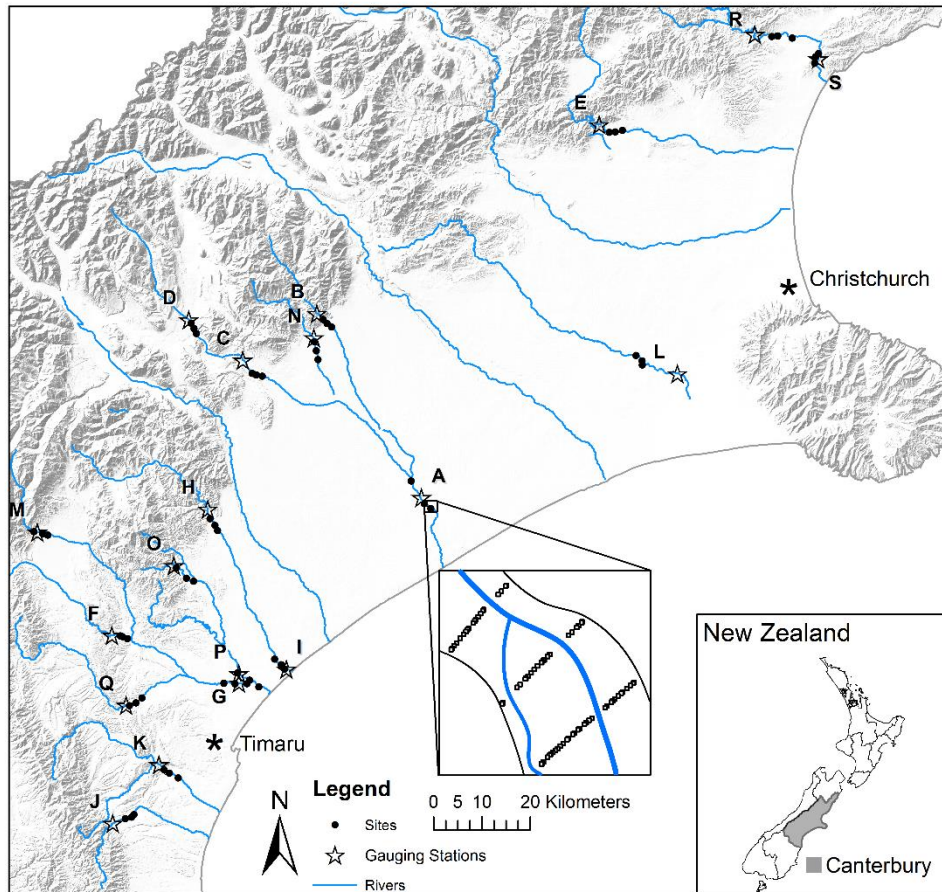
Figure 3.1. Sampling locations for the vegetation survey in the Canterbury province of New Zealand (grey area in country overview). Plots were sampled along three transects perpendicular to the dominant direction of river flow (inset map) at three sites randomly spaced 500 to 2,000 metres apart (black circles) on each of 19 river reaches (A-S) that contained a gauging station (hollow stars) with at least seven years of flow records.

3.3.3 Vegetation data

The same observer visually estimated aerial percent cover of each vascular plant species in all 1-m^2 plots to the nearest 1%. Response variables of interest were percent cover and species richness for native and alien species. Cover estimates were summed across species and were log-transformed after adding 0.25% to account for zeros in the response and achieve approximate normality (0.5% was the smallest cover recorded if a species was present in a plot but at less than 1% cover). Species that occurred in two or fewer plots in the study were removed to minimise the influence of uncertain observations (61 aliens and 35 natives).

3.3.4 Predictor variables

Predictors were chosen based on the set of processes we hypothesised to be shaping species distributions and abundance in the riverbeds (Table 3.1). Analysis of the ecologically-relevant aspects of flow regime for the rivers in our study region revealed three primary axes of variation: flow magnitude, flow variability, and low flow events (detailed in Brummer *et al.* 2016a). Six specific flow indices related to these axes of hydrologic variability were chosen that loaded most strongly on the three factors (following Olden & Poff 2003; Kennard *et al.* 2010): flow magnitude (median daily flow and maximum annual flow), flow variability (variability in winter flows, the variability in 7-day mean flow); low flow events (low flow frequency and duration).

The character of the regional species pool was estimated using land-cover adjacent to the sampling sites (Landcare Research 2014). Artificial surfaces, cropping, and alien grassland land-cover were expected to be associated with different suites of alien species that could invade riverbeds. Similarly, native propagule pressure was captured using adjacent native land-cover. Land-cover variables were defined as the proportion of cells (10 m resolution) in a radius around a sample site occupied by a given land cover category. We built models with land-cover calculated at three radii (2, 5 and 10 km) while controlling for all other predictor variables. Radius did not matter for alien cover or richness, but 10 km land-cover variables were best for native cover and richness models (see Appendix A, Figure A.1), thus all analyses presented here use 10 km land-cover variables.

We included three major axes of climatic variation relevant to plants: growing season rainfall, growing season water deficit and average annual growing degree days. Climate data were derived from National Institute of Water and Atmosphere 500 m resolution interpolations. Altitude was considered (from a digital elevation model) as it is an important predictor of alien and native species abundance, although it can be hard to interpret as it incorporates both climatic and land-cover differences (Overton & Lehmann 2003; Williams & Wiser 2004).

To account for floodplain scale disturbance, inundation, and resource availability, we measured the elevation of each plot relative to elevation of the river channel at base flow (referred to as "riverbed elevation"). Riverbed elevation was estimated using a high resolution Global Positioning System (GPS; Trimble GeoExplorer® 6000 series) at each plot. To calculate riverbed elevation, the edge of all channels in each transect were marked with the GPS and the elevation of each plot was subtracted from the elevation of the nearest river point within a transect. Points that had >10 cm vertical error were excluded from the analyses to minimise the effects of measurement error (total sample size was 2,592 after these 338 plots were removed). The distance to water was also calculated as the minimum distance to a channel edge GPS point within the same transect. A substrate texture index was calculated from field estimates of the percent cover of sediment and stones in five different size classes within each plot (continuous variable following Williams & Wiser 2004). Evidence of human disturbance (e.g. excavation of river gravels, recreational motor sport activity) was included as presence/absence. See Appendix A, Table A.1 for correlations among the predictor variables.

3.3.5 Analytical methods

Boosted regression trees (BRTs) were used to evaluate the effects of the predictor variables on alien and native cover and richness (Elith, Leathwick & Hastie 2008). Boosted regression trees are flexible explanatory and predictive modelling tools. They avoid many of the limitations of linear modelling by accounting for interactions, non-linear responses, and various types of response variables. They are robust to outliers and provide tools to describe the relative importance of predictors, as well as methods to visualise their shape and effect size. For our purposes, Gaussian loss functions were specified for BRTs that modelled log-transformed cover as these data were best approximated as normally distributed and Poisson loss functions were specified for the species richness models as count data are generally well approximated by Poisson error distributions.

Boosted regression trees are optimised by determining the complexity at which independent (out-of-sample) prediction error changes from decreasing to increasing to avoid overfitting that compromises model generalisability. This is typically achieved using 10-fold cross-validation, however, because of our nested spatial sampling design we expected residual dependence between plots to be highly likely. Thus, we used custom folds at the scale at which residuals were independent, which is analogous to h-block cross-validation (Burman et al. 1994), where h-blocks are spatial subunits larger than the scale of residual autocorrelation. Interrogation of residual spatial autocorrelation plots (semivariograms) suggested residual correlation at the scale of plots and transects but not at the scale of sites. Thus, we considered sites to be independent for the cross-

validation routine and they were assigned randomly to 10 folds when fitting BRT models using the 'gbm.step' function in the 'dismo' package in R v3.1.1 (R Core Team 2014; Hijmans *et al.* 2015). We also plotted model residuals for each response variable grouped by river reach and site to determine whether there remained explainable variation at each of those scales (see Appendix A, Figure A.2; methods following Buston & Elith 2011). Some of the residuals were positively or negatively biased at the scale of sites and river reaches suggesting residual explainable variation at those scales. This was not considered an issue statistically because of our cross-validation and null modelling approaches (see below) to determining statistical significance.

Determining statistical significance of predictors measured at multiple scales can be challenging as this increases the chance for spurious relationships to be driven by clustered sampling. Thus, we adopted a null modelling approach to determine the null distribution of relative importance for each predictor. The null model was designed to determine the relative importance values we could expect randomly, given the observed set of values for each of the predictors. To achieve this, each predictor was permuted at the scale at which it was measured, while holding all other variables in the model at their observed values. By permuting one predictor at a time, this maintained the importance of the other predictors in the model, only altering the relative influence of the permuted predictor. This was essential as variable importance is measured relative to all the other predictors in the model. Predictors measured at the river scale were permuted at the river scale (e.g. the 19 unique values for each flow variable were permuted across rivers and one permuted value was applied to all the plots in that river). This maintained the clustered structure of the variables that were measured at site and reach scales, and thus any random effects of clustering were captured in the null distribution. We used a one-tailed test and considered any predictor with a relative importance value greater than the 95% quantile of the null distribution to be statistically significant.

An additional analysis to determine the absolute explanatory power (cf. relative importance as above) of each of the classes of predictors was carried out via a set of model comparisons. Model explanatory power was measured by cross-validation R^2 ("R2cv"; percent of variation explained in validation/withheld data; Efron 1986) for models built using each class of variables alone (e.g. flow regime, land-cover, climate or floodplain), compared to a model built using all variables. Season was included in all models to control for seasonality, while altitude was excluded as it is strongly associated with hydrological, climate and land-cover variables (see Appendix A, Table A.1). An analysis showed that overall model performance was not significantly reduced when altitude was excluded suggesting its effect is accounted for in the land-cover and climate predictors.

3.4 Results

3.4.1 General patterns

There were 154 alien and 31 native species found in more than two plots. The aliens were by far the most frequent, with 42 alien species occupying more transects than the most frequent native species (Figure 3.2). Of the 154 alien species, 39 are classified as environmental weeds, species with real or perceived impacts on natural areas, and of concern to management (Figure 3.2; Howell 2008). Per plot alien species richness ranged from 0 – 39 while native richness ranged from 0 – 8. Alien cover and richness were positively correlated (Spearman rank correlation (rho; 2,592 pairs of plots for all correlations) = 0.83; p ≈ 0) as were native cover and richness (rho = 0.95; p ≈ 0). Alien richness and native richness were also weakly positively correlated (rho = 0.31; p ≈ 0) as were alien cover and native cover (rho = 0.24; p ≈ 0). The five alien species that occurred most frequently were: *Plantago lanceolata* L. (34%), *Holcus lanatus* L. (28%), *Cytisus scoparius* L. (Link) (27%), *Festuca rubra* L. (26%) and *Trifolium repens* L. (25%). The five most frequent natives were: *Pseudognaphalium luteo-album* (L.) Hilliard & B.L.Burtt (6%)*, Muehlenbeckia axillaris* (Hook. f.) (5%)*, Raoulia hookeri* Allan (5%)*, Epilobium microphyllum* A. Rich. Essai (4%)*,* and *Epilobium melanocaulon* Hook. (2%). Only the latter three are endemic to New Zealand and *Pseudognaphalium luteo-album* has a cosmopolitan distribution (GRIN, http://www.ars-grin.gov).
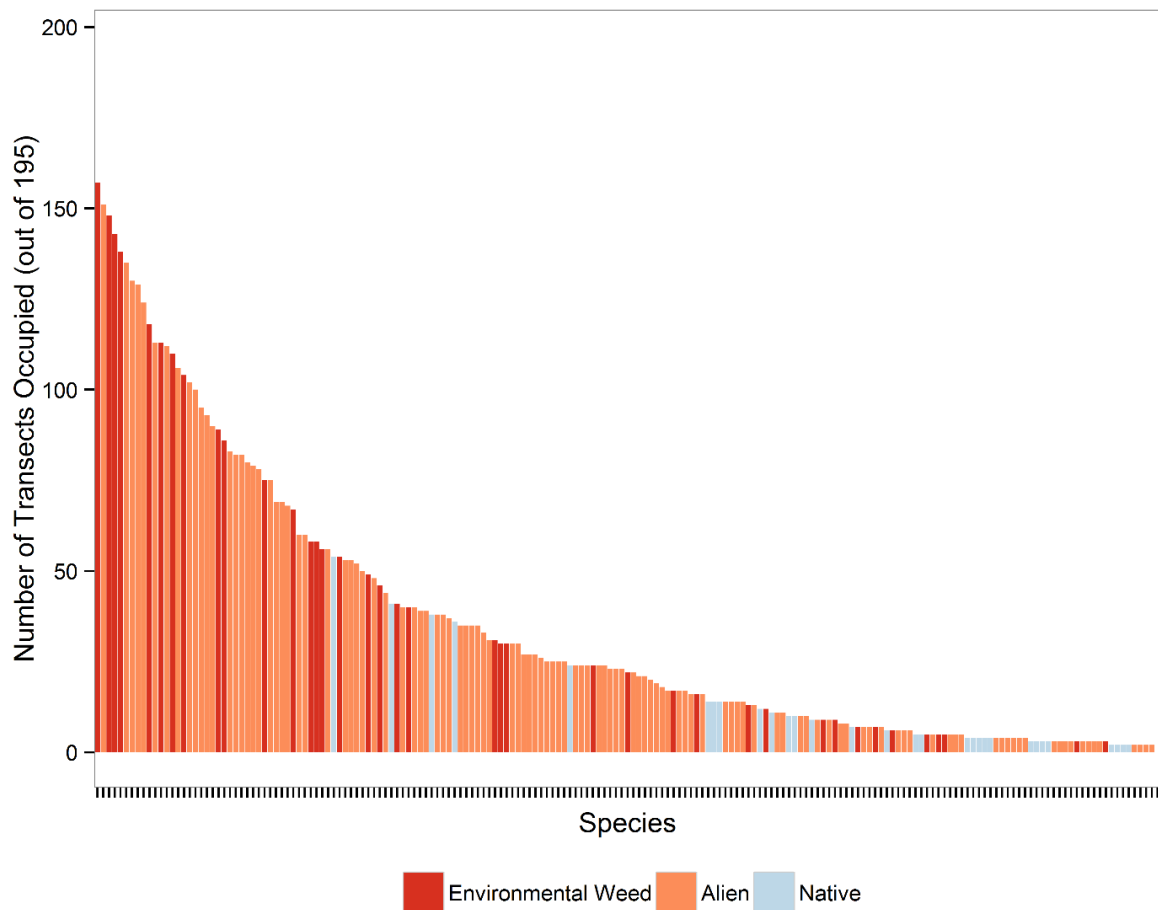
Figure 3.2. Number of transects occupied by 185 species found in the gravel riverbed plant survey classified by origin (ordered from most to least frequent). Environmental weeds (all of which are alien) were classified from a consolidated list of species that have real or perceived environmental impacts in natural areas in New Zealand and are of concern to the Department of Conservation (Howell 2008). Occupancy frequency was counted by transect which are at least 125 metres apart. Thus, following Richardson *et al.* (2000), species in more than two transects could be considered invasive.
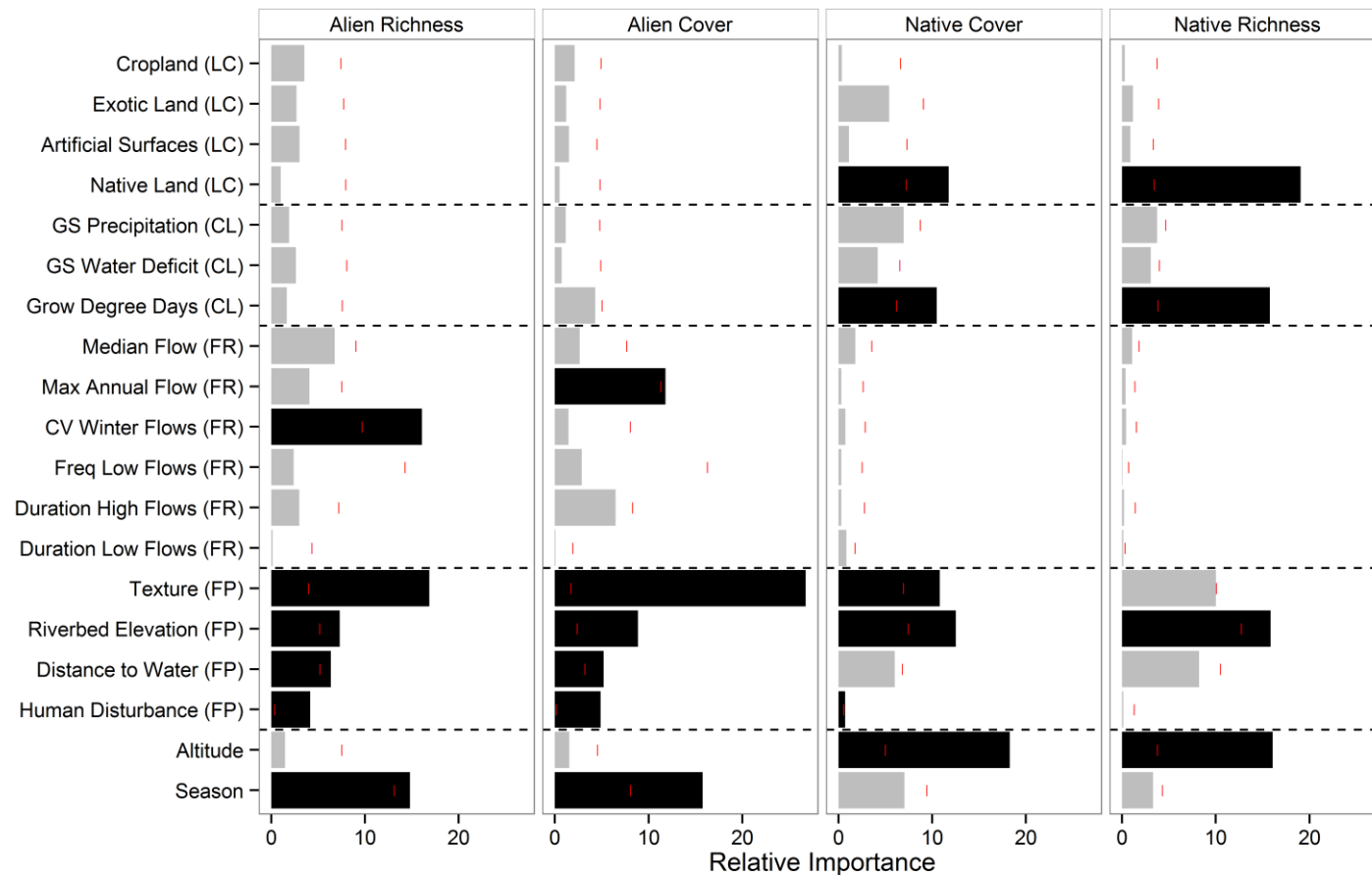
Figure 3.3. Relative importance of the 19 predictors of richness and cover of alien and native species in braided river floodplains. Predictors are grouped from top to bottom by land-cover (LC), climate (CL), flow regime (FR), and floodplain (FP) factors. The same set of predictors were used for each response variable so the magnitude of relative importance is comparable between responses. Black bars depict significant effects compared to the null distribution of relative importance. The 95% quantile of 500 permutations of the null relative importance distribution is shown as a vertical bar. (See Table 3.1 for predictors; GS - growing season, CV – Coefficient of Variation)
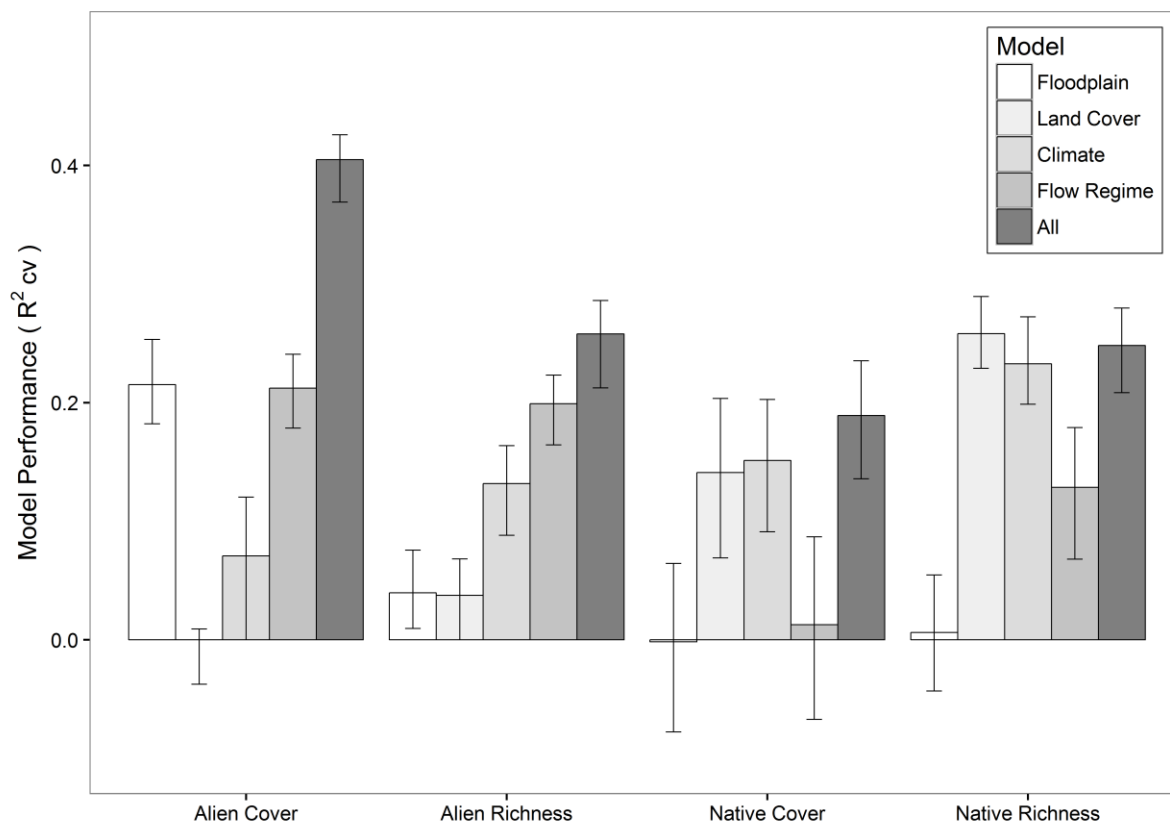
Figure 3.4. Absolute model performance as measured by R²cv (from 10-fold cross validation) for boosted regression tree models that use just floodplain, land-use, climate or flow predictors separately, and a model that includes all the predictors. This effectively partitions out the contribution of each of the variable classes to the overall model performance to better understand the drivers of the four different response variables (alien and native x cover and richness). Altitude is not included in these models because it was correlated with both climate and land-use predictors, making its variable class ambiguous. Models with all predictors except altitude were as good as models with altitude suggesting the effect of altitude is captured by the more proximal climate and land-use predictors. Julian date is included in all models to control for seasonal effects. Error bars are the 95% quantile intervals from 500 runs of the model fitting/cross-validation routine (bars represent the mean).
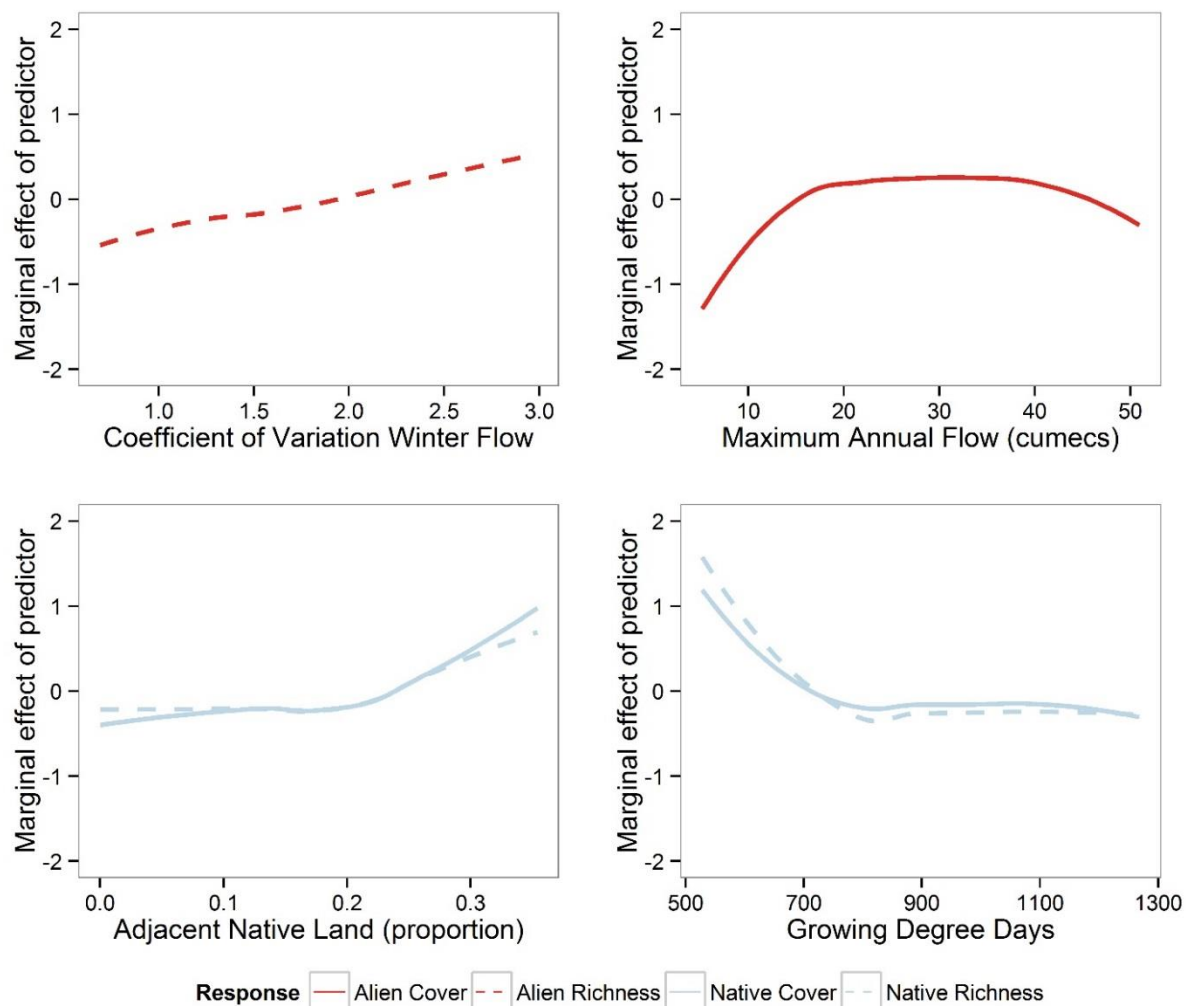
Figure 3.5. Marginal effects of flow, land-use and climate predictors on alien and native cover and richness (only significant effects are plotting thus all lines are not in all panels). The y-axis is a standardized effect size (holding all other predictors at their mean value) while the x-axis is the range of the predictor in the dataset. Lines are the mean prediction from 100 runs of the boosted regression tree model fitting routine.
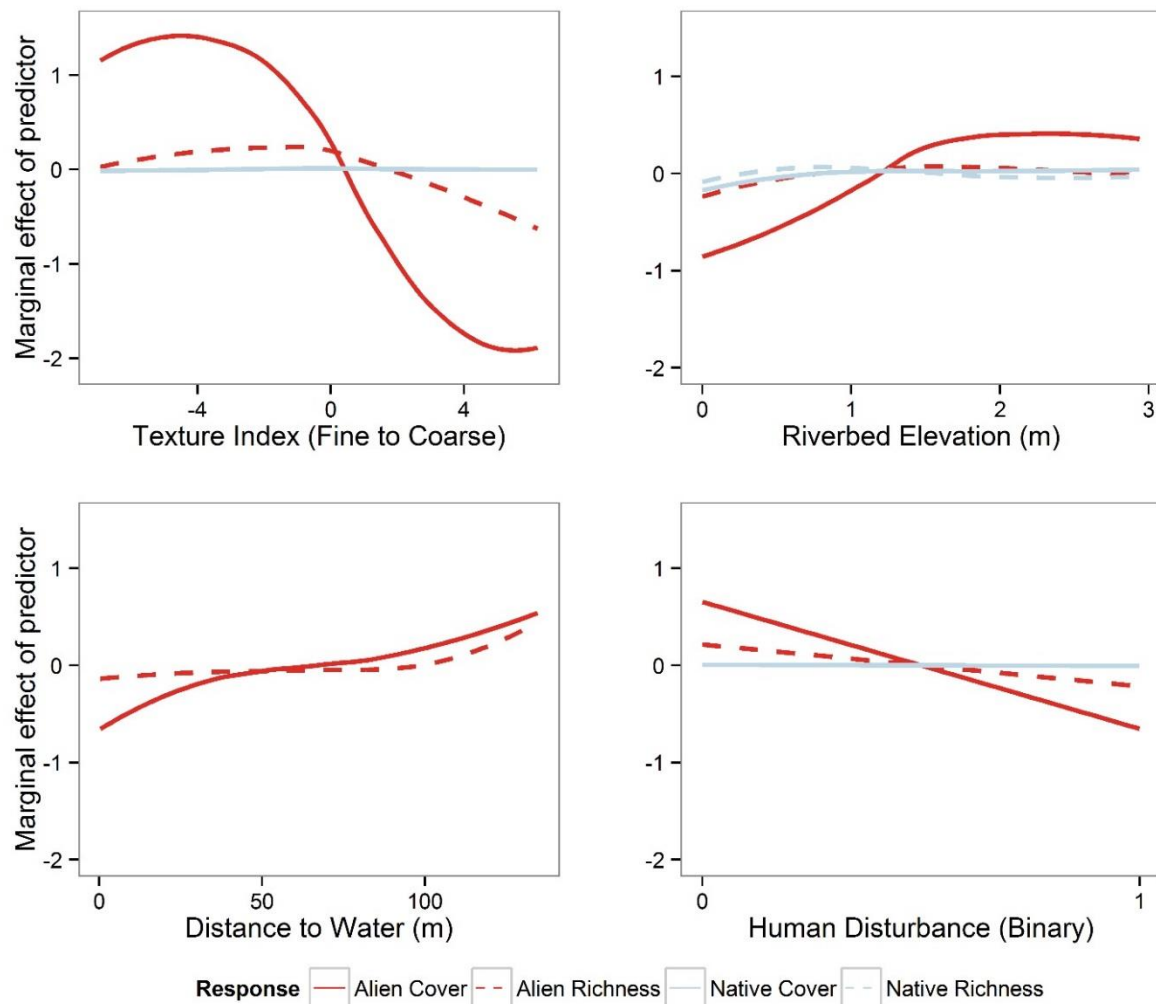
Figure 3.6. Marginal effect of significant floodplain predictors on alien and native cover and richness. The y-axis is a standardized effect size (holding all other predictors at their mean value) while the x-axis is the range of the predictor in the dataset. Human disturbance is a binary variable (0 - no disturbance and 1 - disturbance). Lines are the mean prediction from 100 runs of the boosted regression tree model fitting routine.

3.4.2 Predictors of alien and native cover and richness

Season was a significant predictor of alien cover and richness (Figure 3.3), displaying a positive asymptotic relationship with alien cover and richness saturating around the 40-50th sampling day but was not a significant predictor of native cover and richness. Season was retained in model comparisons to control for the seasonal effects.

The relative importance analysis revealed winter flow variability was a significant predictor of alien richness whereas maximum annual flow was a significant predictor of alien cover (Figure 3.3). Alien richness and cover were significantly associated to all local variables (texture, riverbed elevation, human disturbance and distance to water). No flow variables were significantly associated with either native richness or cover, however significant relationships between native cover and richness were found with growing degree days and the percent adjacent native land (Figure 3.3). Native richness was associated with riverbed elevation, and native cover was associated with texture, though the effect size was small relative to that of aliens (Figure 3.3).

In terms of absolute model performance (measured by out-of-sample R^2), flow regime explained approximately 20% of the overall variation in alien cover and richness (Figure 3.4). Land-cover explained a small amount of variation in alien richness but not alien cover, though this was due to partial confounding between winter flow variability and native land-cover. Floodplain scale variables explained over 20% of the variation in alien cover and around 4% of the variation of alien richness (Figure 3.4), but did not contribute to absolute model performance for either native response variable despite having weak but significant contributions in the analysis of relative importance. Climate and land-cover explained approximately 15% of the overall variation in native cover and 22% of the variation in native richness. Land-cover was equally explanatory of variation in native cover and richness as climate (Figure 3.4). Overall, examination of absolute model performance highlighted that patterns in alien richness and cover were shaped strongly by flow regime and to a lesser extent local floodplain variables; in contrast, native richness and cover were more strongly associated with neighbouring land-cover and climate variables (Figure 3.4).

At the river reach scale, the effects of the significant predictors demonstrated linear, threshold and humped relationships (Figures 3.5 & 3.6). Alien richness increased linearly as winter flow variability increased, while alien cover had a humped relationship to maximum annual flow, with low cover at low and high ends of the maximum flow gradient (Figure 3.5). Native richness and cover were associated to adjacent native land and growing degree days by threshold relationships, with highest richness and cover in areas with more adjacent native land and fewer growing degree

days (Figure 3.5). At the floodplain scale, there were also non-linear response curves (Figure 3.6). Although native cover and/or richness were significantly associated with texture, riverbed elevation and human disturbance, the magnitude of change across any of the variables was small relative to alien cover and richness (Figure 3.6). Alien richness was greatest at intermediate textures, riverbed elevations and absent human disturbance. Alien cover was greatest at the fine end of the texture gradient, high in the river cross section and absent human disturbance (Figure 3.6).

3.5 Discussion

The floodplain ecosystems we studied were heavily invaded with over 79% of the plots sampled containing at least one alien species, many of which are classed as environmental weeds and had greater occupancy frequencies than native species (Figure 3.2). Our study reaffirms the assertion of Williams & Wiser (2004) that NZ braided rivers are among some of the most invaded ecosystems globally and even more so than other riparian ecosystems around the globe (Planty-Tabacchi *et al.* 1996; Planty-Tabacchi, Tabacchi & Bonillo 2001; Catford *et al.* 2012b). Our finding that natives were much lower in abundance and distribution than aliens, even when surrounded by mostly intact ecosystems, supports the view that the native flora lack disturbance-adapted species because of geographic isolation, habitat configuration and the absence of large mammalian herbivores over evolutionary time scales (Craine 2009; Wilson & Lee 2012).

Richness and cover of both alien and native species were driven by distinctly different ecological variables in the braided river floodplains we sampled. At the broadest scale where we examined average differences in cover and richness among river reaches, no predictors were shared between the New Zealand alien and native plant communities. Native richness and cover were associated with climate and land-cover while alien richness and cover were respectively associated with winter flow variability and maximum annual flow magnitude. This contrasts with other studies in which alien and native richness have been associated with similar drivers in the same direction (Fridley *et al.* 2007), or the same variables but in opposite directions (Polce *et al.* 2011; Greet *et al.* 2013; Tomasetto *et al.* 2013; Pouteau *et al.* 2015). Our findings highlight why considering cover can provide essential information, especially in the context of alien species, as alien richness and cover were shaped differently by both regional and local drivers. Although our results differed from the findings of these other studies, they did match our expectation that natives and aliens would differ in their responses to flow regime, land-cover, and climate, as broad-scale climate and land-cover variables have previously been found to act on New Zealand alien and native communities in different ways (Atkinson & Cameron 1993; Williams & Wiser 2004; Pouteau *et al.* 2015).

That aliens were associated with variability in winter floods and maximum annual flow, which captured variation in disturbance regimes among rivers, is consistent with the idea that alien species distribution and abundance is strongly controlled by disturbance (Lite *et al.* 2005; Catford *et al.* 2009; Jauni *et al.* 2015) and with studies that have found river regulation is associated with more aliens and fewer natives (Greet *et al.* 2013). We expected aliens on average to be better suited to more disturbed rivers, with larger more unpredictable floods, due to pre-adaptations to deal with disturbance (Lite *et al.* 2005; Catford *et al.* 2009, 2012a). Our study demonstrates that even semi-natural disturbance gradients (unregulated flow regimes) influence alien species richness and cover which contrasts to the majority of studies that focus on anthropogenic disturbance either though agriculture or ecosystem modification (e.g. regulated flow regimes). The relationship between winter flow variability (which is when most flooding events occur in New Zealand) and alien richness was linear, which did not conform to the intermediate disturbance hypothesis (IDH) prediction of a diversity peak at intermediate levels of flow disturbance (Catford *et al.* 2012a). However, we sampled rivers across the realistic range of this flow measure, suggesting that the alien flora may be so disturbance-adapted that we never observe the expected IDH curve (Catford *et al.* 2012a). Such adaptations (e.g. traits like fast relative growth or prolific seed production and dispersal) enable aliens to establish at the most disturbed end of the disturbance gradient in these river systems (Catford & Jansson 2014). Regardless of the specific mechanisms, alien richness was greater in rivers with greater winter flood variability, the time of year when the majority of large flood events occur in the systems. This suggests that more variable flood disturbance regimes could facilitate the invasion of more alien species in this system.

Although we expected more alien species in areas adjacent to and alien dominated cropland, forestry and grasslands (Vilà & Ibáñez 2011) and at lower altitudes where the climate was warmer (Marini *et al.* 2012) due to propagule pressure, we found no strong effect of surrounding land-cover or climate on alien species richness or cover. This differed from Williams & Wiser (2004), who found adjacent cropland and buildings were associated with alien communities in similar New Zealand braided riverbeds. However, they investigated composition rather than richness and cover, and sampled sites that extended into intact native communities. Thus, our results suggest that alien richness and cover, within the extensively-modified landscape of lowland braided rivers, are not limited by climate and propagule supply. In contrast, native richness and cover were strongly associated with adjacent native land-cover and climate, which followed the pattern found by Williams & Wiser (2004) and is likely driven by a combination of dispersal and climate limitation, as many of the extant natives in braided rivers are adapted to mountain rock-slip environments (Wardle 1991).

At the local riverbed scale, areas more distant from the river channel, at higher riverbed elevation and with finer textured substrate (which were all correlated with each other) had higher alien cover, while alien species richness followed a hump shaped relationship with peak richness at an intermediate riverbed elevation. This pattern matches both theoretical models and empirical studies that show that water level/riverbed elevation strongly controls recruitment processes with greatest recruitment and diversity at intermediate levels of inundation or drought (Nilsson *et al.* 1989; Gurnell, Bertoldi & Corenblit 2012; Fraaije *et al.* 2015a; b). Although the richness pattern is likely partially due to drought effects on recruitment, based on our field observations it may also be due to competition when *Cytisus scoparius* L. and other nitrogen-fixing woody plants, which formed closed canopies at the higher end of the riverbed elevation continuum. In contrast, riverbed elevation and texture were relatively unimportant for native richness and cover. The fact that at the floodplain scale, aliens occupied a much broader breadth of floodplain conditions than natives, and areas that were more removed from the influence of river flows had higher alien cover, suggest that if rivers were significantly altered to reduce the disturbance regime (e.g. by damming or diversion) this may facilitate increasing cover of aliens as is frequently found in other systems (Richardson *et al.* 2007; Caruso *et al.* 2013; Garssen *et al.* 2015). This type of a change in flow would likely alter the low riverbed elevation areas in the floodplain to be more similar to the conditions currently at high riverbed elevation that have higher alien cover.

When managing for the joint goals of promoting native biodiversity and constraining the spread of alien species, strategies will need to address these different drivers of alien and native floras. This is a distinctly different challenge than managing ecosystems when aliens and natives are driven by the same variables but with opposite effects, which has been found in other riparian studies where aliens were promoted by flow alteration while natives were negatively impacted (e.g. Catford *et al.* 2011, 2014; Greet *et al.* 2013). In those situations, managing for natives implicitly manages against aliens and vice versa (Greet *et al.* 2015). This is not the case for the braided rivers in New Zealand. Promotion of natives will require consideration of increasing propagule supply to establish populations in lower altitude reaches and determining whether this is even possible without restoration of native vegetation on adjacent river margins. Furthermore, our study suggests that most extant native species in the rivers are more suited to alpine climates (Wardle 1991). This begs the question as to whether the remaining native taxa would even be suited to lower altitude environments except in the form of casual 'sink' populations.

3.6 Conclusions

Consistent with our original expectations, alien and native floras responded differently to flow regimes, however, the majority of this effect was likely mediated through propagule pressure (or lack thereof for natives) rather than ecophysiological differences between the floras. Alien species responded to flow disturbance gradients supporting the disturbance hypotheses in invasion ecology (Catford *et al.* 2009). Contrary to expectation, alien richness and cover were not related to human land-cover, suggesting aliens are not strongly dispersal limited in the region. Finally, at the river scale, aliens and natives were driven by completely different variables, whereas at floodplain scales similar variables were associated with aliens and natives but affected them in very different ways.

From a management perspective, the primary lesson our study highlights is: alien and native floras can be driven by different variables in the same ecosystem; thus, practitioners cannot presume managing against aliens will in turn promote natives. The contrasting effects of drivers across scales suggests future flow management that stabilises flows (e.g. flood harvesting/dams) may decrease the total number of aliens in a river, but may allow more problematic alien species to increase in cover and impact by altering local disturbance processes (Hicks *et al.* 2008). Further studies should simultaneously compare native and alien species richness and cover across multiple scales as we found drivers of cover and richness can vary, those differences can be informative ecologically, and cover is many times more informative from a management perspective (Catford *et al.* 2012b). This will lead to more generality as to when natural resource managers should expect aliens and natives to be associated with the same or different ecological drivers and how those drivers shape alien and native species distribution and abundance.

3.7 Acknowledgements

Chapter 4 - Growth and regenerative traits explain level of invasion of alien plant species across disturbance and drought gradients in floodplain ecosystems

4.1 Abstract

Conceptualising species by their function is one potential way to reduce the complexity of understanding multi-species invasions into ecosystems. By examining the traits of species that come to dominate ecosystems and understanding how species with different combinations of traits respond to environmental gradients, we may be able to prioritise species for management and predict the outcome of environmental change. We took a functional trait approach in a disturbance prone ecosystem to ask: do growth and regenerative traits predict overall alien plant frequency and do those same traits predict how alien species respond to disturbance and drought gradients within that ecosystem? We sampled the occurrence of all alien plant species across multiple gravel riverbeds with different flow regimes and categorised species by longevity, nitrogen-fixation status, clonal versus seed reproduction and woodiness. The most prevalent species in the riverbeds were nitrogen fixing and either perennial, herbaceous, and clonal or perennial and woody, however the combined frequency of the annuals and biennials were greater than other trait combinations. We found that higher winter flow variability promoted annual and biennial lifeforms, and clonal perennial herbs, while non-vegetative perennial herbs were more suited to the flow regimes characterising drought. Our results suggest that if winter flow regimes become more variable as a result of climate change, the invasion of annual and biennial herbs and to a lesser extent perennial herbs may be promoted. On the contrary, if flow regimes become more stable/predictable due to water diversion or damming, the aggregate impacts of ruderal species may decline, shifting the vegetation to a more perennial, less disturbance-adapted, flora.

4.2 Introduction

Functional traits have been heralded as the key to developing generalisations about which species will invade a new region or ecosystem (e.g. Thuiller *et al.* 2006; Dawson, Burslem & Hulme 2009; Pyšek *et al.* 2009; van Kleunen *et al.* 2010; Catford & Jansson 2014). The functional trait approach has a long and varied history in invasion ecology but has provided insights under three primary themes. It has been used to predict naturalisation success at local (Dawson *et al.* 2009) and biogeographic scales (van Kleunen *et al.* 2010; Mcgregor *et al.* 2012), predict species distribution at

local (Lloret *et al.* 2004; Pouteau *et al.* 2015) and biogeographic scales (Dawson, Fischer & van Kleunen 2011), and to compare alien and native species traits to study biotic resistance, empty niches and contrasting competitive abilities (Cross, Green & Morgan 2015). Less studied are how species traits and trait combinations (i.e. syndromes) vary in response to environmental gradients within ecosystems (but see Catford *et al.* 2014; Pouteau *et al.* 2015). This general lack of hypothesis-driven trait-gradient research on alien invasions is limiting our ability to make predictions about current and future invasions at scales commensurate with ecosystem management. This study addresses two questions: (1) do growth and regenerative traits predict overall alien plant frequency within a disturbance-driven ecosystem ("trait-dominance"), and (2) do those same traits predict how alien species respond to disturbance and drought gradients within that ecosystem ("trait-gradient")? These two questions are key to understanding which alien plants assemble into disturbance-prone ecosystems and how variation in disturbance modifies the ability of alien species to invade.

Previous approaches to addressing invasion drivers at ecosystem or regional scales have been heavily focused on environmental niche modelling (i.e. species distribution modelling), which relates species occurrences or abundances to a multidimensional environmental space to determine where a species is most likely to establish and thrive (Elith & Leathwick 2009). Spatio-temporal models have also been used to predict colonisation of individual species through space and time (e.g. Catterall *et al.* 2012). Alternatively, researchers have related integrated measures such as alien species richness or total alien cover to environmental conditions to address questions about drivers of the level of invasion and invasibility (Planty-Tabacchi *et al.* 1996; Marini *et al.* 2009; Catford *et al.* 2012b; Tomasetto *et al.* 2013). Individual species results are used to predict where species will invade in time and space (Uden *et al.* 2015) while the integrated methods are used to determine which parts of an ecosystem are likely to increase or decrease in the level of invasion under different environmental change scenarios such as climate change or human disturbance (Catford *et al.* 2012b).

Single species approaches are limited in generality as they only focus on one or a few species. Conversely, community studies of invasion lack the ability to make predictions about which species to prioritize for management (Marini *et al.* 2009; Tomasetto *et al.* 2013; González-Moreno *et al.* 2014; Catford *et al.* 2014). Thus, there is much to be learned applying an intermediate approach that examines the response of each species within the whole invading flora simultaneously to environmental gradients and determine if the responses are general for species trait syndromes. Studies adopting this approach are beginning to emerge, yielding insights about how annual versus perennial aliens respond to perturbation relative to perennial natives (Pouteau *et al.* 2015). We build

on this approach, testing whether the combinations of four traits that we hypothesise to respond to disturbance and drought predict individual species responses of the invading flora. This study and others will help us generalise about the characteristics of successful invaders in ecosystems, and determine which components of the alien flora are most likely to change under future management or disturbance regimes.

We chose braided riverbeds in New Zealand as our study system to study trait-dominance and trait-gradient relationships, with a specific focus on how trait syndromes respond to disturbance and drought. Braided riverbeds fit into the broader classification of riparian ecosystems (ecotones on the interface between aquatic and terrestrial systems) that are strongly shaped by frequent and intense disturbances in the form of river flows, floods and droughts (Lake 2000; Richardson *et al.* 2007). We hypothesised that species with different combinations of longevity (annual, biennial, perennial), regeneration method (vegetative versus seed only), woodiness and nitrogen fixation ability would vary in overall success (occupancy) and in response to gradients of disturbance and drought (Mcintyre, Lavorelt & Tremont 1995; Lavorel *et al.* 1997; van Kleunen *et al.* 2010; Monks *et al.* 2012; Catford & Jansson 2014; Greet *et al.* 2015).

Of these traits, we hypothesised that being herbaceous, reproducing vegetatively, fixing nitrogen and regenerating quickly (annual and biennial longevities) would all be advantageous traits and lead to higher mean frequencies of occurrence ('level of invasion') within the braided river ecosystem (Barrat-Segretain, Henry & Bornette 1999; Xiong *et al.* 2001; Karrenberg, Edwards & Kollmann 2002; Karrenberg *et al.* 2003; Riis & Sand-Jensen 2006). We sampled plant occurrence across a gradient of flow variability and flow magnitude, and expected plants with fast generation times to be more frequent on average at higher flow variability and flow magnitude (Kyle & Leighman 2009; Catford *et al.* 2011; Catford & Jansson 2014). We also looked at gradients of drought (low flows) and expected perennial, vegetative plants, and woody species with the ability to reach the water table, to be more suited to the more drought prone end of the gradient. These expectations represent our general hypotheses, however we also expected combinations of traits ('syndromes') to lead to variable success in the ecosystem as a whole and across the gradients. Thus, we tested the effects of interactions facilitated by our natural experiment.

4.3 Methods

4.3.1 Study system

Nineteen braided riverbed ecosystems were studied in the Canterbury region of New Zealand that differed in flow regime (Chapter 2). The riverbed substrate consists of unconsolidated sedimentary

rock (glacially influenced greywacke) eroded from catchments in the Southern Alps and their foothills. The substrate, steep topography and frequent heavy rainfall causes rivers with multiple mobile channels to form in a floodplain of frequently reworked river gravels. Intense bed transforming flows occur frequently, making disturbance a dominant characteristic of these ecosystems (Gray & Harding 2007; Hicks *et al.* 2008). Rivers were selected that have been instrumented with flow recording stations ("gauging stations"). This 15-minute continuous time series of flows from 7 to 40 years before present provides a rich dataset with which to quantify flow regimes (Brummer *et al.* 2016a; Chapter 2).

4.3.2 Vegetation and trait data

A detailed description of the vegetation sampling can be found in Chapter 3. In brief, within the 19 river reaches, three sites were sampled, and within each site three transects of 1-m^2 plots were measured. Percent cover of each vascular plant species was visually estimated in each plot. Each site was sampled in a single day but the different sites within a reach were sampled randomly at early, mid or late season to account for seasonal effects. In the total survey, 154 alien plant species were identified that occurred in at least two plots in the study and aliens made up the majority of the highly abundant species in the system (only 31 native species were found; all occupied the tail of the rank-abundance curve; Chapter 3). A prior analysis to determine drivers of alien species richness and cover showed that higher alien richness was associated with greater flow variability in winter, and that higher alien cover was found in rivers with higher maximum annual flows. These general patterns motivated this study: to determine which functional groups were driving the observed patterns, and whether there were associations that were not captured by using an aggregated measure across all species.

Species functional traits were collected that we expected to be functionally associated with overall success in disturbed environments and across disturbance and drought gradients. Four categorical traits were considered: longevity, which was defined as a 3-level categorical variable: annual, biennial, or perennial; regeneration method which was defined as the presence or absence of vegetative reproduction; nitrogen-fixation status (legumes); and woody versus herbaceous lifeform. These traits were primarily sourced from the LEDA trait database and the Ecological Flora Database (Fitter & Peat 1994; Kleyer *et al.* 2008) as well as supplements from floras and in-field observations. Data were available for all species that met our minimum occurrence criteria. Although there was the possibility of 18 syndromes (the possible combinations of longevity (3-levels), regeneration strategy (2-levels), nitrogen-fixation status (2-levels) and woodiness (2 levels)), species were only found in 10 of these combinations (Table 4.1).

Table 4.1. Number of species in each combination of trait (for the species that occur in at least 20 plots in the study region). Of the four traits, three had 2 levels while one had 3 levels leading to 24 combinations. Of these, 8 were not biologically sensible (e.g. woody biennial and annual species are improbable strategies). The four that were absent in the dataset are listed at the bottom of the table. The last combination (*) is not biologically probable although it is possible. The abbreviations are Y - Yes, N - No, H - Herbaceous, W - Woody, A - Annual, B - Biennial and P – Perennial.

Vegetative reproduction	Nitrogen-fixation	Woody vs Herbaceous	Longevity	Number of Species (>2)	Number of Species (>20)
N	N	H	A	53	35
Y	N	H	P	44	35
N	N	H	P	17	13
N	N	H	B	14	11
N	Y	H	A	6	4
Y	N	W	P	8	4
N	Y	W	P	3	3
Y	N	H	A	6	3
N	Y	H	P	2	2
Y	Y	H	P	2	2
N	Y	H	B	1	1
N	N	W	P	8	1
Y	Y	W	P	0	0
Y	N	H	B	1	0
Y	Y	H	B	0	0
Y	Y	H	A	0	0*

4.3.3 Disturbance variables

Previous research showed significant associations between alien plant richness and winter flow variability which is when most flooding occurs in the braided river ecosystems (Brummer *et al.* 2016b; Chapter 3). We wanted to determine whether this relationship was driven by specific functional groups; thus, this variable was used as one of the gradients in the trait-gradient analysis. The same study also found associations between alien cover and average maximum flow, leading us to include that variable in this analysis. Finally, a variable that captured drought frequency was also included. The previous study did not find a significant effect of drought on alien richness or cover, however we hypothesised that potential patterns would be revealed when species were grouped by traits, so we included it in this analysis. Specific formulations of the flow variables were: (1)

variability in winter flow regimes, which was defined as the coefficient of variation of August flows and was highly correlated with variability in flows across the winter months, (2) average annual maximum flow, and, (3) frequency of flows less than 1/3*median flow, which captured drought frequency. These flow variables were calculated from continuous river flow data at gauging stations on each of the river reaches in the study system (detailed in Brummer *et al.* 2016a; Chapter 2)

4.3.4 Response variables

We carried out two analyses to determine whether species traits predicted overall alien dominance (mean frequency/occupancy) and response to disturbance gradients. First, to determine overall frequency, we modelled the proportion of the 2,896 plots occupied. A plot was considered occupied if there was an established plant within the quadrat (>2 true leaves). In this analysis, species were treated as independent replicates within different trait combinations and were included if they occurred in at least two or more plots, in order to facilitate understanding of the drivers of rarity and commonness (163 species).

Second, to determine alien species' response to the three flow gradients, we modelled the proportion of plots where each species had established at a site. In this analysis, reaches were the independent level of spatial replication. Species served as replicates within the different combinations of traits. Because the aim of this analysis was to detect species-level responses to the flow gradients, more data were needed compared to the first analysis. Thus, species were retained in the analysis if they occurred in more than 20 plots (114 total species). We tried this analysis using 10 plots as a cut-off to increase the number of species (species level sample size), however this compromised model convergence and so few data are unlikely to be sufficient for detecting selection along gradients, which was the goal of the analysis. Further, species within syndromes with very low replication were removed, as the goal of the analysis was to determine group level effects. Thus, we retained groups with at least four species, resulting in six syndromes.

4.3.5 Statistical methods

The proportion of plots occupied by a species was analysed using Generalised Linear Models, and treated as a binomial count (binomial distribution – logit link function). The effects of longevity, regeneration method, woodiness and nitrogen fixation status were examined, as well as their possible interactions. Only a subset of the full interaction model could be considered due to replication within different combinations of the trait categories (and some combinations, such as woody annual and biennial species, were not biologically possible). A log-likelihood ratio test was used to determine whether the interaction model was an improvement over the additive model.

The response of species within different functional groups to three flow variables was modelled using Generalised Linear Mixed Effects Models (package "lme4" in R; Bates *et al.* 2015). Random effects were necessary to account for both spatial and subject clustering (non-independence). A random intercept term was included for species. Random intercepts were also tested for site and reach to account for the spatial sampling design. Site accounted for a significant amount of variation (χ^2 (1) = 2069.9, p < 2.2e-16), however reach explained very little variation (χ^2 (1) = 5.2, p = 0.02). This is likely due to the fact that 'site' was nested within 'reach' so reach level correlation was accounted for by the site random intercept. Thus, in order to keep the random effects structure as simple as possible, reach was not included in the inferential model. Each unique combination of the four categorical traits was treated as a group in the analysis. For this analysis, we were interested in whether different species functional groups responded differently to the flow disturbance gradient. Thus, we fit three models that each interacted one of the three gradients with each of the different syndromes. Season was accounted for as a covariate. The 95% confidence intervals for the slope of the relationship between occupancy probability and each gradient were estimated using parametric bootstrapping. The 95% quantiles were estimated from 1000 replications of the bootstrapping routine. Bootstrapping was carried out in parallel on a high-performance computing cluster. All analyses were conducted in R (R Core Team 2015).

4.3.6 Syndrome effect

The number of species within each combination of functional traits varied widely (Table 4.1). Thus, in addition to analyses that estimated the average effect per species within a syndrome, we calculated an index describing effect of each trait syndrome. This was simply defined as the mean effect size multiplied by the number of species within each syndrome. This approach allowed us to determine which syndromes were most likely to change with shifts in the underlying gradient.

4.4 Results

4.4.1 Overall occupancy

Longevity, woodiness, nitrogen fixation status and regenerative strategy all had significant effects on the overall frequency of species in braided river ecosystems. These effects were not strictly additive, as evidenced by significant model improvement when the testable interactions between those functional traits were included (log-likelihood ratio test between the additive and interaction model: χ^2 (6) = 3270, p < 0.0001) and an improvement in pseudo-R^2 from 0.14 for the additive model to 0.23 for the interaction model (Table 4.2). Plants that fix nitrogen always had higher average occupancy in the ecosystem after controlling for regenerative strategy (Figure 4.1). Perennial plants that

Table 4.2. Comparison of the variation explained in the response variable for different models that predict the occupancy frequency of plant species using species traits. The first two models use all four predictors (nitrogen-fixing ability, woody vs. herbaceous, presence of vegetative reproduction and longevity) with all the possible interactions (Interaction) or purely additively (Additive). The bottom four models remove terms from the interaction model that include each of the four traits, to determine their relative importance in explaining species occupancy frequency. Thus, the model with the most influential trait is degraded the most when that trait is removed (-nitrogen-fixing in this case). The four variables are ordered in decreasing importance. McFadden's pseudo-R^2 is reported and should only be treated as indicative of the proportion of the variation in the response variable that is explained by the traits.

Model	$R^2_{Mcfadden}$
Interaction	0.23
Additive	0.14
Interaction	0.23
-Nitrogen-fixing	0.11
-Woody/Herb	0.16
-Vegetative Reproduction	0.18
-Longevity	0.19

regenerate vegetatively were found at a greater frequency than those that do not after controlling for nitrogen-fixation status, though this effect was not observed in biennial or annual species. The effects of longevity depended strongly on the other three traits, with woody nitrogen-fixers and vegetative reproducing, nitrogen-fixing perennials being the most frequent on a per species basis (Figure 4.1).

When the mean frequency on a per species basis was multiplied by number of species in each combination of functional traits, the picture of the most successful syndromes (at present) at the ecosystem scale shifted (Table 4.1). Even though perennial, vegetative-reproducing herbs and non-nitrogen-fixing annual species did not have the highest mean occupancy (per species), they were the dominant syndromes in the ecosystem. Additionally, even though nitrogen fixation was a big advantage on a per species basis, when weighted by the number of species in each group, most nitrogen-fixing groups had an intermediate score for their syndrome effect compared to the non-nitrogen-fixing herbaceous annuals, biennials and perennials (Table 4.1).

4.4.2 Response to disturbance and drought

There were no significant associations between maximum annual flow and any of the six syndromes with sufficient replication (>4 species) to analyse general responses to flow variation (Figure 4.2). Perennial herbaceous non-vegetative species was the only syndrome positively associated with the frequency of low flow events (estimated increase in odds of occupancy of 37% CI[13%, 68%] for a one unit increase in standardised low-flow frequency).

Annual and biennial non-nitrogen-fixing plants were positively associated with winter flow variability, but the effect size did not differ between those groups (estimated increase in odds of occupancy of 128% CI[92%, 172%] and 107% CI[75%, 148%] respectively, for a one unit increase in standardised winter flow variability; Figure 4.2). Perennial, herbaceous, vegetative-reproducing plants had a significant positive association with winter flow variability although it was smaller in magnitude compared to the annuals and biennials (estimated increase in odds of occupancy of 35% CI[14%, 61%], for a one unit increase in standardised winter flow variability; Figure 4.2). Woody, vegetative reproducing non-nitrogen-fixing species did not respond to changes in winter flow variability, and there were too few nitrogen-fixing woody species to determine whether that syndrome responded more generally to any of the flow gradients.
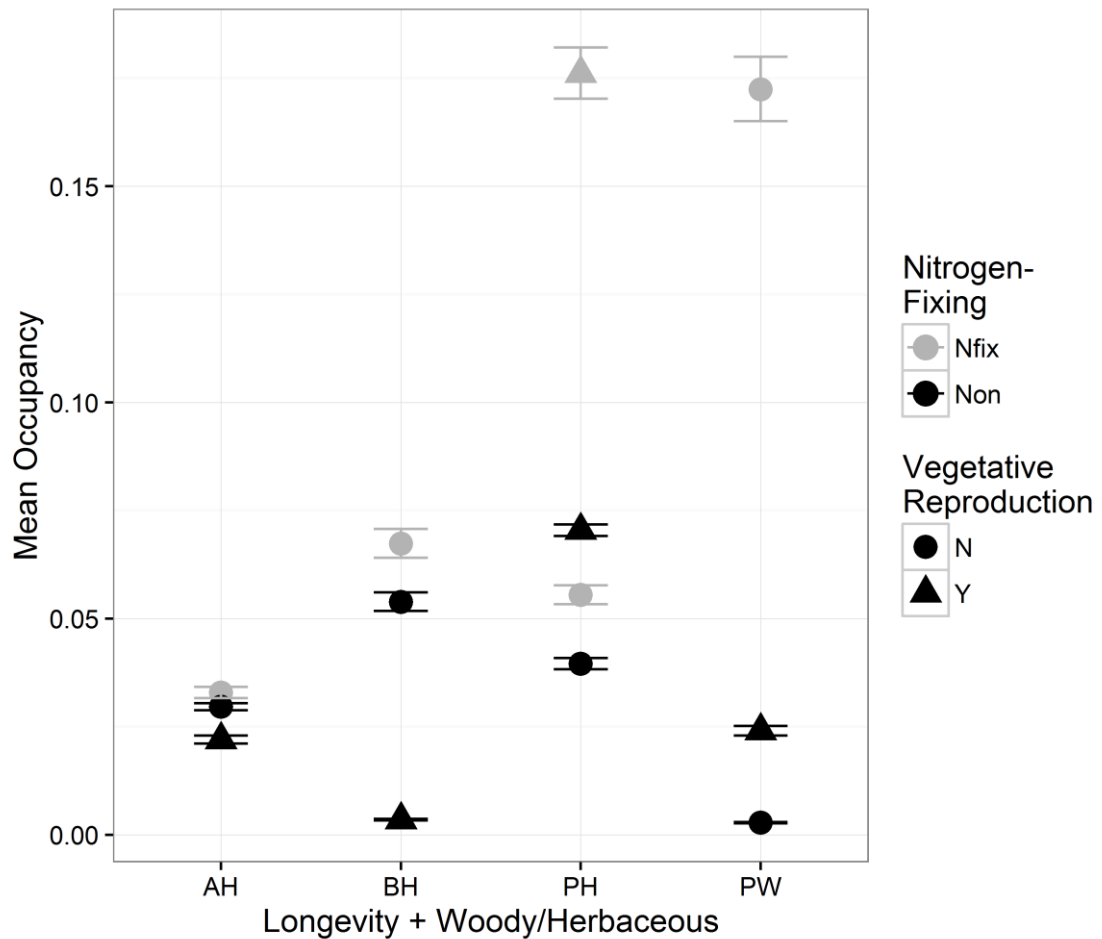
Figure 4.1. Mean proportion of plots (Y-axis) in the braided riverbed study occupied by species of different functional trait combinations. Functional traits considered were longevity (A-annual, B-biennial, and P-perennial) and herbaceous (H) versus woody (W) on the x-axis, whether they fixed nitrogen or not (grey versus black) and whether they regenerate vegetatively (point symbols). Error bars represent 95% confidence intervals around the mean. Displayed are model-based estimates that allow for estimable interactions among the four traits.
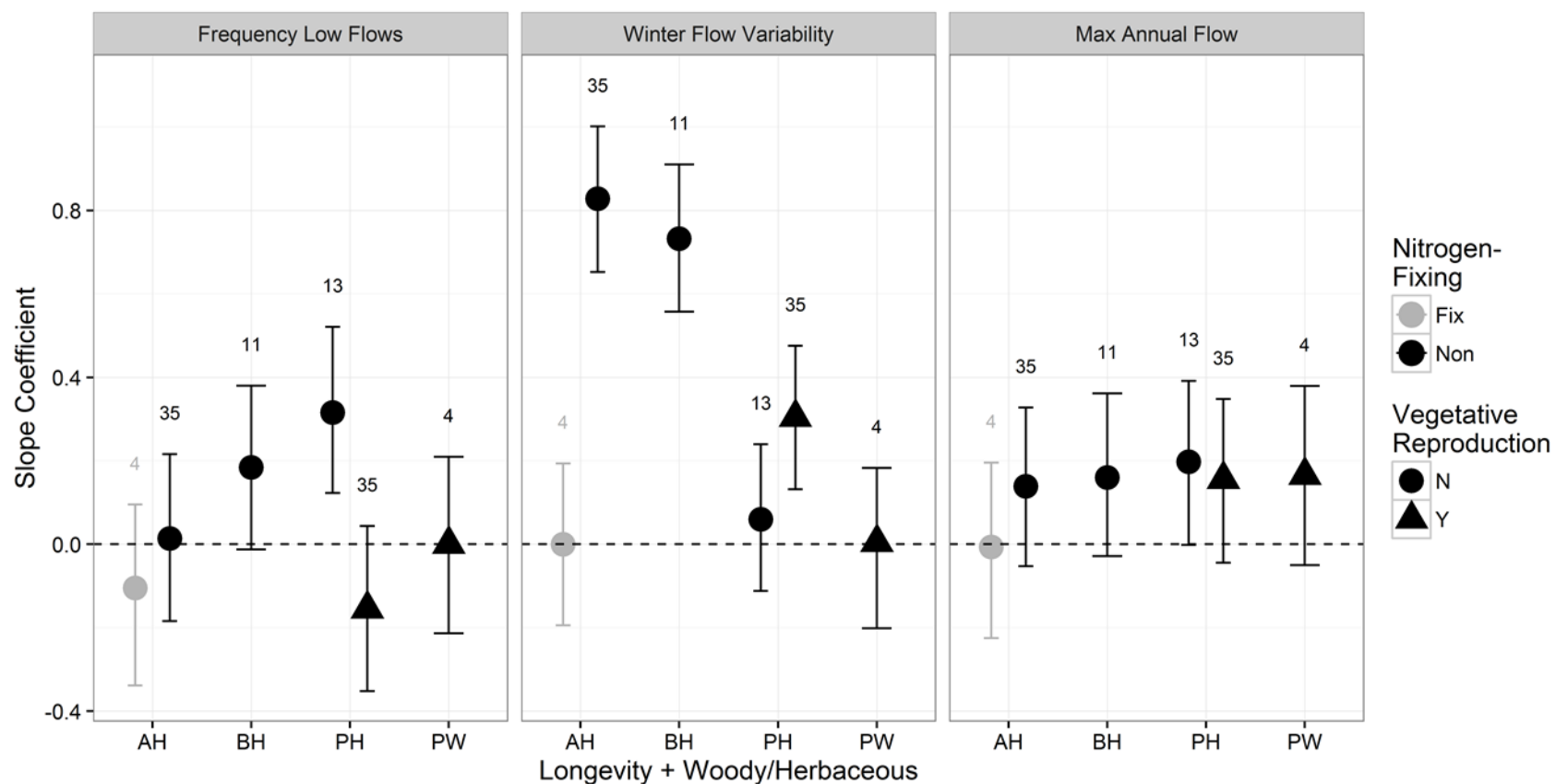
Figure 4.2. Estimated slope coefficient for the relationship between the frequency of different alien plant functional trait combinations and three flow indices (panels). A positive value, above the dashed line, indicates the species within the group increased in frequency as flow indices increased. All three flow indices were centred and standardised so effect sizes are comparable among indices. The x-axis groups responses by longevity (A-Annual, B-Biennial), and herbaceous (H) versus woody (W) species; shapes indicate whether the plants resprout vegetatively (Y-Yes, N-No); and grey/black indicates whether or not they fix nitrogen. Numbers indicate the number of species in that combination of functional traits. Error bars are 95% confidence intervals about the mean slope derived from empirical quantiles of 1000 replicates of parametric bootstrapping.

4.5 Discussion

Generalisations about the trait syndromes that are associated with higher levels of invasion in ecosystems, and how those trait syndromes will respond to future environmental change are critical for making predictions to inform ecosystem management. In our study, we studied both aspects to: (1) understand the combination of traits that drives the level of invasion in the ecosystem as a whole and (2) to determine whether trait syndromes predict species' responses to flow gradients. We highlight how our findings can be integrated into current management of the ecosystem and used in targeting preventative management to minimize the risk of future invasions.

4.5.1 Which alien species should we prioritise for control?

Plants in braided riverbeds must tolerate or escape periods of intense disturbance from periodic floods as well as periods of growth-limiting drought in the well drained, coarse textured bed material (Lake 2000; Bertoldi *et al.* 2011; Catford & Jansson 2014). Our findings suggest that the most successful invaders in braided riverbeds fix nitrogen and are either perennial, herbaceous, and clonal or are perennial and woody. Nitrogen-fixing species' high relative abundance is not surprising considering riverbed material is generally nitrogen poor and water stressed, conditions that lead to a growth advantage for nitrogen-fixers (Monks *et al.* 2012). Further, nitrogen-fixing ability was observed as a key difference between the native and alien flora in braided river systems in a previous study (Williams & Wiser 2004) and suggested as one of the reasons aliens are so successful in this ecosystem. However, nitrogen-fixing perennial herbs that only reproduced via seed were much less frequent per species, suggesting that at least for this growth form, the ability to clonally reproduce provides a strong advantage. This may be due to the ability of their root architecture to survive flooding (c.f. annuals or biennials that may be less resistant to scouring (Karrenberg *et al.* 2003)), and/or the ability for the species to resprout quickly after disturbances (Bellingham & Sparrow 2000; Barrat-Segretain 2001).

That clonal, nitrogen-fixing perennial herbs (e.g. *Trifolium repens*) are some of the most abundant species in the gravel riverbeds is a hard reality for management prioritisation as these species are ubiquitous in the agricultural matrix surrounding the riverbeds (Goh & Bruce 2005). Thus, management of these species is likely to be transient in effectiveness due to intense propagule pressure from neighbouring land use (Von Holle & Simberloff 2005). However, management actions designed to mitigate the effects of the other most abundant syndrome, nitrogen-fixing perennial woody plants (e.g. *Lupinus arboreous*, *Cytisus scoparius* and *Ulex europaeus*), may be met with more success as there are active eradication campaigns to remove those species from the agricultural

matrix and in upland wildlands where the species have invaded. Thus, coordinated programmes could have long term benefits as propagule pressure is reduced, and floods discharge and bury extant seed.

Although targeting individual species can be effective, this may ignore suites of species that have small individual effects but large group effects. Our results show this is the case as clonal perennial herbs and annual herbs have very large syndrome effects, while their per species effects are relatively small. This reiterates the point made by Peltzer et al. (2009) who found the low aboveground biomass herbs had disproportionately large impacts in a riverbed succession experiment. Thus, management to mitigate current impacts should consider the effects of suites of impactful species rather than taking a solely species focused approach (Kuebbing, Nuñez & Simberloff 2013).

4.5.2 Which alien species are likely to become problems in the future?

The second question we were interested in addressing was: do trait syndromes respond predictably to variation in flow regime? Our results showed that higher winter flow variability promoted annual and biennial lifeforms, and clonal perennial herbs, while non-vegetative perennial herbs were more suited to the flow regimes characterizing drought. The flow variability relationships match other empirical studies that find changes in disturbance promote ruderal strategies (Nilsson *et al.* 1991; Catford *et al.* 2011, 2014; Greet *et al.* 2013, 2015). They also match plant strategy theory that suggests that short generation times and prolific investment in seeds can improve a plant's chances to establish in highly disturbed settings (Grime 2001). The current predominant view is that invasive plant species are those adapted to disturbance by producing many seeds, having short generation times (e.g. annual life-cycle) and reproducing vegetatively (van Kleunen *et al.* 2010; Thompson & Davis 2011). Our results agree with these general findings as species with these characteristics were more frequent at the higher end of the disturbance gradient.

The relationship between drought and non-vegetative perennial herbs does not have a lot of precedence in the literature, generally due to a lack of research on riparian community responses to hydrologic drought. However, species-focused studies suggest this observation could be driven by differential investment in underground vertical roots that can more easily reach the water table compared to vegetative perennial herbs that invest more resources in lateral underground structures (Naumburg *et al.* 2005) or perhaps due to variation in drought induced juvenile mortality (Smith *et al.* 1991) that may relate to consistent traits within the trait syndrome we defined. The absence of a negative relationship between the annual/biennial species and low flows was

surprising, however this may be due to the ability of those species to quickly take advantage of favourable growth conditions, even if the river has, on average, a greater number of low flow events (Catford & Jansson 2014).

In terms of the practical implications, our results suggest that if winter flow regimes become more variable as a result of climate change (Hirabayashi *et al.* 2013), the invasion of annual and biennial herbs and to a lesser extent perennial herbs may be promoted. On the contrary, if flow regimes become more stable/predictable due to water diversion or damming, the aggregate impacts of ruderal species may decline, shifting the vegetation to a more perennial, less disturbance-adapted, flora (Deiller, Walter & Tremolieres 2001; Catford *et al.* 2011). Counterintuitively, we did not find evidence that this would also promote slower growing life forms, at least in the functional trait groupings examined, leaving the question of what will replace the annual and biennials that may decrease in abundance. However, due to low replication within the syndrome of the nitrogen-fixing woody species (largely *Cytisus scoparius, Ulex europaeus,* and *Lupinus arboreus*) we were not able to assess their general responses to the disturbance gradient, though they may be the species that slowly come to dominate a less disturbed floodplain.

4.6 Acknowledgements

Chapter 5 - Do invasive woody legumes behave the same in heavily disturbed gravel riverbed ecosystems? Insights from a demographic species distribution modelling approach

5.1 Abstract

Strategic management of alien species at ecosystem scales requires a fundamental understanding of the factors driving their invasion. This study takes the power of the species distribution modelling approach combined with detailed data on the demographic stage of invasive species to determine: what are the key environmental drivers of three woody, nitrogen-fixing invasive species? Data on the seedbank, establishment and percent cover across local and regional scales were collected along with data on flow regime, land-cover, climate, and local floodplain variation. Despite the three species having similar functional traits (woody legumes) they were driven by different regional variables. Contrary to expectation, flow regime played only a minor role in one species' distribution. At local floodplain scales, the establishment of the three invasive legumes was greatest in areas with fine textured soil that was removed from the active river channels. These results suggest that changes to flow regimes at the regional scale may significantly alter the distribution of these three species. However, that they all preferred the less disturbed, less inundated parts of the floodplains suggests that if river levels are consistently lowered and floods less frequent, these species may expand locally to occupy more of the floodplain habitat.

5.2 Introduction

Understanding the drivers of alien species' invasion, distribution and abundance across scales is a challenging task that requires investment in data collection and predictive modelling (Gallien *et al.* 2010). Approaches to studying species' invasion have been varied and span a gradient of effort and information density. One common approach is detailed demography: gathering data about the lifecycle of an invading species over multiple years, across the region or range the species is invading (Holt *et al.* 2005; Normand *et al.* 2014; Seipel *et al.* 2016). Such data provide a rich basis to understand and predict the target species' invasion, but are costly in both physical labour and in time to reaching conclusions to inform management (Ibáñez *et al.* 2014). At the other end of the spectrum, researchers collate observations of a species' presence and model them relative to the possible environmental conditions the species could select from to determine the drivers of alien species distributions (Guisan & Zimmermann 2000; Guisan & Thuiller 2005; Elith & Leathwick 2009).

These species distribution models (SDMs) tend to be coarse in spatial resolution because of data uncertainty, and generally only address questions for which there are reliable geospatial data to relate presences to, limiting questions and inferences to climate and large scale land-cover variables (reviewed in Elith & Leathwick 2009). Studies that combine distribution modelling methodologies with demographic data are relatively rare but growing in application and perceived value (Franklin 2010; Schurr *et al.* 2012). However, the fact remains: detailed demographic data are costly to collect. This study aimed to incorporate data that could closely approximate demographic processes into a modelling framework, to improve our understanding of the drivers of target species invasion while maintaining the efficiencies associated with SDM approaches.

Presence and absence data used in the SDM approach, while easy and reliable, can have the effect of obfuscating interpretation of species' behaviour in the environment. We do not know whether the species was present as a seed, seedling, adult or reproductive individual. Furthermore, within the resolution of aggregation (e.g. 1 km x 1 km grid cells) it is difficult to determine where a species invades within an ecosystem, as large scale patterns are many times the sum of processes at a local scale (Austin 2007). In this study, we take a species distribution modelling analytical framework, but apply it to original, fine resolution data collected at nested spatial scales (Pyšek & Hulme 2005). Easy-to-collect attributes tied to different demographic stages were gathered in addition to presence and absence to create a more complete picture of the environmental drivers of the invasion of three functionally similar species. Specifically, we collected data on the seedbank, the life-stage of plants growing in each sampled plot and their abundance as measured by percentage cover. Although these measurements were significantly more detailed than data collected for empirical species distribution models, they could still be applied to many species within the ecosystem to facilitate a comparative study. We asked: can this more demographic approach to distribution modelling tell us how three alien species are invading New Zealand's braided riverbeds?

Alien woody legumes have clear and well documented impacts in New Zealand riverbed environments (Hicks *et al.* 2008; Drake 2011; Caruso *et al.* 2012, 2013) and are considered ecosystem engineers, creating feedbacks by slowing flows causing sediment deposition and creating more habitat for more woody invasion (Francis, Corenblit & Edwards 2009; Gurnell *et al.* 2012; Corenblit *et al.* 2014; Gurnell 2014). Despite knowing invasive woody legumes are a problem for the last ~40 years (Williams 1978, 1981), resulting in extensive control programmes, there has been little effort to try and understand the regional and local scale drivers of establishment and abundance of these species in gravel riverbeds, nor how their distributions and subsequent impacts in this ecosystem may change in the future. This chapter focuses on three woody legumes that have

invaded the riverbeds of New Zealand: *Cytisus scoparius* (L.) Link (Scotch Broom), *Ulex europaeus* L. (Gorse), and *Lupinus arboreus* Sims (Tree Lupin). We ask: are these species driven by the same environmental variables? Are they associated with river flow regimes which may be subject to change in the future? And, is there any reason for differential prioritisation of these species when looking across regional scales?

Field observations suggest that *C. scoparius* is the most prolific invader and transformer of floodplain ecosystems in the study region (Williams 1978; Meurk & Williams 1989; Brummer *et al.* 2016b; Chapter 3). In contrast, *U. europaeus* and *L. arboreus* are present but at lower abundance and frequency than *C. scoparius*. However, *U. europaeus* is more broadly distributed than *L. arboreus*. These observations suggest that different factors are driving the distribution and abundance of these species. All three legumes share commonalities through their life-history, but originated in different regions (Peterson & Prasad 1998; Clements, Peterson & Prasad 2001), and appear to have different ecological drivers, suggesting their niches may not completely overlap. This is what we aimed to test through a more demographic approach to species distribution modelling.

5.3 Methods

5.3.1 Study System and Species

The study system is described in detail in the introduction and in Chapters 2 & 3. This study targeted three specific species: *Cytisus scoparius, Ulex europaeus* and *Lupinus arboreus*. All three species are members of the Fabaceae family, fix nitrogen, and are woody shrubs. They were all introduced in the mid to late 19th century during European colonisation (1872, 1862 and 1899 respectively) and have since spread by human and natural pathways into riverbeds (Williams 1978; Owen 1998; Williams & Cameron 2006). *Cytisus scoparius* is native to Europe and ranges broadly across all maritime regions throughout. The species grows in moderate to very dry climates and is limited by severe winter temperatures (Peterson & Prasad 1998). *Ulex europaeus* is native to central and western Europe and northern Africa, and is most prevalent in Mediterranean regions (Clements *et al.* 2001). *Ulex europaeus* generally grows in areas with cool and wet maritime climates, where mean monthly temperatures remain above freezing (similar to *C. scoparius*). Although gorse thrives in wet environments, it is well adapted to survive periods of drought (Clements *et al.* 2001). *Lupinus arboreus* is endemic to the Mediterranean climates of California in the United States where it grows in coastal sand dune or coastal scrub environments (Jepson Flora Project 2016).

All three are prolific seed producers and disperse via explosive seed pods. Individuals of *C. scoparius* can produce more than 10,000 seeds (Wayloff & Richards 1977), they can float for a short

time and travel in the bed load of rivers during which time scarification seems to decrease germinability (Watterson & Jones 2006). Records have shown *U. europaeus* can produce 40,000 seeds m^{-2} in established stands. These seeds are highly viable, but up to 90% fall as hard seed that can remain dormant until scarified. Seeds are long-lived, up to 30 years with ~10% of seed remaining viable after 5 years (Clements *et al.* 2001). *Lupinus arboreus* and *C. scoparius* also produce hard seed that can remain dormant for long periods until scarified (Williams 1981; Maron & Simms 1997). None of the species reproduce vegetatively, with seed being the primary reproductive pathway.

Cytisus scoparius has been shown to grow faster than similar native species in Australia (Fogarty & Facelli 1999) which could be due to its specific adaptation of stem photosynthesis. *Ulex europaeus* is evergreen allowing for year-round photosynthesis (Clements *et al.* 2001). Both *U. europaeus* and *C. scoparius* have very fast growth rates and short juvenile times, often reaching flowering stage within two years (Peterson & Prasad 1998; Clements *et al.* 2001). Nitrogen fixation has been shown to be a particularly advantageous trait in water and nitrogen limited environments in New Zealand (Monks *et al.* 2012), which are two characteristics of freshly deposited riverbed gravels as they are particularly well drained and nitrogen poor (Bellingham *et al.* 2005). However, these species are generally not well suited to inundation suggesting that local and regional differences in river flows may influence their relative success (Fitter & Peat 1994).

5.3.2 Plant Survey

The same plant survey data were used as in Chapters 2 & 3. The survey was nested, spanning 13 catchments and 19 river reaches (sections of river associated with flow recording stations). Within each reach, three sites were located within 500 to 2000 metres of each other. Within each site, three transects were placed perpendicular to the flow of the river and plots were sampled every five metres along the transects. Percent aerial cover of the three target species was estimated in 2,930 1-m^2 plots across 195 transects that were distributed among 57 sites which were distributed among the 19 river reaches. The lowest percent cover recorded if a species was present at less than 1% cover was 0.5%. The most advanced growth stage was also recorded within each plot. The stages of interest to this study were seedling and established plants. Seedlings were defined as plants that were either in the cotyledon stage through the two true-leaf stage. Anything with three true-leaves or more was considered an established plant. The aim of this distinction was to determine where species were germinating but potentially not establishing. Thus, two response variables were derived from the plant survey data: *established* - a binary variable that indicated where the species had at least three true leaves (i.e. plots where the species was present as a very young

seedling/germinant were excluded from the analysis), and *cover* which was modelled for the plots where the species was present.

5.3.3 Seedbank Survey

Seedbank samples were collected at each site (except one where the sample was lost). Nine litres of gravel material were collected in a targeted random walk where shovelfuls (5-10 cm depth) were collected from near the channel, and up through the riverbed cross section. Areas with dense closed canopy vegetation were excluded from sampling as we were most interested in the seedbank (potential invaders) of the open gravel areas. Areas with visually different erosion and deposition patterns were targeted in order to have the best chance of collecting areas where different seeds were deposited. This material was then sorted through a 4 mm sieve to concentrate the sample which was larger than the largest seeds expected in the ecosystem (Heerdt *et al.* 1996). Two litres of each sample were distributed among two sample trays with an equal amount of potting mix to help retain water. Trays were kept in a glasshouse at Lincoln University, Canterbury, New Zealand and watered daily. Seedling counts of the germinated seedlings began in November 2013 and were conducted for 19 months. Counts were undertaken weekly initially, then bi-weekly when germination rates slowed. Species that could not be identified at seedling stages were potted and grown to more mature stages.

5.3.4 Analysis Methods – Seedbank

Presence and absence of the three species in the seedbank were determined at the site and reach scale and compared to above ground presence and absence using Fisher exact tests for two-way contingency tables. The sampling intensity below ground was orders of magnitude less than the above ground sampling, but we wanted to explore whether the frequency of the species above ground predicted the number of individuals found in the seedbank sample. Thus, the number of individuals germinated in each seedbank sample was regressed against the proportion of plots at a site occupied by the same species using a generalised linear mixed model, assuming a Poisson error distribution and including 'reach' as a random intercept as sites were clustered within reaches.

5.3.5 Analysis Methods - Establishment and Cover

Basic patterns in species associations were explored using χ^2 tests of independence on two-way contingency tables of each of the three species relative to one another. The data were dependent by the sampling design, so a non-parametric bootstrapping routine that recreated the nested sampling regime was used to examine the sampling distribution of the χ^2 statistic. An alpha significance level of 0.05 was used to determine significance which corresponds to a χ^2 value of 3.84 for a two-way

table. Thus, an association between two species was considered significant if 95% of the test statistics in the bootstrap distribution were greater than 3.84. We also reported the median χ^2 to get an idea of the effect size. The larger this value, the stronger the association between the two species.

To determine the drivers of establishment and cover, a boosted regression tree approach similar to Chapter 3 was adopted (Elith *et al.* 2008; Brummer *et al.* 2016b). Bernoulli loss functions were specified for establishment as those were binary variables, while Gaussian loss functions were specified for cover. Cover was only modelled for plots where the species were present, thus the associations are conditioned on the species being present. The same 19 predictor variables were used that captured land-cover, climate, flow regime, and floodplain variables. To determine the statistical significance of each predictor, the null modelling approach described in Chapter 3 was employed. In brief, each predictor variable was permuted at the scale at which the data were collected while holding the other predictor variables at their observed values. If the observed relative importance of the predictor was greater than the 95% quantile of the distribution of the relative importance that could arise from permutation, the predictor effect was considered statistically significant (this is a one tailed test as the hypothesis is that the observed relative importance is greater than relative importance values that arise through random permutation).

5.4 Results

5.4.1 Species associations: general patterns

The occurrence of *C. scoparius* and *U. europaeus* at the plot scale were strongly associated with each other (refer to Table 5.1 for all test statistics). The occurrences of *L. arboreus* and *C. scoparius* were weakly associated with each other. There was no evidence of association between *L. arboreus* and *U. europaeus*. All three species occurred simultaneously in only 50 of 2,864 plots.

5.4.2 Above versus below ground distributions

Cytisus scoparius and *U. europaeus* were distributed similarly across the study reaches and sites, being found in all reaches and only absent from 4 and 6 sites respectively (Table 5.2; Figure 5.1). *Lupinus arboreus* was less widely distributed and was absent from seven of 19 reaches and 30 of 57 sites. *Lupinus arboreus* distribution was geographically concentrated in the river reaches of southeast Canterbury Plains (Figure 5.1). *Cytisus scoparius* was broadly distributed, but had highest abundances in the mid-altitude reaches of the southern rivers. *Ulex europaeus* was also broadly distributed with less obvious occupancy concentrations (Figure 5.1).

Absolute emergence from seedbank samples was greatest for *C. scoparius* (100 individuals) followed by *U. europaeus* (32 individuals) and none for *L. arboreus*. When the number of individuals in the seedbank was regressed against the proportion of plots occupied at the site scale to determine if seedbanks were only likely to be detected where plant abundance was high (Figure 5.2), there was a marginally significant positive correlation for *U. europaeus* (est. = 2.27, se=1.22, z = 1.86, p = 0.06) and a significant correlation for *C. scoparius* (est. = 1.93, se = 0.59, z = 3.27, p = 0.001). Neither of the relationships were very explanatory (Marginal R^2 = 0.06 and 0.09 for *U. europaeus* and *C. scoparius* respectively)

Table 5.1: Contingency tables for the two-way associations between the three study species. A χ² test of independence between the species pairs is reported below each table. *Ulex europaeus* and *C. scoparius* were strongly associated with one another while *L. arboreus* and *C. scoparius* were only weekly associated. There was no statistical evidence that *U. europaeus* and *L. arboreus* were associated with one another. Results were determined by a non-parametric bootstrapping routine that estimated the sampling distribution of the χ² statistic (500 randomisations). The probability that the test statistic was larger than the predetermined significance level of 0.05 is reported along with the median value of the χ² statistic.

		U. europaeus	
		-	+
C. scoparius	-	1946	141
	+	472	305

$p(\chi^2 < 3.84) < 0.002$
median $\chi^2 = 434$

		L. arboreus	
		-	+
C. scoparius	-	1958	129
	+	648	129

$p(\chi2 < 3.84) = 0.036$
median $\chi^2 = 73$

		U. europaeus	
		-	+
L. arboreus	-	2225	381
	+	193	65

$p(\chi2 < 3.84) = 0.236$
median $\chi^2 = 18$

Table 5.2: Comparison of seedbank versus aboveground distribution. '+' indicates the species was present, while '-' indicates the species was absent either aboveground 'abv' or belowground 'blw'. Fisher's exact tests of associations between above and below ground occurrence were not significant for any species (p-values all greater than 0.1).

Species	Scale	+abv +blw	+abv -blw	-abv +blw	-abv -blw
Cytisus scoparius	Site	26	26	0	4
Ulex europaeus	Site	16	34	0	6
Lupinus arboreus	Site	0	26	0	30
Cytisus scoparius	Reach	12	7	0	0
Ulex europaeus	Reach	9	10	0	0
Lupinus arboreus	Reach	0	12	0	7

Table 5.3: Comparison of seedling (Sdl; < 3 true leaves) versus established (Est; > 2 true leaves) plant distributions from the vegetation survey data. The values in the table indicate the number of times seedlings and established plants of the same species occurred in the same transect or reach.

Species	Scale	Sdl+ Est+	Sdl+ Est-	Sdl- Est+	Sdl- Est-
Cytisus scoparius	Transect	147	22	0	27
Ulex europaeus	Transect	123	32	0	41
Lupinus arboreus	Transect	59	7	0	130
Cytisus scoparius	Site	53	3	0	1
Ulex europaeus	Site	51	2	0	4
Lupinus arboreus	Site	26	1	0	30
Cytisus scoparius	Reach	19	0	0	0
Ulex europaeus	Reach	19	0	0	0
Lupinus arboreus	Reach	12	0	0	7
Cytisus scoparius	Catchment	10	0	0	0
Ulex europaeus	Catchment	10	0	0	0
Lupinus arboreus	Catchment	8	0	0	2

At any site, the three species were never found only in the seedbank and not aboveground (Table 5.2). There were many instances where the species were found aboveground but not in the seedbank and *L. arboreus* was never found in a seedbank sample. Fisher exact tests of association between above and below ground occurrence at the site scale showed no significant associations (*C. scoparius*: p = 0.12; *U. europaeus*: p = 0.17).

5.4.3 Seedling versus established distributions

When the distributions of seedlings and established plants were compared, it was evident that at the transect and site scales there were instances where all three species were present as seedlings but not as established plants (Table 5.3). When the reach and catchment scale were examined, there were no instances where seedlings were present but established plants absent, and only *L. arboreus* was completely absent from reaches and catchments. At the finest scale, there were 194, 211, and 39 plots where, respectively, *C. scoparius*, *U. europaeus* and *L. arboreus* were present only as seedlings.

5.4.4 Drivers of establishment

At the floodplain scale, all three species were associated with riverbed elevation and texture, with diminished establishment probabilities at low riverbed elevation and higher establishment in finer textured areas (Figure 5.3). *Cytisus scoparius* and *L. arboreus* had lower establishment probabilities close to water and *C. scoparius* and *U. europaeus* had slightly lower establishment in human disturbed plots (Figure 5.4). At the reach scale, *C. scoparius* had higher establishment in reaches with moderate values of cumulative water deficit. *Ulex europaeus* established more in rivers with larger maximum flows, lower median flows, and lower water deficit. *Lupinus arboreus* had higher establishment probabilities when there was more adjacent cropping land and at lower altitudes (Figure 5.4).

5.4.5 Drivers of cover

At the floodplain scale, all three species had higher cover in areas with finer textured substrate (Figure 5.5). *Cytisus scoparius* had higher cover at higher riverbed elevations and *U. europaeus* had more cover at greater distance to water. At the reach scale, *C. scoparius* had higher cover at higher altitudes, and *U. europaeus* had a polynomial relationship relative to growing degree days, however the effect size was very small.
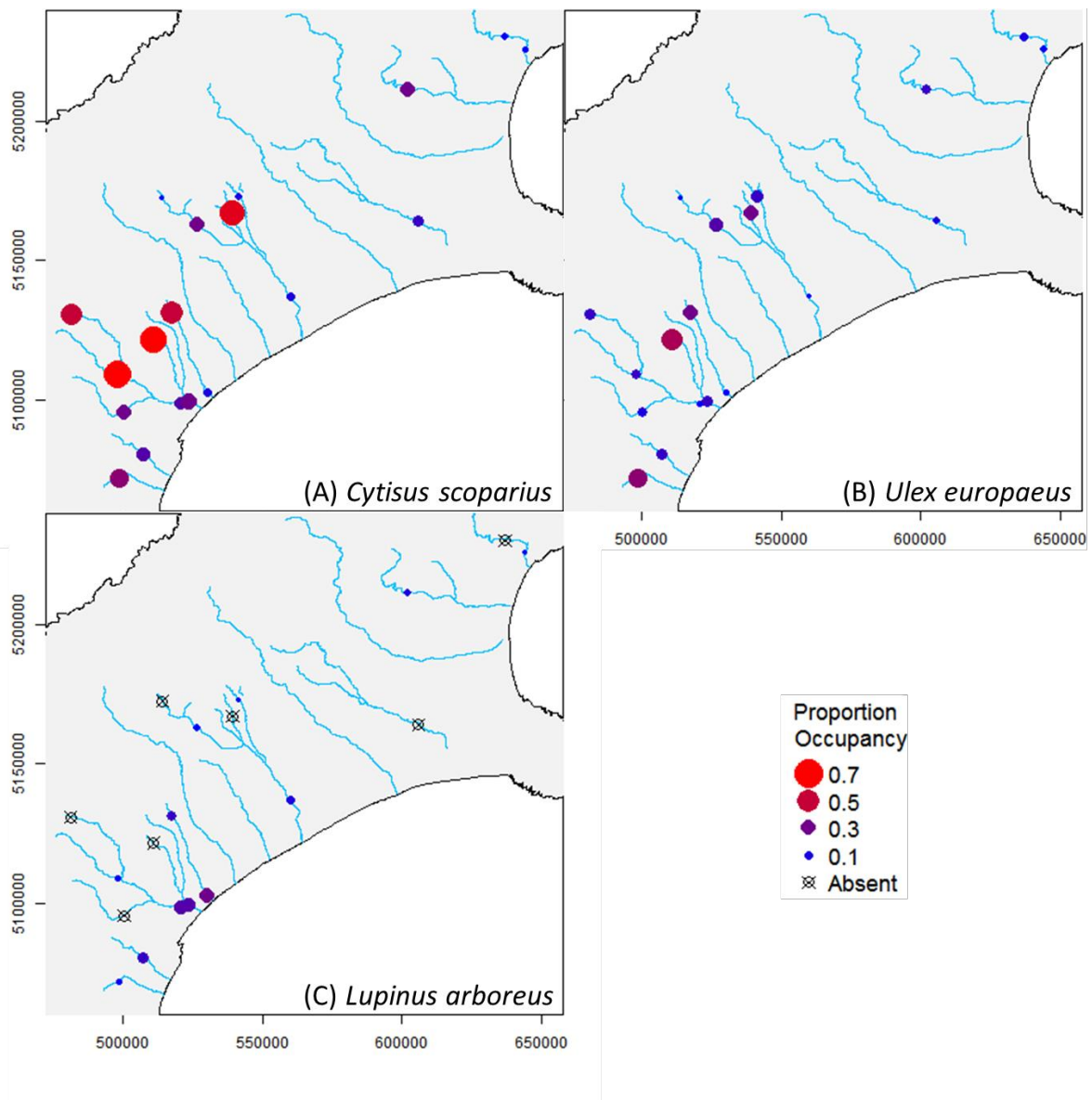
Figure 5.1: Proportion of plots occupied within the 19 river reaches studied by the three target species (A-C). The circles that indicate the location of the river reaches are coloured and sized on the same scale to facilitate comparison among species. The maximum proportion of plots occupied by any of the three species was 0.68 and was defined as the upper limit for the colour scale. The political boundary shown is the Canterbury Province and the aquamarine coloured lines represent high order rivers. The coordinate system and projection are NZGD2000, UTM Zone 59S.
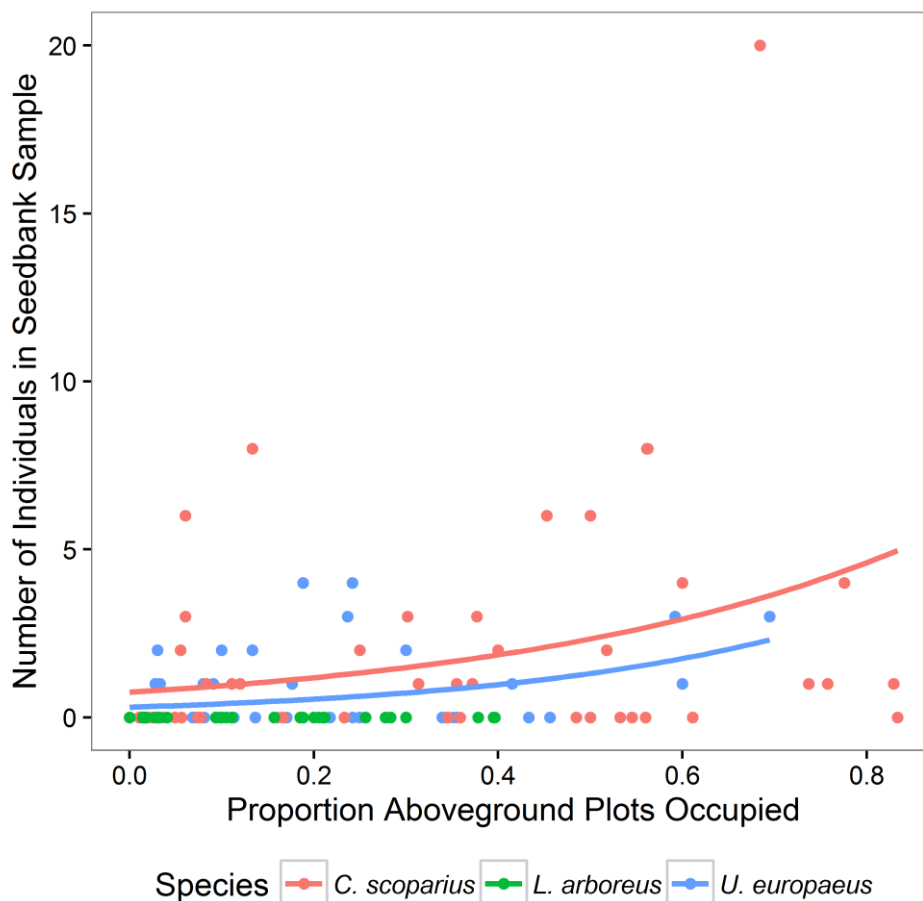
Figure 5.2: Number of individuals of the three target species found in the seedbank samples plotted against the proportion of the plots occupied by the same species above ground at that same site. *Lupinus arboreus* **was never found in the seedbank samples. The two lines are the best fit from a Poisson regression model with river reach included as a random effect.**
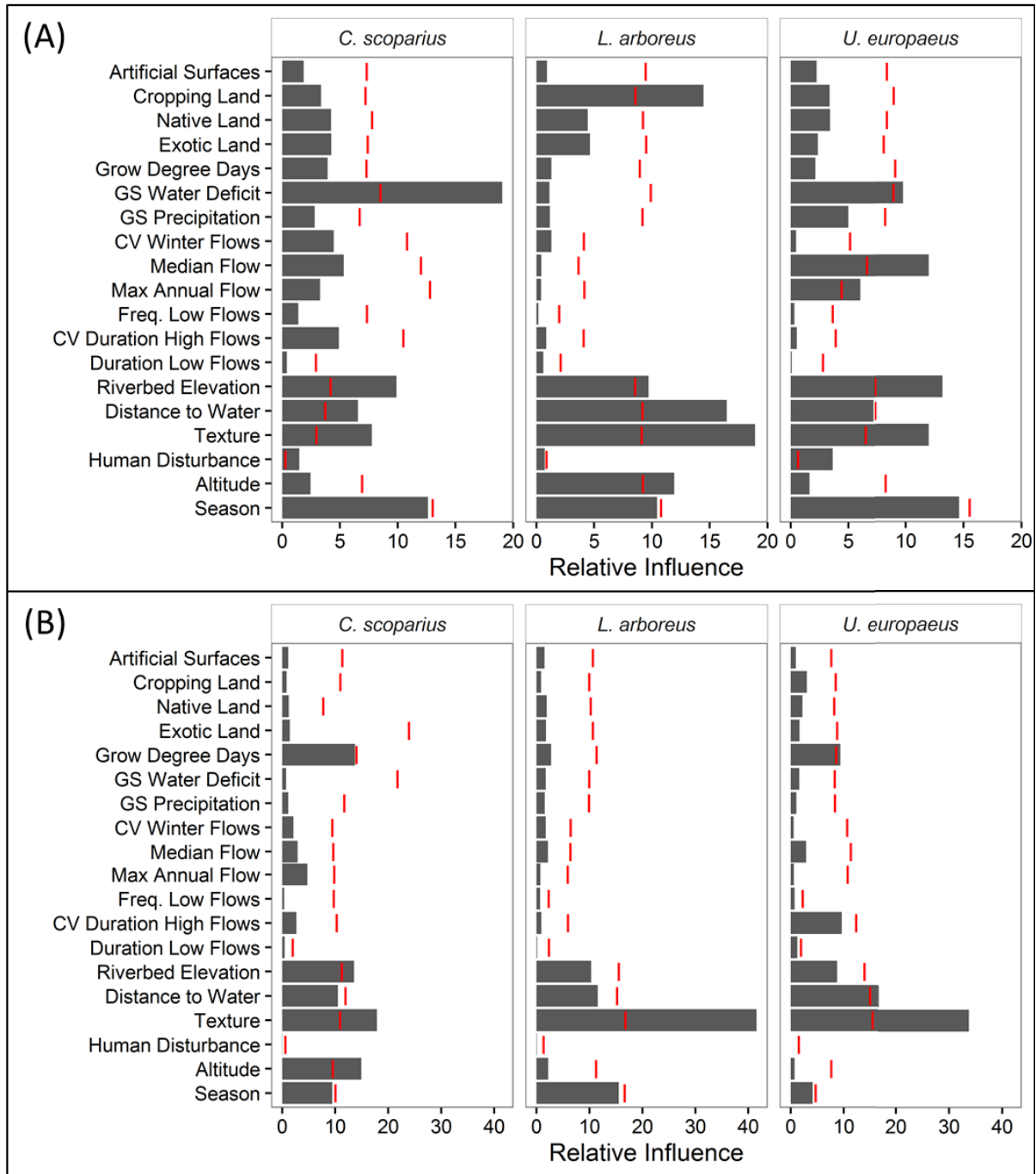
Figure 5.3: The relative influence of different predictors on the establishment (Panel A) and cover (Panel B) of the three woody nitrogen fixing legumes invading riverbed ecosystems in Canterbury. The red bars indicate the 95 percentile of relative influence values we could observe through random permutations of the sampled values. Thus, any bar that is larger than the red line indicates a statistically significant effect. Relative influence is weighted by the amount of deviance in the response variable explained, thus, predictors with larger influence values account for more of the variation in the response variable.
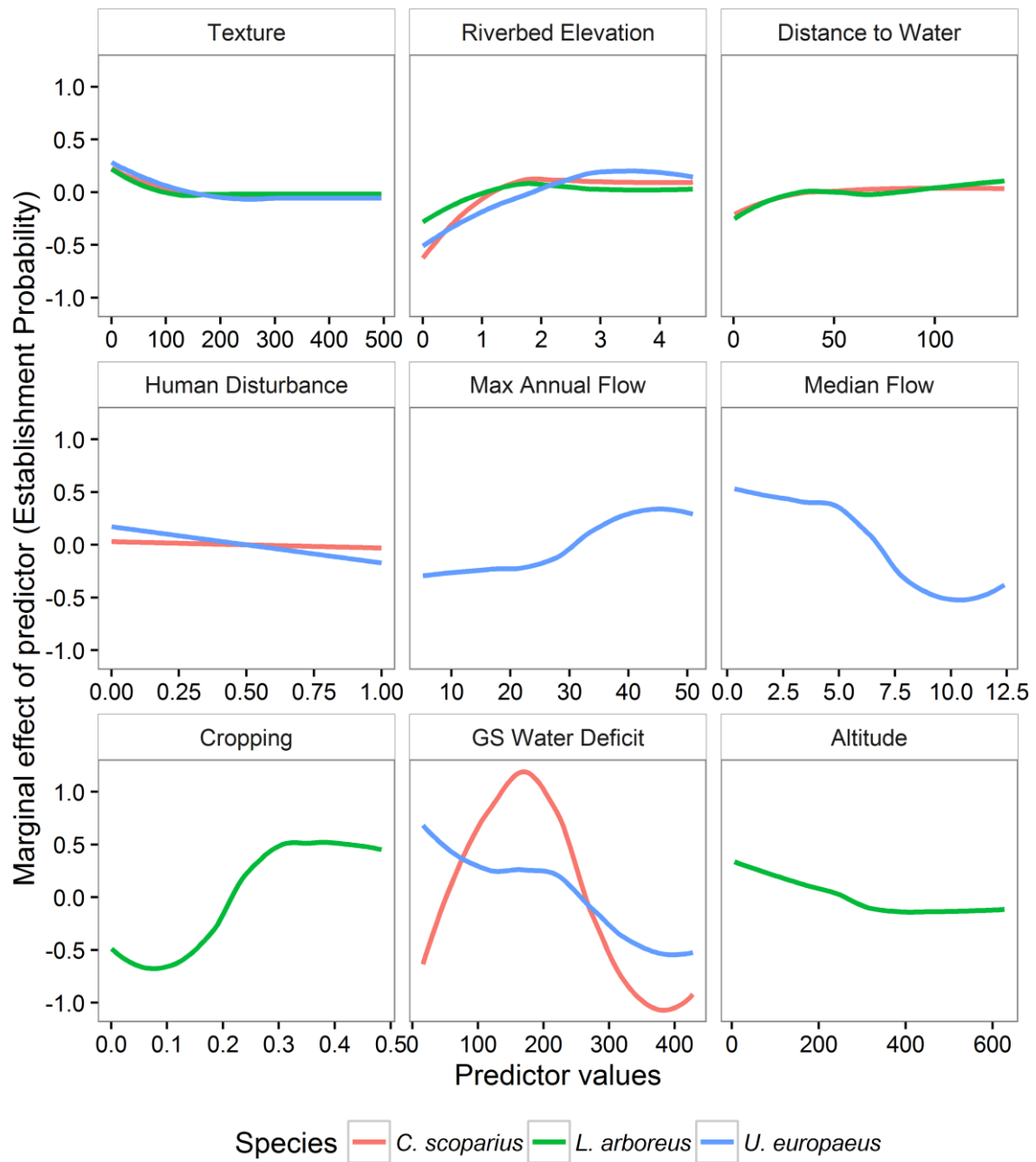
Figure 5.4: Marginal effect of significant predictors on the establishment probability of three invasive alien legumes. Only the statistically significant relationships are shown (out of a total possible 19 predictors). Thus, the absence of a species from a panel indicates that the predictor was not important for that species.
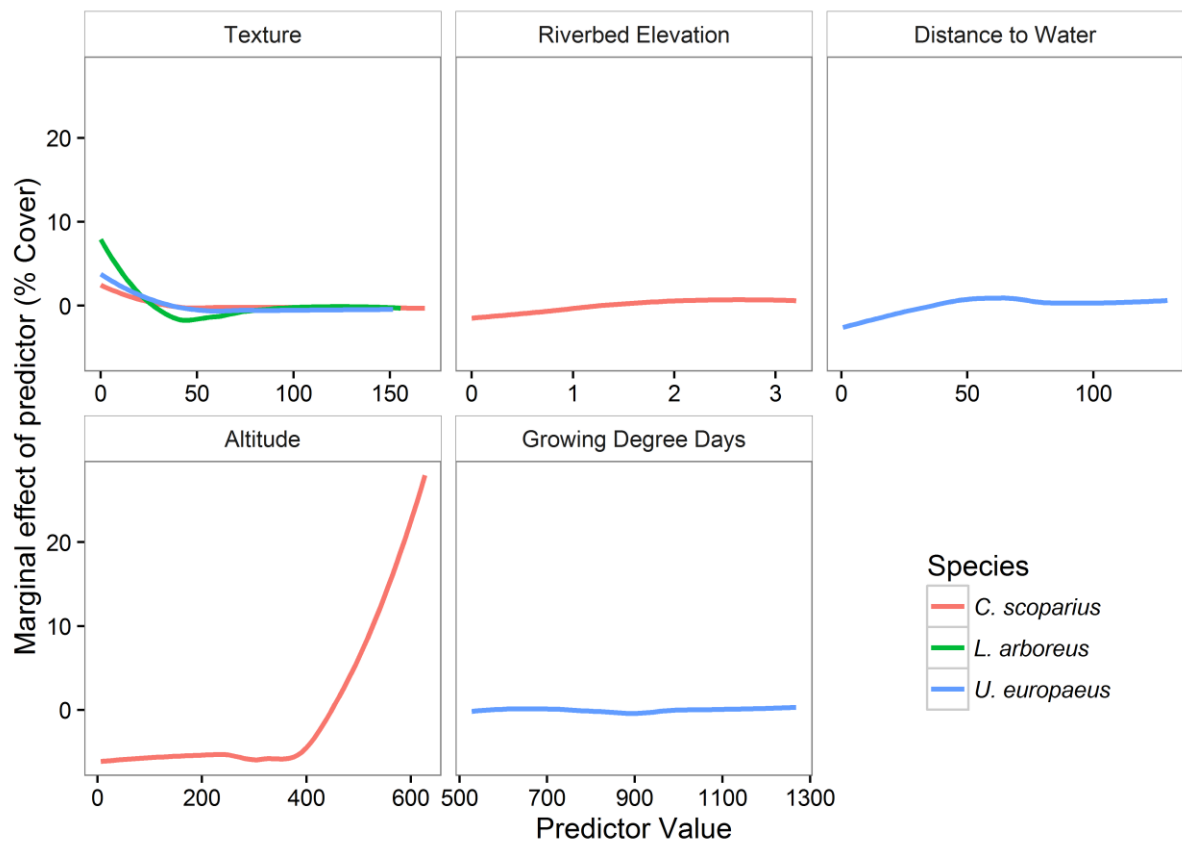
Figure 5.5: Marginal effect of predictors on the percent cover of three invasive alien legumes in braided rivers in NZ. Only the statistically significant relationships are shown (out of a total possible 19 predictors). Thus, the absence of a species from a panel indicates that the predictor was not important for that species.

5.5 Discussion

5.5.1 Do woody legumes behave the same in heavily disturbed gravel riverbed ecosystems?

The central biological question addressed in this study was: are three alien woody legumes behaving similarly in the gravel floodplains of New Zealand? The answer was mixed. At a regional scale, two of the species, *U. europaeus* and *C. scoparius* were associated with each other while *L. arboreus* was not strongly associated with either. The positive association between *U. europaeus* and *C. scoparius* matches many other observations from New Zealand and other parts of the native and invaded range (Williams 1981; Peterson & Prasad 1998; Clements *et al.* 2001). The weak or absent association between *L. arboreus* and the other two species was not unexpected, given that it evolved in coastal dunes in California, very different environments compared to the other two species. Thus, its restricted range which tended to be lower altitude may follow from the species eco-evolutionary history (Molloy, Partridge & Thomas 1991). However, *L. arboreus* has been identified as a threat in the upper reaches of the Rakaia River in New Zealand, begging the question of why this species is not common in the upper reaches of the hill and plains fed rivers (Harding 2013). The pattern of differing habitat preferences also manifest in the analysis of the environmental drivers of species establishment and cover. *Lupinus arboreus* was related to altitude and adjacent cropping (which are correlated with one another), whereas *C. scoparius* and *U. europaeus* were related to climate and flow respectively.

Although these differences existed at the regional scale, there were strong similarities among the species' environmental preferences at the floodplain scale. In general, the three species preferred areas at higher riverbed elevation, away from the active channels and with finer textured sediment. This finding is in line with the species biology as these areas are less prone to prolonged inundation which none of the three species tolerate well (Fitter & Peat 1994), and inundation is considered one of the primary limits on the encroachment of terrestrial vegetation into river channels (Miller *et al.* 2013). In sum, woody legumes appear to invade differently at a regional scale, but locally prefer similar habitats. This highlights why examining multiple scales is critical to understanding invasions (Pyšek & Hulme 2005).

5.5.2 How do river flows influence these species?

No research to date has determined whether river flows promote or constrain how these three species invade riverbeds. Despite expectations, river flows were not explanatory of species establishment or cover, except in the case of *U. europaeus* which was associated with two measures of flow magnitude: maximum annual flow (positive) and median annual flow (negative). This association was not readily explained, but the two variables are negatively correlated so species

could be responding more to one than the other (Appendix A, Table A.1). However, one reason for this relationship could be generally lower water tables during most of the year (*U. europaeus* prefers well drained soils; (Clements *et al.* 2001)) coupled with big disturbances that open up new sites for colonisation. Studies from other areas in the world suggest that flow stabilisation can cause invasion by woody species (Poff & Zimmerman 2010; Miller *et al.* 2013) but we found no association between more stable flows and woody invasion.

The climate variable growing season water deficit was associated with both *C. scoparius* and *U. europaeus* establishment. This variable is probably the hardest to interpret as it is negatively associated with growing season precipitation, adjacent native vegetation, and altitude, and positively associated with low flows, cropping and human disturbance (Appendix A, Table A.1). Land-use played little apparent role in predicting the distribution of the three species except in the case of *L. arboreus* which was associated with the amount of adjacent cropping land. This may suggest a propagule pressure effect, or it may be indicative of the geographic concentration of the species in lowland sites which is also evidenced by the significant association to altitude (altitude and cropping land are negatively associated with one another). The species' native and invaded habitat is most often coastal dunes (Molloy *et al.* 1991), suggesting lower altitude environments may be closer to the species optimal climate niche.

Regional variables appeared to play little role in predicting cover for any of the species, with the exception that higher altitude was strongly associated with higher *C. scoparius* cover. Explanations for this could be many. The higher altitude rivers we sampled tended to be less confined than lower altitude rivers, thus creating wider, less intensely disturbed floodplains. This disturbance regimes may allow broom to dominate because the local intensity of disturbance is distributed across a wider floodplain. Thus, this could be a flow relationship, indirectly mediated by altitude and river management activities.

5.5.3 Did seedbank data provide important insights?

The total number of individuals found in the seedbank samples matched the relative abundance of the species aboveground, with *C. scoparius* most prevalent and *L. arboreus* not detected. The abundances were exceedingly small (100, 32 and 0), however these were comparable to a previous study that looked at germinable seed for *C. scoparius* in river gravels (Williams 1981). Not finding *L. arboreus* in the seedbank at all was surprising given it was locally abundant at a few of the sampling sites. *Lupinus arboreus'* absence and the other two species low frequency in seedbank samples was likely due to the low relative abundance of *L. arboreus* in the whole sampling area, and that we were sampling in areas in the tail of the primary dispersal kernel (i.e. not underneath closed canopy woody communities). We only found 100 individuals of broom in all the seedbank samples which was

relatively small when we consider a single broom individual can produce >10,000 seeds annually (Wayloff & Richards 1977), and these seeds easily become part of the bed load (Watterson & Jones 2006). The low numbers of germinated individuals were consistent with Williams (1981) who found relatively low densities of *C. scoparius* seeds in river gravels (12-116 per m^2) and low germinability (0-37% on average) depending on site and whether there was a recent flood. Although these low numbers made it difficult to draw conclusions about dispersal processes and dispersal limitation, seedbank samples tied to above ground samples can still be useful in further demographic distribution modelling studies, if recovery sampling methods are improved upon (e.g. a more complete approach that recovers dormant seed as well).

5.5.4 Did more detailed data improve knowledge gain?

Additional data collected about species cover, life-stage and seedbank gave mixed improvements in our ability to infer the drivers of each of the three species in gravel riverbed ecosystems. The seedbank data were less useful, but this was a methodological shortcoming that could be overcome in future studies. Future work targeting the seedbank life-stage should sample greater volumes of material and recover dormant seed rather than only germinable seed to increase detectability. Conversely, percent cover provided vital additional data, because it revealed different drivers of dominance at regional scales compared to establishment. Furthermore, the fact that there were few constraints on species cover suggested that primary constraints on each of these species were in the establishment phase.

5.6 Management implications

We have identified key drivers of the abundance of three woody legumes that characterise braided river gravel floodplains in New Zealand. Native nitrogen-fixers are not common in these New Zealand ecosystems (Williams & Wiser 2004), so invasive woody legumes are hypothesised in turn to promote the establishment of a host of other alien plants (McQueen, Tozer & Clarkson 2006). Thus, drivers that promote these species will need to be managed or mitigated to prevent or slow future invasions at local and regional scales. That the most widely distributed and abundant species, *C. scoparius*, was not associated with river flows, suggests that changes in water extraction rates or climate change are unlikely to dramatically change the distribution of woody legumes in this ecosystem in the future. However, that all the species preferred areas at higher riverbed elevations and further away from active channels suggests that if flows are progressively decreased and/or stabilised, the species could spread across more of the flood plain, with the assumption that this pattern is related to inundation or flow disturbance.

Chapter 6 - General Discussion

6.1 Thesis Aims

The overall aim of my thesis was to better understand whether river flows structured the richness and abundance of alien plants in New Zealand gravel riverbeds. I aimed to determine the drivers of current invasion patterns in the system and infer what may happen under future conditions. This aim came with a set of three challenges.

1. Could I study the effects of flow-disturbance in a reasonable time-frame?

2. Were there any emergent generalisations that could convincingly demonstrate that the results were not system-specific?

3. What practical advice can I give to managers of braided river in New Zealand?

Each chapter has already presented a detailed discussion of main findings so I have limited the general discussion below to highlighting how this thesis addressed each of these general questions. In doing so, I highlight points of novelty, and discuss avenues for future research that can draw from this body of work.

6.2 Lessons for ecohydrological studies

One of the largest challenges arose during the conceptualisation of this project. How could I logistically study the effects of flow regimes on invasion in a three year PhD? Past studies of invasions in New Zealand rivers had either (1) tracked or manipulated plant community development for 4-10 years in one geographic location (Bellingham *et al.* 2005; Holdaway & Sparrow 2006; Peltzer et al. 2009; St John *et al.* 2012; Fukami et al. 2013), (2) used aerial imagery to look at changes in vegetation through time (usually large time steps, and coarse vegetation classification) and compared that to flow events in the intervening time (Caruso *et al.* 2012, 2013), or (3) used large scale surveys and statistical modelling to determine the drivers of alien and native plant communities (Williams & Wiser 2004). These studies all added valuable information about vegetation ecology and invasion in riverbed ecosystems, but quantitative relationships between river flows and invasion in these ecosystems were still too river specific, or too low resolution, to provide guidance for management or to inform predictions about future dynamics. The solution I proposed was a flow-gradient analysis. Gradient analyses have proved invaluable to, amongst other fields, climate change research where ecological attributes have been sampled across climate gradients (e.g. altitude, temperature and moisture) to infer how future climate may alter the ecology of an ecosystem (Fukami & Wardle 2005;

De Frenne *et al.* 2013). Similarly, I aimed to use gradient analysis to determine if flow regime was related functionally to invasion in the system, but I had to figure out a robust way to do this.

This resulted in the framework outlined and applied in Chapter 2. The framework addressed several critical challenges that had not yet been considered in the ecohydrology literature. The framework accounted for uncertainty in estimating the individual flow indices, determined whether time trends could confound differences among rivers in the network, and reduced the dimensionality of the many flow indices that are often considered when describing flow regimes. The mathematical approach and logical framework is unique in that it allows for trade-offs to be assessed between adding more gauged reaches in a network (which represent more data points for a gradient analysis) versus excluding them due to inadequacies in the data. It also borrows information from stations with longer records to assess time trends and applies a statistical approach to extracting defensible gradients from the many flow indices. My framework unites challenges that have hitherto been problematic since ecohydrological gradient analyses were first proposed up to a decade ago (Olden & Poff 2003; Monk *et al.* 2007; Kennard *et al.* 2010). This provides a standardised approach so that flow-gradient analyses can be comparable globally across future studies.

The framework has broad reaching applications across ecohydrology. It is directly relevant to the international framework driving ecohydrological research – the Ecological Limits of Hydrological Alteration (ELOHA) (Poff *et al.* 2010), that highlights a clear need for more quantitative studies linking flows to the ecology of rivers. These relationships can be used to apportion environmental flows (water left in the river for environmental reasons) and to predict the impacts of human modification on river ecology (Poff *et al.* 2003; Davies *et al.* 2014; Webb *et al.* 2015).

However, whilst gradient analyses have considerable advantages, they are not a panacea. I think they have the greatest value when monitoring networks are initially established. Ecological data collected on a network of rivers that vary in flow regime can be used in the gradient analysis framework to derive an initial set of flow-ecology relationships. These can then be refined and tested using time series data across the same network. Snapshot data (single time point), such as those collected in this thesis, have some limitations, especially in disentangling confounded independent variables. Time-series data can resolve some of these issues, whereby more robust flow-ecology relationships can emerge and predictions can be tested.

6.3   Lessons for invasion ecology

Once the study methodology was sorted, I set out to understand how plant species, especially aliens, were responding to river flows across the ecosystem. Although there were many interesting results, I reiterate the general findings that have broad application to invasion ecology. First, Chapter 3

demonstrated that aliens and natives can be driven by fundamentally different ecological variables. This lesson is obvious to ecologists in New Zealand (e.g. Hulme, Pyšek & Duncan 2011; Wilson & Lee 2012) and is a result of the somewhat unique colonisation and species introduction history (Chapter 1). However, this finding that has emerged from my study of gravel riverbeds is an important counter example to an over-generalised message that species origin does not matter when it comes to understanding vegetation dynamics in ecosystems (Davis *et al.* 2011). Obviously, origin in and of itself is not a mechanism of ecological disruption, however it can be an effective surrogate for historical and eco-evolutionary differences in alien flora relative to native (Hulme *et al.* 2011). Importantly, these findings highlight the utility of studies that contrast alien and native vegetation responses to the environment for understanding ecosystem dynamics, which can subsequently be translated into management recommendations.

Not only did I find that aliens and natives differed, but they were associated with completely different environmental drivers, which is a novel discovery. Previous work has either found environmental conditions that favoured natives favoured aliens as well (Stohlgren *et al.* 2003; Fridley *et al.* 2007) or that aliens and natives were related to the same drivers but in opposite directions (Tomasetto *et al.* 2013; Pouteau *et al.* 2015). Therefore, when seeking to understand landscape-scale drivers of invasion in an ecosystem or region, it is possible that native and alien species are driven by completely different factors, thus requiring radically different management strategies. Although this finding was novel, it was not completely unexpected: this study focused on a heavily disturbed ecosystem, where the native flora generally was known to lack disturbance adaptations while in contrast the alien flora is particularly well suited to disturbed conditions (Williams & Wiser 2004; Hulme *et al.* 2011; Wilson & Lee 2012).

Chapters 3 & 4 augment literature that highlights disturbance is a driving force behind alien plant invasion (Catford *et al.* 2009; Jauni *et al.* 2015). Chapter 3 revealed that rivers with greater variability in winter flows (arising from more high-magnitude flood events) had significantly more alien species; Chapter 4 examined this phenomenon in more detail and showed that this was due to increases in annual and biennial alien plants. This pattern fits well within what we have come to understand about plant invasion: that aliens are promoted by disturbance (Colautti *et al.* 2006; Jauni *et al.* 2015) due to life-history adaptations such as short generation time and high fecundity (Ordonez, Wright & Olff 2010; van Kleunen *et al.* 2010). However, I also observed an increase in perennial alien herbs when hydrologic drought increased (Chapter 4), demonstrating a shift in the alien community that does not necessarily follow disturbance predictions. Furthermore, woody species invaded areas of floodplain that had more protection from large hydrological disturbances. Thus, in these braided riverbed ecosystems, the alien flora showed exceedingly diverse responses, with some functional groups following predictions from disturbance theory, and others invading

different ends of disturbance and stability gradients within the floodplains. Thus, I suggest that the utility of generalisations such as "disturbance promotes invasion" often mask the realities of shifts in vegetation communities as environmental gradients (such as disturbance) change. Alien responses to these gradients should therefore be analysed and interpreted more holistically (i.e. using a community and functional ecology approach) rather than simply searching for positive associations between disturbance and alien species richness or cover.

6.4   Lessons for the conservation of New Zealand gravel riverbeds

The most general lesson for conservation from my research highlighted that managing against alien plants will not necessarily promote native plants and vice versa (Chapter 3). This runs counter to most management strategies that assume that removal of alien plants can promote the recovery of native plant biodiversity with the implicit assumption that competitive interference is the underlying mechanism for alien dominance (Levine, Adler & Yelenik 2004). However, my findings fit with a community assembly and succession view of invasion ecology, where dispersal and colonisation traits are more important in post-disturbance assembly, while competition increases in importance as time since disturbance increases or as succession progresses (Catford *et al.* 2012a). Unfortunately for braided riverbed ecosystems, this signifies that they are likely to continue to be invaded unless propagule sources are removed and floodplain populations of aliens simultaneously controlled, as there are no native plant species or communities to provide biotic resistance to alien species or reinvade *en masse* to replace the invaders (Levine *et al.* 2004).

Predicting the future of these systems under altered disturbance regimes was one of the primary goals of each of the three invasion studies in Chapters 3-5. I found that increased disturbance variability was associated with an increase in the number of alien species and, specifically, an increase in the frequency of annuals and biennials (Chapter 4). However, at a local scale, dominance of woody legumes was greatest in areas with lower levels of disturbance and inundation from the active river channels. This could suggest that woody legumes are currently limited by inundation or disturbance locally. Thus, one could imagine that if climate change or water abstraction were to decrease the water table (via longer or more severe drought periods: Mullan *et al.* 2008), then we may see these woody species encroach across larger areas of the floodplain. Hence on the one hand, changes in variability in winter flows (i.e. more flooding; Hirabayashi *et al.* 2013) may keep woody legumes where they are but promote the invasion of annual and biennial species, whereas more frequent or severe drought (Mullan *et al.* 2008) may promote woody legumes and perennial herbs as low flow dynamics shift (Chapters 4 & 5). The effect of altered composition of the vegetation on the collective impact of these species remains to be seen, but at the very least

more woody legumes will likely lead to more channelisation and more nitrogen input into the ecosystem as a whole (Hicks *et al.* 2008; Drake 2011; Gurnell 2014).

Although I observed local patterns of invasion with the three woody invaders, there were no compelling relationships between average flow regimes and the regional-scale abundance or distribution of these individual species. However, this does not necessarily mean that river flows do not affect the distribution and abundance of these species in some way. One of the limitations of the study was its inability to capture the effects of discrete and/or extreme events on the riverbed vegetation. Rather, it was only capable of addressing how the general behaviour of the river (average flow regime from the past decade) was related to the current status of the vegetation. We know that large flow events affect woody vegetation in specific rivers (Hicks *et al.* 2008; Caruso *et al.* 2012, 2013). Thus, it would be highly beneficial to collect the same data each year (at least at a subset of the rivers that span the flow gradients) so that vegetation dynamics can assessed relative to individual flow events. This would provide another dimension to the knowledge gained from this study and give a more complete picture of how river flows affect invasion in this system.

6.5 Future work

Discerning cause and effect relationships in observational studies is impossible and inference is made more difficult when data are from a single snapshot in time. My studies have provided a strong foundation or baseline for future work to monitor changes in the plant invasion and composition in floodplain ecosystems, and further explore the effects of flow regimes and individual flow events on the assembly and dynamics of invasion. Weather patterns and catchment areas are sufficiently variable across the range of rivers sampled to examine the effects of different extreme events on plant community destruction and reassembly. Thus, the relevance and robustness of the flow-invasion relationships found in Chapters 3 & 4 could be explored further by monitoring vegetation dynamics across the sites in this study. That all 2,930 plots have highly precise GPS locations provides the perfect opportunity to assess vegetation dynamics with the confidence of a direct comparison of the same location through time.

In addition to further validating the flow-ecology relationships that were the focus of the thesis, interesting questions remain to be explored about the succession of species in gravel floodplains and the interaction between alien and native species. In particular, I would be interested to know whether alien nitrogen fixing plants facilitate the invasion of alien non-nitrogen fixing species in this relatively nutrient poor ecosystem (Simberloff 2006), particularly considering the dominance of nitrogen fixing species in this ecosystem (Williams & Wiser 2004; Drake 2011; Brummer *et al.* 2016b; Chapters 3-5). The finding that herbaceous perennial nitrogen-fixing aliens had high abundance in addition to the woody legumes (Chapter 4) adds weight to the evidence for

potentially dramatic changes to the biogeochemical cycles of these ecosystems compared to their presumed uninvaded state. Furthermore, the four studies in my thesis do not address whether alien species impact native species. The analyses in Chapter 3 suggested that natives were dispersal limited, suggesting that aliens do not directly impact natives. However, this pattern could also be caused by intense propagule pressure by disturbance-adapted aliens at lower altitudes that prevent the establishment of natives. Analyses of the current dataset could assess the correlations between nitrogen-fixer abundance and alien species richness and abundance, as well as the correlation between alien and native richness and abundance (e.g. Bernard-Verdier & Hulme 2015). If correlations are present, these results could be used to inform manipulative experiments to establish causality and explore the ecosystem scale consequences of nitrogen-fixer mediated invasion, and alien impacts on native species.

Finally, I suggest that there remains scope to investigate the role of propagule flows from the adjacent terrestrial ecosystems (especially cropping and pastoral systems), riparian zone and gravel riverbeds. The findings of this study suggest propagule flow is critical for native species (Chapter 3), but what was left unclear is how it affects aliens, while it is of known importance in other riverbed and riparian ecosystems (e.g. Truscott *et al.* 2006; Eschtruth & Battles 2009). To what degree might the riparian zone act as a contributor to the gravel riverbed communities? Could native riparian restoration coupled with instream control of alien species make real gains in shifting the ecosystem to a less invaded state? In other words, is it possible to take a whole-system approach to controlling communities of invasive species from the top of the riverbed profile down, just as we think about controlling individual invasive species within a catchment from the headwaters to the mouth (but see Wadsworth *et al.* 2000 for a comparison of different control strategies in river ecosystems). Furthermore, experimental tests of whether assisted dispersal could successfully establish native plants in lower altitude reaches could confirm whether the restricted distribution of natives is primarily due to low propagule pressure, as suggested in Chapter 3.

6.6   Parting words

To answer the questions at the beginning of this discussion: 1) gradient analyses can serve as investigative tools in freshwater ecosystems just as they do in other ecological disciplines, 2) the general findings that management against aliens does not necessarily mean management for natives and the associations between species traits and disturbance and drought gradients were important lessons to add to the global literature, and 3) I was able to make recommendations for river managers. While these were important lessons in improving our understanding of how the system works, it still has not solved the greater conservation issue. We still need strategies to control established alien communities (not just species) at a landscape scale, and we still need a better

understanding of how dispersal drives invasion dynamics in these systems to try and reduce the level of invasion and reinvasion across gravel floodplains in New Zealand. More ambitiously, if we are to preserve or restore the biodiversity values of New Zealand braided rivers, we need to figure out how to do less water intensive agriculture so that natural flow regimes can be maintained or reclaimed.

Appendix A

Supplemental tables and figures for Chapter 3

Table A.1. Table of Spearman rank correlation coefficients between the 19 predictor variables used in the boosted regression tree modelling. Asterisks denote statistical significance (P < 0.05) as computed using the 'rcorr' function in the package 'Hmisc' (Harrell, 2015). Significant positive correlations are highlighted in blue while significant negative correlations are highlighted in red. Correlations and their significance were determined at the river reach scale. The mean of site and plot scale variables were calculated to calculate the correlations to ensure the degrees of freedom in the statistical tests was most appropriate. Names correspond with descriptions in Table 3.1 in the main text.

	Cropping	Exotic Grassland	Artificial Surfaces	Native Land	Growing Degree Days	GS Precipitation	GS Water Deficit	Median Flow	CV August Flows	Max Annual Flow	Low flow days	Duration Low Flows	CV Max 7day Means	Texture	Riverbed Elevation	Distance to water	Human Disturbance	Altitude
Cropping																		
Exotic Grassland	-0.39																	
Artificial Surfaces	0.81*	-0.45																
Native Land	-0.79*	0.01	-0.75*															
Growing Degree Days	0.34	0.15	0.48*	-0.47*														
GS Precipitation	-0.79*	0.16	-0.76*	0.85*	-0.54*													
GS Water Deficit	0.76*	-0.08	0.75*	-0.82*	0.69*	-0.95*												
Median Flow	-0.04	-0.47*	0.05	0.16	-0.36	0.23	-0.32											
CV August Flows	0.59*	0.18	0.42	-0.67*	0.33	-0.65*	0.58*	-0.41										
Max Annual Flow	0.40	0.15	0.27	-0.46*	0.45	-0.51*	0.49*	-0.73*	0.76*									
Low flow days	0.39	0.22	0.36	-0.40	0.76*	-0.55*	0.71*	-0.51*	0.49*	0.51*								
Duration Low Flows	0.40	0.16	0.49*	-0.48*	0.78*	-0.61*	0.73*	-0.49*	0.53*	0.52*	0.93*							
CV Max 7day Means	0.45	0.29	0.52*	-0.68*	0.57*	-0.62*	0.65*	-0.4	0.80*	0.54*	0.70*	0.81*						
Texture	-0.46*	0.37	-0.62*	0.48*	-0.24	0.53*	-0.49*	-0.18	0.11	0.15	0.05	-0.06	0.00					
Riverbed Elevation	0.30	-0.01	0.05	-0.21	0.15	-0.21	0.24	-0.22	0.50*	0.33	0.44	0.43	0.49*	0.28				
Distance to water	0.42	-0.22	0.40	-0.37	0.40	-0.47*	0.43	-0.16	0.41	0.30	0.26	0.37	0.45	-0.41	0.46*			
Human Disturbance	0.75*	-0.16	0.64*	-0.77*	0.46*	-0.76*	0.74*	-0.13	0.53*	0.39	0.42	0.50*	0.53*	-0.47*	0.23	0.49*		
Altitude	-0.85*	0.16	-0.78*	0.91*	-0.53*	0.93*	-0.87*	0.20	-0.75*	-0.58*	-0.45	-0.53*	-0.66*	0.47*	-0.34	-0.57*	-0.78*	
Season	-0.69*	0.11	-0.46*	0.53*	-0.46*	0.74*	-0.72*	0.25	-0.56*	-0.58*	-0.62*	-0.54*	-0.38	0.14	-0.21	-0.11	-0.68*	0.65*
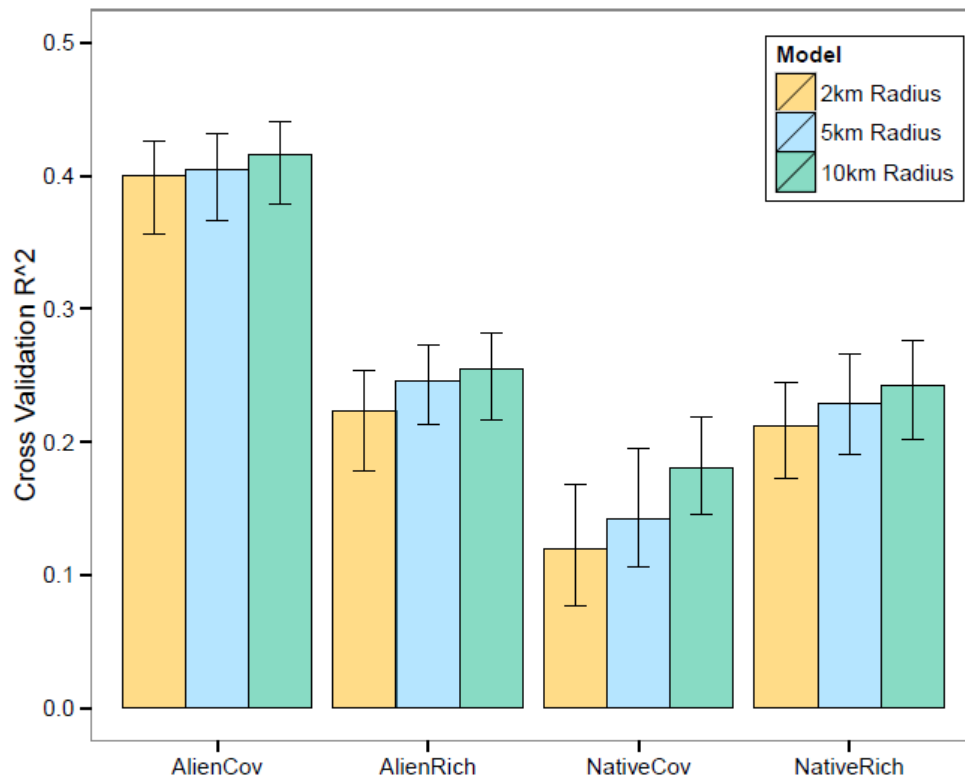
Figure A.1. Comparison of models built using all the variables in Table 3.1 while varying the radius used to generate the land-use predictors. Bars represent mean cross validation R2 while the error bars are 95% quantile intervals for 500 runs of the model fitting and cross-validation routine. Radius did not influence models of alien cover or richness while the 10 km radius produced higher performing models compared to two km radius land-use predictors for native cover and richness. Thus, all land-use predictors for the analyses used land-use predictors calculated with a 10 km radius. An analysis that included all land-use variables at the three different scales showed no improvement over the 10 km radius models, suggesting that different land-use predictors were not influencing the responses at different scales.
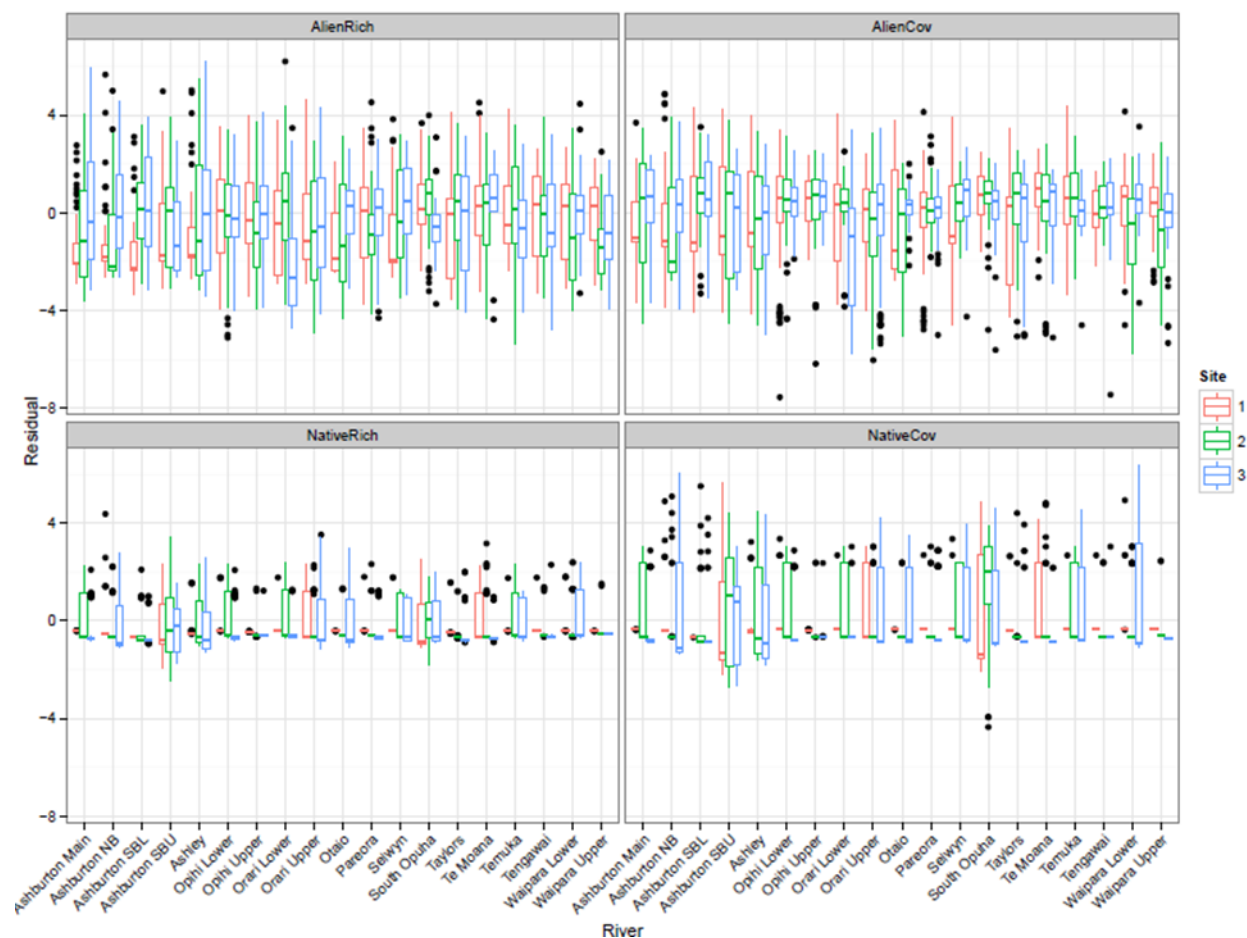
Figure A.2. Model residuals grouped by river reach and site combinations for the four different response variables following Buston & Elith (2011). Sites and river reaches with consistent positive or negative residuals indicate missing site or reach level variables in the model. Reference: Frank E Harrell Jr, with contributions from Charles Dupont and many others. (2015). Hmisc: Harrell Miscellaneous. R package version 3.16-0. https://CRAN.R-project.org/package=Hmisc

Appendix B

Species List

B.1   Species list from the riverbed survey

Table B.1: List of species identified in the riverbed survey and the number of transects, sites and reaches each occupied (total number of each given in parentheses). Some species were only identified to genus but were still differentiated from other species within the genus. Origin is included. Native species that labelled as either endemic or non-endemic. An '*' denotes a species considered an environmental weed by Howell (2008). Nomenclature follows Breitwieser I., Brownsey P.J., Nelson W.A., Wilton A.D. eds. (2016) Flora of New Zealand Online. Accessed at www.nzflora.info.

Scientific Name	Origin	Transects (196)	Sites (57)	Reaches (19)
Acacia sp.	Alien*	1	1	1
Acaena sp1		2	2	2
Acaena sp2		6	5	5
Acer pseudoplatanus	Alien*	5	4	4
Achillea millefolium	Alien	110	46	17
Agrostis capillaris	Alien*	70	34	19
Agrostis stolonifera	Alien	133	45	17
Aira caryophyllea	Alien	27	18	11
Alnus glutinosa	Alien*	7	5	3
Alopecurus geniculatus	Alien	7	4	3
Anagallis arvensis	Alien	52	26	12
Anaphalioides bellidioides	Endemic	3	2	1
Anthemis cotula		1	1	1
Anthoxanthum aristatum	Alien	6	3	3
Anthoxanthum odoratum	Alien	129	53	19
Aphanes arvensis	Alien	4	4	3
Arabidopsis thaliana	Alien	5	3	3
Arenaria serpyllifolia	Alien	45	31	16
Aristotelia serrata	Endemic	5	3	2
Arrhenatherum elatius	Alien	92	37	17
Barbarea intermedia	Alien	79	27	12
Barbarea vulgaris	Alien	6	4	3
Betula pendula	Alien	2	1	1
Bromus diandrus	Alien	89	40	18
Bromus hordeaceus	Alien	20	17	14
Bromus tectorum	Alien*	14	6	4
Bromus willdenowii	Alien*	18	13	7
Buddleja davidii	Alien*	8	2	1
Calandrinia menziesii	Alien	4	4	3

Callitriche stagnalis	Alien	14	11	9
Calystegia silvatica	Alien*	26	14	7
Capsella bursapastoris	Alien	19	13	9
Cardamine hirsuta	Alien	42	24	13
Carduus nutans	Alien*	32	19	11
Carex spp.		19	13	11
Carmichaelia corrugata	Endemic	2	1	1
Centaurium erythraea	Alien	2	2	2
Centipeda cunninghamii	Non-endemic	1	1	1
Cerastium fontanum	Alien	95	39	15
Cerastium glomeratum	Alien	17	10	7
Chenopodium album	Alien	27	18	11
Chenopodium pumilio	Alien	1	1	1
Cirsium arvense	Alien*	51	33	17
Cirsium vulgare	Alien*	34	21	14
Clematis vitalba	Alien*	62	28	12
Colobanthus apetalus	Non-endemic	4	4	2
Conium maculatum	Alien	54	25	12
Conyza spp.	Alien	44	20	9
Coprosma atropurpurea	Endemic	1	1	1
Coprosma propinqua	Endemic	11	7	5
Coriaria plumosa	Endemic	1	1	1
Coriaria sarmentosa	Endemic	26	17	9
Coronopus didymus	Alien	23	10	4
Cotoneaster spp.	Alien*	2	1	1
Cotula australis	Non-endemic	1	1	1
Crataegus monogyna	Alien*	3	2	1
Crepis capillaris	Alien	117	49	18
Cynosurus cristatus	Alien	7	4	3
Cytisus scoparius	Alien*	147	53	19
Dactylis glomerata	Alien*	149	57	19
Daucus carota	Alien	35	16	6
Dianthus armeria	Alien	23	15	8
Dichelachne crinita	Non-endemic	1	1	1
Digitalis purpurea	Alien	37	20	9
Discaria toumatou	Endemic	6	4	4
Echium vulgare	Alien*	106	43	18
Elymus solandri	Endemic	4	4	3
Elytrigia repens	Alien	18	12	9
Epilobium brunnescens	Endemic	10	9	7
Epilobium ciliatum	Alien	31	20	11
Epilobium melanocaulon	Endemic	15	8	4
Epilobium microphyllum	Endemic	37	20	10
Epilobium rostratum	Endemic	4	2	1
Erodium cicutarium	Alien	3	2	2
Eschscholzia californica	Alien	25	9	4
Euchiton involucratus	Non-endemic	1	1	1
Euchiton sphaericus	Non-endemic	9	7	5

Festuca rubra	Alien*	154	55	19
Foeniculum vulgare	Alien	9	3	1
Fumaria officinalis	Alien	32	16	7
Galium aparine	Alien	73	33	17
Galium murale	Alien	2	2	1
Galium palustre	Alien	4	2	1
Geranium dissectum	Alien	1	1	1
Geranium molle	Alien	2	1	1
Glyceria fluitans	Alien*	16	12	7
Griselinia littoralis	Endemic	1	1	1
Gunnera sp.	Endemic	1	1	1
Haloragis erecta	Endemic	2	2	2
Helichrysum depressum	Endemic	2	1	1
Hieracium lepidulum	Alien*	10	9	5
Hieracium praealtum	Alien*	6	4	3
Holcus lanatus	Alien*	160	54	19
Hydrocotyle heteromeria	Endemic	3	3	2
Hydrocotyle microphylla	Endemic	1	1	1
Hypericum perforatum	Alien*	56	29	14
Hypochaeris radicata	Alien	84	41	17
Impatiens glandulifera	Alien	3	2	1
Isolepis aucklandica	Non-endemic	13	10	8
Juncus articulatus	Alien*	78	39	17
Juncus bufonius	Alien	105	47	19
Koeleria novozelandica	Endemic	1	1	1
Lachnagrostis lyallii	Endemic	1	1	1
Lamium purpureum	Alien	1	1	1
Lapsana communis	Alien	35	19	11
Leontodon taraxacoides	Alien	18	11	10
Leucanthemum vulgare	Alien	102	40	14
Leucopogon fraseri	Non-endemic	2	2	2
Leycesteria formosa	Alien*	6	3	2
Linaria arvensis	Alien	2	1	1
Linum catharticum	Alien	34	21	10
Logfia minima	Alien	2	2	2
Lolium italicum	Alien	10	6	4
Lolium perenne	Alien*	59	33	19
Lotus pedunculatus	Alien*	95	42	16
Lupinus arboreus	Alien*	59	26	12
Lupinus polyphyllus	Alien*	1	1	1
Luzula rufa	Endemic	1	1	1
Luzula spp.		5	3	2
Lythrum hyssopifolia	Alien	4	3	2
Mahonia aquifolium	Alien	1	1	1
Marrubium vulgare	Alien	2	2	2
Matricaria discoidea	Alien	3	2	2
Medicago lupulina	Alien	52	20	8
Medicago minima	Alien	6	4	2

Melilotus albus	Alien	28	10	4
Mentha spicata	Alien	4	4	3
Mimulus guttatus	Alien*	113	50	19
Mimulus moschatus	Alien	10	6	6
Muehlenbeckia australis	Non-endemic	2	1	1
Muehlenbeckia axillaris	Non-endemic	39	21	12
Muehlenbeckia complexa	Non-endemic	14	9	6
Muehlenbeckia ephedroides	Endemic	1	1	1
Myosotis arvensis	Alien	8	6	5
Myosotis laxa	Alien	14	13	10
Myosotis stricta	Alien	5	5	3
Myricaria germanica	Alien*	3	3	2
Nasturtium microphyllum	Alien	38	23	13
Navarretia squarrosa	Alien*	15	9	5
Oenothera stricta	Alien	44	18	7
Origanum vulgare	Alien	4	3	2
Orobanche minor	Alien	4	4	3
Oxalis exilis	Non-endemic	5	5	4
Papaver rhoeas	Alien	24	12	6
Parentucellia viscosa	Alien	12	10	6
Pastinaca sativa	Alien	20	9	5
Persicaria hydropiper	Alien	72	30	14
Persicaria maculosa	Alien	96	40	17
Persicaria prostrata	Alien	18	8	6
Phalaris aquatica	Alien	1	1	1
Phleum pratense	Alien	2	2	2
Pilosella officinarum	Alien*	43	25	14
Pimelea prostrata	Endemic	3	2	1
Pittosporum tenuifolium	Endemic	1	1	1
Plantago lanceolata	Alien	158	52	19
Plantago major	Alien	24	15	9
Poa annua	Alien	29	22	14
Poa lindsayi	Endemic	11	4	2
Poa maniototo	Endemic	1	1	1
Poa pratensis	Alien	23	14	11
Poa trivialis	Alien	82	37	17
Polycarpon tetraphyllum	Alien	11	7	4
Polygonum arenastrum	Alien	28	15	11
Polygonum aviculare	Alien	56	25	11
Polystichum vestitum	Non-endemic	1	1	1
Populus nigra	Alien	9	6	6
Populus sp.	Alien	1	1	1
Prunella vulgaris	Alien	40	25	15
Pseudognaphalium luteoalbum	Non-endemic	56	28	14
Ranunculus acris	Alien	1	1	1
Ranunculus flammula	Alien	1	1	1
Ranunculus repens	Alien	70	31	15

Ranunculus sceleratus	Alien	1	1	1
Raoulia australis	Endemic	10	4	2
Raoulia haastii	Endemic	5	3	1
Raoulia hookeri	Endemic	43	21	10
Raoulia tenuicaulis	Endemic	15	7	5
Reseda luteola	Alien	18	10	5
Ribes sanguineum	Alien*	2	2	2
Rorippa palustris	Non-endemic	5	5	5
Rosa rubiginosa	Alien*	13	8	6
Rubus fruticosus	Alien*	36	27	14
Rumex acetosella	Alien	135	51	17
Rumex crispus	Alien	25	13	10
Rumex obtusifolius	Alien	89	39	17
Rytidosperma buchananii	Endemic	2	1	1
Rytidosperma pumilum	Non-endemic	3	2	1
Rytidosperma racemosum	Alien	3	2	1
Rytidosperma spp.		5	5	4
Sagina apetala	Alien	1	1	1
Sagina procumbens	Alien	81	41	16
Salix alba	Alien	4	3	3
Salix cinerea	Alien*	52	29	16
Salix fragilis	Alien*	122	51	19
Sanguisorba minor	Alien	1	1	1
Schedonorus arundinaceus	Alien*	92	36	15
Sedum acre	Alien*	46	23	11
Senecio glomeratus	Non-endemic	0	0	0
Senecio jacobaea	Alien*	8	6	4
Senecio quadridentatus	Non-endemic	5	3	2
Senecio vulgaris	Alien	11	10	8
Silene gallica	Alien	22	13	8
Silene latifolia	Alien	5	2	1
Sisymbrium officinale	Alien	22	13	6
Solanum chenopodioides	Alien	7	3	3
Solanum dulcamara	Alien*	27	18	10
Solanum nigrum	Alien	9	5	4
Sonchus asper	Alien	24	16	12
Sonchus oleraceus	Alien	42	25	15
Sophora microphylla	Endemic	1	1	1
Spergularia arvensis	Alien	24	14	7
Spergularia rubra	Alien	28	16	9
Stellaria alsine	Alien	26	13	7
Stellaria gracilenta	Endemic	2	2	1
Stellaria graminea	Alien	43	23	11
Stellaria media	Alien	62	29	14
Taraxacum officinale	Alien	41	25	16
Thymus vulgaris	Alien*	1	1	1
Trifolium arvense	Alien	63	34	16
Trifolium dubium	Alien	57	33	17

Trifolium glomeratum	Alien	1	1	1
Trifolium pratense	Alien	29	17	9
Trifolium repens	Alien	139	53	19
Trifolium striatum	Alien	1	1	1
Trifolium subterraneum	Alien	5	4	4
Tripleurospermum inodorum	Alien	33	13	5
Ulex europaeus	Alien*	123	51	19
Urtica urens	Alien	3	3	3
Verbascum thapsus	Alien	116	45	19
Verbascum virgatum	Alien	2	1	1
Veronica anagallis-aquatica	Alien	56	25	10
Veronica arvensis	Alien	27	15	8
Veronica persica	Alien	14	9	6
Veronica salicifolia	Non-endemic	4	2	2
Vicia hirsuta	Alien	15	9	5
Vicia sativa	Alien	58	30	14
Vinca major	Alien*	3	3	3
Vittadinia australis	Endemic	1	1	1
Vulpia myuros	Alien	99	46	19
Wahlenbergia albomarginata	Endemic	1	1	1
Wahlenbergia gracilis	Endemic	2	1	1

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