DRIVERS, IMPACTS, AND FEEDBACKS OF GLOBAL *PINUS CONTORTA* (LODGEPOLE PINE) INVASIONS

by

Kimberley Terrill Taylor

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

Doctor of Philosophy

in

Ecology and Environmental Science

MONTANA STATE UNIVERSITY
Bozeman, Montana

March 2016

ACKNOWLEDGEMENTS

I would like to first acknowledge and thank my advisor Dr. Bruce Maxwell who has provided valuable guidance, advice, support and encouragement throughout the process. I am very grateful for his tireless work both as a mentor and as a field assistant in far flung corners of the Southern Hemisphere. His enthusiasm for ecology, the natural world, and adventure in general is inspiring and I could not have asked for a better mentor or traveling companion. I would like to thank the rest of my committee, Dr. Lisa Rew, Dr. Aníbal Pauchard, Dr. Cathy Whitlock, and Dr. Dave McWethy, who all provided their unique form of guidance and support and have broadened my personal and scientific perspectives. I am greatly indebted to our international collaborators Martin Nuñez and Duane Pelzter who helped make this project possible and provided valuable input. I also appreciate the insightful and helpful interactions I had throughout my time at MSU with Dr. Matt Lavin and Dr. Cathy Zabinski. Thank you to all my field helpers and interns, particularly Hannah and Sam, who were willing to travel half way around the world to help me complete my project. Despite Hannah's serious fear of bears, she was always an enthusiastic partner, even deep in Montana's bear country. I am incredibly grateful for the many wonderful interactions I had with fellow students who have provided invaluable support and friendship. Finally, thank you to my family for their constant support and to Phil for sticking with me through it all, reminding me to still take time to enjoy life, and taking care of me when I was too busy to take care of myself.

TABLE OF CONTENTS

TABLE OF CONTENTS - CONTINUED

TABLE OF CONTENTS - CONTINUED

LIST OF TABLES

Table Page

LIST OF FIGURES

Figure Page

ABSTRACT

Pine species (genus *Pinus*) have been introduced across the Southern Hemisphere for forestry and several species have invaded surrounding ecosystems. Pine introduction across biogeographic regions sets up an ideal natural experiment to test underlying theories and assumptions of invasion biology. We studied the factors determining patterns of *Pinus contorta* invasion across nine sites in both the native and introduced ranges to understand how the invasion drivers change across sites and invasion stages. We found that propagule pressure is the most important factor in explaining invasion density in young invasions, but that biotic factors play an important role at later invasion stages. Additionally, we found higher invasion densities in the introduced than native range which may be explained by faster growth and earlier and more prolific reproduction in the introduced range.

We examined the impacts of *P. contorta* invasions on plant biodiversity across sites and found that species richness and native plant cover decline with increasing *P. contorta* cover across sites in both the native and introduced range. There were more significant changes in species composition and individual species cover at grassland and shrubland sites in the introduced range than in the native range or a native forest site in the introduced range.

Finally, there is concern that invasive pines, which are fire adapted, will alter fire regimes in a way that promotes a new fire-prone state further increasing their success over native plants. We examined the potential for *P. contorta* to form a positive feedback with fire by quantifying fuel loads and fire effects across an invasive gradient. We also examined *P. contorta* and native plant recovery following fire across an invasion density gradient. We found that fuel loads and simulated soil heating increased with older *P. contorta* invasions. Following fire, *P. contorta* dominated communities only when the pre-fire density was high. Therefore, we expect that a positive feedback between *P. contorta* invasion and fire will form only above an invasion threshold. Our invasion-fire simulation model suggested that fire in older invasions will increase invasion rates, but that fires in young invasions will not affect the invasion rate.

CHAPTER 1

INTRODUCTION

Prologue

Introduced and invasive species often elicit strong opinions about their impacts and benefits, as well as the appropriate management responses. Points of view vary from those who think complete eradication should be pursued, to those who think the potential benefits of invasive species should be considered, and even to those who think a desire to rid ecosystems of invasive species stems from xenophobia (Simberloff 2013). All sides have some valid arguments. For example, some introduced species can provide ecosystem services such as pollination or habitat for rare species in some systems (Schlaepfer et al. 2011). Furthermore, as climate changes rapidly and species respond by moving on their own or through assisted migration, it becomes increasingly difficult to draw a line as to what is "native" and what is not. Species have had range expansions and contractions throughout all of geological time and thus the question of on what time scale we should assess "nativeness" arises. On the other hand, humans are introducing more new species more quickly in more spatially disparate locations than has happened in the past. Additionally, there are numerous examples of invasive species that significantly reduce native biodiversity (Pysek et al. 2012; Skurski et al. 2014). Many people believe that preserving biodiversity is an important global conservation goal for ecological, economic, cultural and ethical reasons. In this context, it is necessary to better understand which species become dominant and have negative impacts on diversity when introduced

to new ranges. Furthermore, this information can help identify other species that may behave the same way under similar conditions. The ability to predict which species are most likely to spread and have negative consequences has long been a goal of invasion biology, and although difficult, some improvements in this understanding have been achieved (Gordon et al. 2015). Overall, I think there is an opportunity to move away from blanket arguments about whether introduced species are good or bad and towards a recognition that not all invasive species are evil, but that some create serious ecological changes and degrade aspects of natural and agro-systems that we value. When we move beyond thinking that invasive species are inherently bad, to thinking about why we care about invasions and recognizing that our values, and not just science, play an integral role in this, we may be better able to make informed management decisions.

Beyond the implications for global biodiversity conservation, studying invasion biology is also relevant to broader plant ecology questions. The introduction of species to new areas allows us to test theories about what factors most influence plant establishment, community assembly, and range expansion. For example, neutral theory would suggest that all areas can be invaded equally by new species provided dispersal opportunities and chance events. On the other hand, niche-based assembly theory would predict differences in invasibility based on the availability of "empty niches" and that success of an invader species would relate to its ability to fill a niche different than the native species. If niche processes do indeed structure most communities, prediction of which species invade where becomes easier than if neutral processes structure communities.

Studying the introduction of new species to different climates also provides an opportunity to explore the potential impacts of climate change on plant communities. Climate change in the past half a century is occurring at a faster rate than has previously been observed potentially putting plant communities and the processes that structure them in peril. Abrupt changes in environmental conditions could lead to changes in plant community composition, and as a result, landscape-scale processes such as fire and ecosystem services could be disrupted. Human-mediated plant introductions result in exposure to novel climate conditions at a much faster rate than anthropogenic climate change as plants are abruptly transported to areas with new climate conditions. The response of introduced plants to new ranges is variable. Some species have been shown to evolve rapidly and successfully expand in locations where the climate niche substantially differs from that of their native range. For example, flowering time genes of an introduced forb species were found to diverge from native populations prior to the spread of the species in its new range with a different climate (Vandepitte et al. 2014). These findings and others (e.g., Buswell et al. 2011) suggest that certain plants may be able to adapt to climate change faster than expected. Many other important factors can influence the success of introduced plants; however, studying the response of introduced plants to novel climates is one way that we can better understand how plants respond to abrupt changes in environmental conditions. This type of research adds to a larger body of work that investigates how changes in environmental conditions lead to changes in plant community function that includes paleoecological studies and modern gradient studies (e.g., Choler et al. 2001; Higuera et al. 2009).

Examining the response of species to novel climate conditions also allows us to test ideas about whether the current range of species are in equilibrium with present-day climate. When species perform better in introduced climates this could suggest that the native range does not occupy the best potential climate space of the species. We might expect that species could occupy a broader range of climate conditions (i.e., their fundamental niche), but factors, such as dispersal, competition, or predation limit their range (i.e. their realized niche). Alternatively, the native range could represent a local climate optimum within the limits of the dispersal capabilities of the species, but globally better climatic conditions may occur beyond dispersal barriers.

Successful and unsuccessful invasions are also an opportunity to explore evolutionary changes when species are exposed to drastically different selective pressures. Evolution may occur faster when there is an abrupt change in selection pressures and therefore studying introduced species may provide an opportunity to better understand the processes involved in evolution.

This dissertation, which examines pine invasions across biogeographical regions, allows us to address several of these important questions. For example, I compare invasion success across different ecosystem types with different levels of diversity and potentially "vacant niches." I also examine plant growth responses in new geographic ranges. This information is a first step for determining if performance is different between ranges and provides the foundation necessary to assess what factors are responsible for these differences. Is *Pinus contorta* growing in less than ideal climate conditions in its native range, and if so why? Do differences in pathogens, mutualisms, or

competition between native and non-native ranges drive differences in performance? Examining growth early in invasion provides important baseline data about the potential limitations to range posed by pathogens, competitors, or herbivores. Invasions can help us to determine how long it takes for pathogens and herbivores in introduced ranges to host switch and adapt to new species. Studying these types of processes, which are not specific to invasion, may be most easily accomplished in an invaded system.

This study also addresses important questions about abrupt regime shifts. Studying how the introduction of one species can lead to changes in disturbance regimes and feedbacks that result in rapid and large scale shifts in the dominant vegetation may help to explain the mechanisms behind rapid shifts in disturbance or vegetation observed in recent times and in the past. Studying current tree invasions allows us to understand if changes in vegetation result in changes in fire regimes (e.g., Stevens & Beckage 2009) or vice versa (e.g., Heyerdahl et al. 2006). Evidence of the current impacts of tree invasions on plant communities and disturbance may help us to better understand the consequences of landscape recolonization by different tree species in the past following glaciation.

Invasions Processes Across Ecosystems and Invasion Stages

Increasing globalization has resulted in widespread introductions of plant and animal species to new regions of the world. While many species arrive to new systems, only a few successfully establish and reproduce. It is widely recognized that not all introduced species become invasive (Williamson & Fitter 1996). Therefore, many initial studies of biological invasions focused on the questions of what makes certain species invasive and certain ecosystems invasible (Drake et al. 1989; Richardson et al. 1994;

Simberloff 2011a). This body of literature led to generalizations that attempted to describe the traits of invasive species (e.g. Baker 1965; Rejmanek & Richardson 1996; Sutherland 2004; van Kleunen et al. 2010) or describe processes that lead to invasion (such as disturbance (Sher & Hyatt 1999)).

There are many hypotheses about the mechanisms causing invasions (e.g. evolution of increased competitive ability (Blossey & Notzold 1995); enemy-release (Keane & Crawley 2002); novel weapons (Callaway & Ridenour 2004)), but the best that any single hypothesis can do is to explain some of the success of some invaders in some situations (Catford et al. 2009). Broad understanding of the dominance of different invasion mechanisms is limited (Catford et al. 2009; Kueffer et al. 2013). Therefore some argue that the focus of invasion biology should shift away from making new hypotheses that try to provide general explanations, to quantifying the relative importance of different mechanisms driving invasions (Catford et al. 2009). Additionally, the importance of context dependence and the need for multi-site studies is becoming increasingly recognized (Kueffer et al. 2013; Kumschick et al. 2015; Melbourne et al. 2007).

There are different ways that biological invasions can be context dependent. Some suggest that the interactions between ecosystems and recently introduced species, as well as the differences across invasion stages, are the most important variables to understand (Kueffer et al. 2013). Similarly, others have suggested that the reason that prior studies have failed to find a consistent suite or ranking of factors that promote invasion success may be that studies often compare invasions at different stages (Theoharides & Dukes

2007). Drivers of invasion may shift over time and the only way to fully understand this process is to study invasions of the same species at different stages of invasion (Dietz & Edwards 2006).

Pine (genus *Pinus*) is an ideal genus to examine context dependency because pine plantations have been established around the world, most notably in the Southern Hemisphere, and thus provide a large propagule source for pine invasions in different biophysical settings (Richardson & Higgins 1998; Simberloff et al. 2010). Twenty-four pine species are invasive in at least one region of the world, while *Pinus pinaster*, *P. radiata*, and *P. patula* all invade in at least 5 different regions (Rejmanek & Richardson 2013). *Pinus contorta* invades in four regions globally (Rejmanek & Richardson 2013) despite being less widely planted than many other pine species (Richardson & Higgins 1998). The specific species traits that make certain pine species, including *P. contorta*, more invasive include: small seeds, short juvenile period, and short interval between large seed crops (Rejmanek & Richardson 1996). Certain habitat types, such as dunes or grasslands, have been found to be more invasible than forests (Richardson et al. 1994).

I aimed to better understand the context-dependency of pine invasion success and impacts both across different types of ecosystems and also different stages of invasion. While certain pine species as a whole are highly likely to invade in the Southern Hemisphere, few studies have compared the same species across biogeographic regions to determine how abiotic and biotic factors alter invasion density in different settings. Therefore, the first chapter of my dissertation explores the relative importance of abiotic and biotic factors, as well as propagule pressure, in determining *Pinus contorta* invasion

success, and how this varies between invasion stages and across six ecoregions. These questions are important from an applied perspective given the widespread nature of pine invasions across the Southern Hemisphere and the potential for pines to significantly alter native soil biota and nutrient cycling (Dehlin et al. 2008; Dickie et al. 2014; Dickie et al. 2011), hydrologic processes (Farley et al. 2005; Fernandez et al. 2009), and native plant communities (Dickie et al. 2011; Ledgard & Paul 2008; Urrutia et al. 2013).

Understanding the patterns of *P. contorta* invasion can help managers to prioritize high risk areas for control efforts. Beyond the practical benefits of understanding the patterns of *P. contorta* invasion in different ecosystems, this study tested several theoretical invasion models. For example, Dietz & Edwards (2006) predicted that early in invasion propagule pressure is the most important variable for invasion success, while at later invasion stages habitat characteristics become more important. The range in invasion age from 22 to 53 at our study sites allowed us to test this model. Similarly, there is an ongoing debate about the relative importance of propagule pressure versus other factors in determining invasion success (Catford et al. 2009; Lockwood et al. 2005; Simberloff 2009; Theoharides & Dukes 2007; Von Holle & Simberloff 2005). We specifically examined the importance of propagule pressure relative to other biotic and abiotic factors in explaining invasion density. This information helps assess the importance of propagule pressure across ecosystems and at different invasion stages for one pine species.

Biogeography of Invasions

Many invasion biology theories depend on the idea that there are differences between the native and introduced ranges of species, prompting the question of whether and why invasive species behave differently in the introduced region than in their native range. There has been evidence both for naturally weedy or abundant species becoming invasive elsewhere (Firn et al. 2011; Parker et al. 2013; Shah et al. 2014) and for species that were not abundant in their native range becoming highly abundant in the introduced range (Parker et al. 2013; Xiao et al. 2013). Evidence for differences in performance (e.g. growth, reproduction) between the native and introduced ranges is also mixed (Parker et al. 2013). Several main theories of why introduced species can become invasive hinge on the idea that there are fundamental differences between the native and introduced region including changes in soil feedbacks (Klironmos 2002), release from natural enemies (Keane & Crawley 2002), reduced herbivory (Blossey & Notzold 1995), changes in invader competitive ability between ranges (Callaway & Aschehoug 2000; Callaway & Ridenour 2004; Callaway et al. 2012) or differences in competitive effects of native species on the invader in the native and introduced ranges (Callaway et al. 2011). There is mixed support for most of these hypotheses (Colautti et al. 2004; Felker-Quinn et al. 2013; Joshi & Vrieling 2005; Parker et al. 2006; Parker et al. 2013; Willis & Blossey 1999; Willis et al. 1999). One of the best ways to thoroughly address these types of questions is through a biogeographic study of a species in its native and introduced range. Therefore, in the first chapter I assessed differences in invasion density, patterns of

invasion, growth rates, and reproduction between *P. contorta*'s native and introduced ranges.

Impacts of Invasions

As with drivers of invasion, impacts of invasive species are also context dependent (Hulme et al. 2013; Pysek et al. 2012) and in order to better predict impacts and improve management we need a better understanding of this context dependence (Kumschick et al. 2015). Concern about the impacts of invasive species has existed for a long time (e.g. Elton 1958) and a few early studies did quantify impacts (e.g. Mack & D'Antonio 1998; Stock et al. 1995; Wardle et al. 1995); however, in the past decade studies examining the impacts of particular species and papers reviewing all impact studies have proliferated (Kumschick et al. 2015; Skurski et al. 2014).

Some argue that highly invasive species likely have some sort of impact on native communities or ecosystem processes even if that impact has not been detected yet (Simberloff 2011b). However, given the number of introduced and invasive species in many regions of the world, it is not practical to manage all invasive plant species (Hulme et al. 2013). Therefore, while invasion biologists are interested in the theory behind why some species have stronger impacts than others, understanding this issue is also integral for land managers with making decisions about how to utilize limited resources (Blackburn et al. 2014; Kumschick et al. 2012; Parker et al. 1999).

The impacts of pine invasions on soil communities, native biodiversity, and hydrology have been widely studied (Dickie et al. 2014; Dickie et al. 2011; Farley et al. 2005; Fernandez et al. 2009; Howell & McAlpine 2016; Ledgard & Paul 2008; Urrutia et

al. 2013), but most studies assess impacts in a single site or sites within one biogeographic region. By examining *P. contorta* invasions across climatic and geographic regions (New Zealand, Patagonia, Montana) we hoped to capture a wide range of variability to make more robust generalizations about the impacts of pines on plant diversity (Chapter 2) and fire regimes (Chapter 3). Our multi-region study allowed us to assess if invasions at certain stages have different impacts, and if a tipping point exists beyond which recovery of native systems is unlikely. We were able to determine how the interaction between native ecosystem properties and *P. contorta* traits resulted in potentially unique outcomes across sites and to test the hypothesis that impacts of invasive species will be greatest where the species is a novel life form or adds new traits to the system (Levine et al. 2003).

Plant Invasions, Feedbacks and Regime Shifts

The idea of stable states, thresholds, feedbacks and regime shifts has recently been applied to many ecological systems (Folke et al. 2004; Gaertner et al. 2014; Kitzberger et al. 2012; Lindenmayer et al. 2011; Scheffer et al. 2001). It has been suggested that the likelihood of regime shifts to less desirable states (in terms of diversity and/or ecosystem services) increases when humans reduce native ecosystem resilience (ability to absorb disturbance and reorganize to maintain similar function, structure, identity, and feedbacks (Folke et al. 2004; Walker et al. 2004)), for example by altering the magnitude, frequency, and duration of disturbance regimes (Folke et al. 2004). It is increasingly recognized that invasive species with the ability to alter ecosystem processes, such as disturbance, have the highest potential to negatively impact native

communities potentially through altering disturbance patterns which leads to regime shifts (Brooks et al. 2004; Gaertner et al. 2014; Levine et al. 2003).

There has been mounting evidence that invasive species, particularly grasses, can create a positive feedback with fire by altering some aspect of the fire regime in a way that promotes its own success over native plants (D'Antonio & Vitousek 1992; Flory et al. 2015; Rossiter et al. 2003; Setterfield et al. 2010; Stevens & Beckage 2009). The majority of these studies focus on invasive grass species (rather than woody invaders) and few address the possibility of an invasion threshold beyond which feedbacks are likely to form. Most studies compare fuel loads or fire behavior in invaded versus uninvaded areas, rather than across an invasion gradient, which limits understanding across a range of conditions (although see Stevens & Beckage 2009). Although much of the theoretical literature discusses alternative ecosystem states, few plant invasion studies have empirically assessed the feedback mechanisms that promote alternative states (Gaertner et al. 2014).

It has been suggested that a positive feedback between pine invasions and fire is likely (Simberloff et al. 2010; Veblen et al. 2008); however, no study has empirically addressed this question. Studies have examined pine plantations after fire and found little native plant recovery (Nuñez & Raffaele 2007), but given that often there is no native understory in plantations, we would not expect to see native recovery post-fire in these settings. However, it remains unknown how invaded plant communities that maintain some native vegetation would respond to fire and if the response depends on the level of invasion. Would the native shrubs, known to resprout following fire, recover or would

dense *P. contorta* dominate as seen after fires in the native range (e.g. in Yellowstone National Park post-1988 fires; Turner et al. 1997)? An important consideration not often mentioned in the discussion of positive pine-fire feedbacks is that *P. contorta* is serotinous in many North American populations which contributes significantly to its ability to dominate after fire (Schoennagel et al. 2003), while many invasive populations in the Southern Hemisphere are not serotinous (personal observation). Thus, one of the main fire adaptations of *P. contorta* is not present or prevalent in Southern Hemisphere populations. Therefore, areas with native fire-adapted species could be expected to show a strong native post-fire recovery instead of dominance by *P. contorta*. In Chapter Three I address the potential for a positive feedback to form between *P. contorta* invasion and fire, and examine which mechanisms are most likely responsible for the positive feedback. I assessed fuel loads and vegetation response to fire across an invasion gradient, which allowed me to identify if a threshold exists above which feedbacks are most likely to form.

Finally, in Chapter Five I use the results from the other chapters to inform an invasion-fire simulation model that allow me to ask how the interactions we found between *P. contorta* and fire will play out on a larger scale and how fires at different stages of invasion will alter invasion density and spread rates. While it is often recognized that disturbance will promote invasion by creating invasion windows (Johnstone 1986; Sher & Hyatt 1999), disturbance in the invaded area may actually decrease invasion rates by killing invading individuals and reducing the seed source (Buckley et al. 2007). Although we found an increase in *P. contorta* density following

fire in highly invaded areas, it was unclear if the increase in density over the long-term will compensate for the loss of individuals killed by the fire. Would fires burning through a young invasion reduce invasion rates, while fire burning through an older invasion increase invasion densities? The actual invasion density threshold, above which a positive feedback between fire and *P. contorta* invasion exists, likely varies by site and over time depending on the fire adaptations of local plant species. To what extent does the effect of fire at different invasion stages depend on the exact density threshold? To answer these important questions, I created a simulation model based on real demographic data to examine the interactions between invasion rates, fire, and invasion thresholds.

Research Objectives

1) To determine biotic and abiotic controls on pine invasion globally within six ecoregions that include both introduced and native ranges. The ecoregions include Canterbury-Otago tussock grassland (New Zealand), South Island montane grassland (New Zealand), Patagonian shrub-steppe (Argentina), Patagonian grass-steppe (Chile), Valdivian temperate forest (Chile), and South-Central Rockies forest-shrub steppe (USA). Specifically, what factors most control invasion density and do patterns in invasion density match differences in *P. contorta* growth and reproduction in native and non-native ranges?
2) To determine if one of the most invasive pine species introduced to the Southern Hemisphere, *Pinus contorta*, has changed plant species richness, composition, diversity, and litter depth. Specifically, how has *P. contorta* invasion altered

native open forest, shrub-steppe and grassland communities and are the changes similar in its native and introduced range.

3) To determine the potential for a positive feedback between *P. contorta* invasions and fire by examining how invasions alter fuel loads and fire effects, as well as plant community responses to fire across an invasion gradient.
4) To examine how the threshold and feedback behavior between *P. contorta* invasion and fire may alter the course of an invasion. Through modelling simulations examine whether fire increases or decreases invasion rates and to what extent does invasion rate depend on the age of the *P. contorta* invaders when they burn? Furthermore, what is the effect of altering the threshold invasion density after which we see a positive feedback between invasion and fire?

References

Baker, H. 1965. Characteristics and modes of origin of weeds. Pages 147-172 in H. Baker, and G. Stebbins, editors. The genetics of colonizing species. Academic Press, New York.

Blackburn, T. M., F. Essl, T. Evans, P. E. Hulme, J. M. Jeschke, I. Kuehn, S. Kumschick, Z. Markova, A. Mrugala, W. Nentwig, J. Pergl, P. Pysek, W. Rabitsch, A. Ricciardi, D. M. Richardson, A. Sendek, M. Vila, J. R. U. Wilson, M. Winter, P. Genovesi, and S. Bacher. 2014. A Unified Classification of Alien Species Based on the Magnitude of their Environmental Impacts. Plos Biology **12**: e1001850.

Blossey, B., and R. Notzold. 1995. Evolution of increased competitive ability in invasive nonindigenous plants - A hypothesis. Journal of Ecology **83**:887-889.

Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. Bioscience **54**:677-688.

Buckley, Y. M., B. M. Bolker, and M. Rees. 2007. Disturbance, invasion and re-invasion: managing the weed-shaped hole in disturbed ecosystems. Ecology Letters **10**:809-817.

Buswell, J. M., A. T. Moles, and S. Hartley. 2011. Is rapid evolution common in introduced plant species? Journal of Ecology **99**:214-224.

Callaway, R. M., and E. T. Aschehoug. 2000. Invasive plants versus their new and old neighbors: A mechanism for exotic invasion. Science **290**:521-523.

Callaway, R. M., and W. M. Ridenour. 2004. Novel weapons: invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment **2**:436-443.

Callaway, R. M., U. Schaffner, G. C. Thelen, A. Khamraev, T. Juginisov, and J. L. Maron. 2012. Impact of *Acroptilon repens* on co-occurring native plants is greater in the invader's non-native range. Biological Invasions **14**:1143-1155.

Callaway, R. M., L. P. Waller, A. Diaconu, R. Pal, A. R. Collins, H. Mueller-Schaerer, and J. L. Maron. 2011. Escape from competition: Neighbors reduce *Centaurea stoebe* performance at home but not away. Ecology **92**:2208-2213.

Catford, J. A., R. Jansson, and C. Nilsson. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Diversity and Distributions **15**:22-40.

Choler, P., R. Michalet, and R. M. Callaway. 2001. Facilitation and competition on gradients in alpine plant communities. Ecology **82**:3295-3308.

Colautti, R. I., A. Ricciardi, I. A. Grigorovich, and H. J. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis? Ecology Letters **7**:721-733.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics **23**:63-87.

Dehlin, H., D. A. Peltzer, V. J. Allison, G. W. Yeates, M.-C. Nilsson, and D. A. Wardle. 2008. Tree seedling performance and below-ground properties in stands of invasive and native tree species. New Zealand Journal of Ecology **32**:67-79.

Dickie, I. A., M. G. St John, G. W. Yeates, C. W. Morse, K. I. Bonner, K. Orwin, and D. A. Peltzer. 2014. Belowground legacies of *Pinus contorta* invasion and removal result in multiple mechanisms of invasional meltdown. AoB Plants **6**: plu056.

Dickie, I. A., G. W. Yeates, M. G. St John, B. A. Stevenson, J. T. Scott, M. C. Rillig, D. A. Peltzer, K. H. Orwin, M. U. F. Kirschbaum, J. E. Hunt, L. E. Burrows, M. M. Barbour, and J. Aislabie. 2011. Ecosystem service and biodiversity trade-offs in two woody successions. Journal of Applied Ecology **48**:926-934.

Dietz, H., and P. J. Edwards. 2006. Recognition that causal processes change during plant invasion helps explain conflicts in evidence. Ecology **87**:1359-1367.

Drake, J. M., H.A., F. Di Castri, R. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson 1989. Biological Invasions: a Global Perspective. Wiley, Chichester.

Farley, K. A., E. G. Jobbagy, and R. B. Jackson. 2005. Effects of afforestation on water yield: a global synthesis with implications for policy. Global Change Biology **11**:1565-1576.

Felker-Quinn, E., J. A. Schweitzer, and J. K. Bailey. 2013. Meta-analysis reveals evolution in invasive plant species but little support for Evolution of Increased Competitive Ability (EICA). Ecology and Evolution **3**:739-751.

Fernandez, M. E., J. Gyenge, and T. Schlichter. 2009. Water flux and canopy conductance of natural versus planted forests in Patagonia, South America. Trees-Structure and Function **23**:415-427.

Firn, J., J. L. Moore, A. S. MacDougall, E. T. Borer, E. W. Seabloom, J. HilleRisLambers, W. S. Harpole, E. E. Cleland, C. S. Brown, J. M. H. Knops, S.

M. Prober, D. A. Pyke, K. A. Farrell, J. D. Bakker, L. R. O'Halloran, P. B. Adler, S. L. Collins, C. M. D'Antonio, M. J. Crawley, E. M. Wolkovich, K. J. La Pierre, B. A. Melbourne, Y. Hautier, J. W. Morgan, A. D. B. Leakey, A. Kay, R. McCulley, K. F. Davies, C. J. Stevens, C.-J. Chu, K. D. Holl, J. A. Klein, P. A. Fay, N. Hagenah, K. P. Kirkman, and Y. M. Buckley. 2011. Abundance of introduced species at home predicts abundance away in herbaceous communities. Ecology Letters **14**:274-281.

Flory, S. L., K. Clay, S. M. Emery, J. R. Robb, and B. Winters. 2015. Fire and non-native grass invasion interact to suppress tree regeneration in temperate deciduous forests. Journal of Applied Ecology **52**:992-1000.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology Evolution and Systematics **35**:557-581.

Gaertner, M., R. Biggs, M. Te Beest, C. Hui, J. Molofsky, and D. M. Richardson. 2014. Invasive plants as drivers of regime shifts: identifying high-priority invaders that alter feedback relationships. Diversity and Distributions **20**:733-744.

Gordon, D. R., S. L. Flory, D. Lieurance, P. E. Hulme, C. Buddenhagen, B. Caton, P. D. Champion, T. M. Culley, C. Daehler, F. Essl, J. E. Hill, R. P. Keller, L. Kohl, A. L. Koop, S. Kumschick, D. M. Lodge, R. N. Mack, L. A. Meyerson, G. R. Pallipparambil, F. D. Panetta, R. Porter, P. Pysek, L. D. Quinn, D. M. Richardson, D. Simberloff, and M. Vila. 2015. Weed Risk Assessments are an Effective Component of Invasion Risk Management. Invasive Plant Science and Management **Early view**.

Heyerdahl, E. K., R. F. Miller, and R. A. Parsons. 2006. History of fire and Douglas-fir establishment in a savanna and sagebrush-grassland mosaic, southwestern Montana, USA. Forest Ecology and Management **230**:107-118.

Higuera, P. E., L. B. Brubaker, P. M. Anderson, F. S. Hu, and T. A. Brown. 2009. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. Ecological Monographs **79**:201-219.

Howell, C. J., and K. G. McAlpine. 2016. Native plant species richness in non-native *Pinus contorta* forest. New Zealand Journal of Ecology **40**:131-136.

Hulme, P. E., P. Pysek, V. Jarosik, J. Pergl, U. Schaffner, and M. Vila. 2013. Bias and error in understanding plant invasion impacts. Trends in Ecology & Evolution **28**:212-218.

Johnstone, I. M. 1986. Plant invasion windows - A time-based classification of invasion potential. Biological Reviews of the Cambridge Philosophical Society **61**:369-394.

Joshi, J., and K. Vrieling. 2005. The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. Ecology Letters **8**:704-714.

Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution **17**:164-170.

Kitzberger, T., E. Araoz, J. H. Gowda, M. Mermoz, and J. M. Morales. 2012. Decreases in Fire Spread Probability with Forest Age Promotes Alternative Community States, Reduced Resilience to Climate Variability and Large Fire Regime Shifts. Ecosystems **15**:97-112.

Kueffer, C., P. Pysek, and D. M. Richardson. 2013. Integrative invasion science: model systems, multi-site studies, focused meta-analysis and invasion syndromes. New Phytologist **200**:615-633.

Kumschick, S., S. Bacher, W. Dawson, J. Heikkilä, A. Sendek, T. Pluess, T. B. Robinson, and I. Kühn. 2012. A conceptual framework for prioritization of invasive alien species for management according to their impact. Neobiota **15**:69-100.

Kumschick, S., M. Gaertner, M. Vila, F. Essl, J. M. Jeschke, P. Pysek, A. Ricciardi, S. Bacher, T. M. Blackburn, J. T. A. Dick, T. Evans, P. E. Hulme, I. Kuehn, A. Mrugala, J. Pergl, W. Rabitsch, D. M. Richardson, A. Sendek, and M. Winter. 2015. Ecological Impacts of Alien Species: Quantification, Scope, Caveats, and Recommendations. Bioscience **65**:55-63.

Ledgard, N. J., and T. S. H. Paul. 2008. Vegetation successions over 30 years of high country grassland invasion by *Pinus contorta* New Zealand Plant Protection **61**:98-104.

Levine, J. M., M. Vila, C. M. D'Antonio, J. S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society B-Biological Sciences **270**:775-781.

Lindenmayer, D. B., R. J. Hobbs, G. E. Likens, C. J. Krebs, and S. C. Banks. 2011. Newly discovered landscape traps produce regime shifts in wet forests. Proceedings of the National Academy of Sciences of the United States of America **108**:15887-15891.

Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution **20**:223-228.

Mack, M. C., and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. Trends in Ecology & Evolution **13**:195-198.

Melbourne, B. A., H. V. Cornell, K. F. Davies, C. J. Dugaw, S. Elmendorf, A. L. Freestone, R. J. Hall, S. Harrison, A. Hastings, M. Holland, M. Holyoak, J. Lambrinos, K. Moore, and H. Yokomizo. 2007. Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? Ecology Letters **10**:77-94.

Nuñez, M. A., and E. Raffaele. 2007. Afforestation causes changes in post-fire regeneration in native shrubland communities of northwestern Patagonia, Argentina. Journal of Vegetation Science **18**:827-834.

Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, B. Von Holle, P. B. Moyle, J. E. Byers, and L. Goldwasser. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions **1**:3-19.

Parker, J. D., D. E. Burkepile, and M. E. Hay. 2006. Opposing effects of native and exotic herbivores on plant invasions. Science **311**:1459-1461.

Parker, J. D., M. E. Torchin, R. A. Hufbauer, N. P. Lemoine, C. Alba, D. M. Blumenthal, O. Bossdorf, J. E. Byers, A. M. Dunn, R. W. Heckman, M. Hejda, V. Jarosik, A. R. Kanarek, L. B. Martin, S. E. Perkins, P. Pysek, K. Schierenbeck, C. Schloeder, R. van Klinken, K. J. Vaughn, W. Williams, and L. M. Wolfe. 2013. Do invasive species perform better in their new ranges? Ecology **94**:985-994.

Pysek, P., V. Jarosik, P. E. Hulme, J. Pergl, M. Hejda, U. Schaffner, and M. Vila. 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Global Change Biology **18**:1725-1737.

Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology **77**:1655-1661.

Rejmanek, M., and D. M. Richardson. 2013. Trees and shrubs as invasive alien species-2013 update of the global database. Diversity and Distributions **19**:1093-1094.

Richardson, D. M., and S. I. Higgins. 1998. Pines as invaders in the southern hemisphere. Pages 450-473 in D. M. Richardson, editor. Ecology and Biogeography of *Pinus*. Cambridge University Press, Cambridge.

Richardson, D. M., P. A. Williams, and R. J. Hobbs. 1994. Pine invasion in the Southern Hemisphere: determinants of spread and invadability. Journal of Biogeography **21**:511-527.

Rossiter, N. A., S. A. Setterfield, M. M. Douglas, and L. B. Hutley. 2003. Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. Diversity and Distributions **9**:169-176.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature **413**:591-596.

Schlaepfer, M. A., D. F. Sax, and J. D. Olden. 2011. The Potential Conservation Value of Non-Native Species. Conservation Biology **25**:428-437.

Schoennagel, T., M. G. Turner, and W. H. Romme. 2003. The influence of fire interval and serotiny on postfire lodgepole pine density in Yellowstone National Park. Ecology **84**:2967-2978.

Setterfield, S. A., N. A. Rossiter-Rachor, L. B. Hutley, M. M. Douglas, and R. J. Williams. 2010. Turning up the heat: the impacts of *Andropogon gayanus* (gamba grass) invasion on fire behaviour in northern Australian savannas. Diversity and Distributions **16**:854-861.

Shah, M. A., R. M. Callaway, T. Shah, G. R. Houseman, R. W. Pal, S. Xiao, W. Luo, C. Rosche, Z. A. Reshi, D. P. Khasa, and S. Chen. 2014. *Conyza canadensis* suppresses plant diversity in its nonnative ranges but not at home: a transcontinental comparison New Phytologist **202**:1286–1296.

Sher, A. A., and L. A. Hyatt. 1999. The disturbed resource-flux invasion matrix: a new framework for patterns of plant invasion Biological Invasions **1**:107-114.

Simberloff, D. 2009. The Role of Propagule Pressure in Biological Invasions. Pages 81-102. Annual Review of Ecology Evolution and Systematics. Annual Reviews, Palo Alto.

Simberloff, D. 2011a. Charles Elton: Neither Founder Nor Siren, But Prophet in D. M. Richardson, editor. Fifty Years of Invasion Ecology. Wiley-Blackwell, Chichester.

Simberloff, D. 2011b. How common are invasion-induced ecosystem impacts? Biological Invasions **13**:1255-1268.

Simberloff, D. 2013. Invasive Species: What Everyone Needs to Know. Oxford University Press.

Simberloff, D., M. A. Nuñez, N. J. Ledgard, A. Pauchard, D. M. Richardson, M. Sarasola, B. W. Van Wilgen, S. M. Zalba, R. D. Zenni, R. Bustamante, E. Peña, and S. R. Ziller. 2010. Spread and impact of introduced conifers in South America: Lessons from other southern hemisphere regions. Austral Ecology **35**:489-504.

Skurski, T. C., L. J. Rew, and B. D. Maxwell. 2014. Mechanisms Underlying Nonindigenous Plant Impacts: A Review of Recent Experimental Research. Invasive Plant Science and Management **7**:432-444.

Stevens, J. T., and B. Beckage. 2009. Fire feedbacks facilitate invasion of pine savannas by Brazilian pepper (*Schinus terebinthifolius*). New Phytologist **184**:365-375.

Stock, W. D., K. T. Wienand, and A. C. Baker. 1995. Impacts of invading N-2-fixing acacia species on patterns of nutrient cycling in 2 cape ecosystems: Evidence from soil incubation studies and n-15 natural-abundance values. Oecologia **101**:375-382.

Sutherland, S. 2004. What makes a weed a weed: life history traits of native and exotic plants in the USA. Oecologia **141**:24-39.

Theoharides, K. A., and J. S. Dukes. 2007. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytologist **176**:256-273.

Turner, M. G., W. H. Romme, R. H. Gardner, and W. W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs **67**:411-433.

Urrutia, J., A. Pauchard, and R. A. Garcia. 2013. Differences in plant composition in an *Araucaria araucana* (Molina) K.Koch and *Nothofagus antarctica* (G. Forst.) Oerst. forest in a *Pinus contorta* Douglas ex Loudon invasion gradient. Gayana Botanica **70**:92-100.

van Kleunen, M., E. Weber, and M. Fischer. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters **13**:235-245.

Vandepitte, K., T. De Meyer, K. Helsen, K. Van Acker, I. Roldan-Ruiz, J. Mergeay, and O. Honnay. 2014. Rapid genetic adaptation precedes the spread of an exotic plant species. Molecular Ecology **23**:2157-2164.

Veblen, T. T., T. Kitzberger, E. Raffaele, M. Mermoz, M. E. Conzalez, J. S. Sibold, and A. Holz. 2008. The historical range of variability of fires in the Andean-

Patagonian *Nothofagus* forest region. International Journal of Wildland Fire **17**:724-741.

Von Holle, B., and D. Simberloff. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. Ecology **86**:3212-3218.

Walker, B. H., and J. A. Meyers. 2004. Thresholds in ecological and social-ecological systems: a developing database. Ecology & Society **9**:3.

Wardle, D. A., K. S. Nicholson, and A. Rahman. 1995. Ecological effects of the invasive weed species *Senecio jacobaea* L (ragwort) in a New Zealand pasture. Agriculture Ecosystems & Environment **56**:19-28.

Williamson, M., and A. Fitter. 1996. The varying success of invaders. Ecology **77**:1661-1666.

Willis, A. J., and B. Blossey. 1999. Benign environments do not explain the increased vigour of non-indigenous plants: a cross-continental transplant experiment. Biocontrol Science and Technology **9**:567-577.

Willis, A. J., M. B. Thomas, and J. H. Lawton. 1999. Is the increased vigour of invasive weeds explained by a trade-off between growth and herbivore resistance? Oecologia **120**:632-640.

Xiao, S., G. Y. Ni, and R. M. Callaway. 2013. Models of experimentally derived competitive effects predict biogeographical differences in the abundance of invasive and native plant species. Plos One **8**: e78625.

CHAPTER TWO

DRIVERS OF PLANT INVASION VARY GLOBALLY: EVIDENCE FROM PINE INVASIONS WITHIN SIX ECOREGIONS

Contribution of Authors and Co-Authors

Manuscript in Chapter 2

Author: Kimberley T Taylor

Contributions: Conceived the study and methodology, collected field data, executed statistical analysis and wrote initial manuscript.

Co-Author: Bruce D. Maxwell

Contributions: Assisted in study design, field data collection, analysis and manuscript preparation.

Co-Author: Aníbal Pauchard

Contributions: Provided guidance in study design and analysis and assisted manuscript preparation.

Co-Author: Martin Nuñez

Contributions: Provided guidance interpreting results and edited manuscript.

Co-Author: Duane Peltzer

Contributions: Provided guidance interpreting results and edited manuscript.

Co-Author: André Terwei

Contributions: Collected field data and edited manuscript.

Co-Author: Lisa J. Rew

Contributions: Provided guidance in analysis and interpreting results and edited manuscript.

Manuscript Information Page

Kimberley T. Taylor, Bruce D. Maxwell, Aníbal Pauchard, Martin Nuñez, Duane A. Peltzer, André Terwei, and Lisa J. Rew
Journal Name: Global Ecology and Biogeography
Status of Manuscript:
____ Prepared for submission to a peer-reviewed journal
____ Officially submitted to a peer-review journal
____ Accepted by a peer-reviewed journal
__x_ Published in a peer-reviewed journal

John Wiley & Sons Ltd
Volume 25, Issue 1 (2016), Page 96-106

The following chapter has been published in the journal *Global Ecology and Biogeography* and appears in this dissertation with the journal's permission.

Abstract

Aim To determine biotic and abiotic controls on pine invasion globally within six ecoregions that include both introduced and native ranges.

Locations Río Negro province, Argentina; Aysén and Araucanía Regions, Chile; South Island (two ecoregions), New Zealand; Greater Yellowstone Ecosystem, USA.

Methods We quantified tree abundance and size across invasion fronts of the widespread invasive tree species *Pinus contorta* at each of nine sites, encompassing both the native and introduced range. We also determined the relative importance of propagule pressure, abiotic characteristics, and biotic factors for invasion success. Finally, key plant population metrics such as individual tree growth rates and reproductive effort were compared between native and introduced ranges.

Results *Pinus contorta* density decreased with increasing distance from source population in all cases, but the importance and shape of this relationship differed among sites due primarily to biotic factors. For example, areas dominated by native southern beech forest (*Fuscospora cliffortioides* or *Nothofagus* spp.) were not invaded, and this biotic resistance was not overcome by high propagule pressure. In contrast, shrublands were more highly invaded than grasslands, contradicting previous generalizations about pine invasions. *Pinus contorta* growth was faster, age to maturity was earlier, and reproductive effort was higher in the introduced ranges compared to the native range, suggesting a demographic shift towards more rapid population growth in introduced regions. Climatic differences between the ranges may explain, at least in part, the observed pattern.

Main Conclusions We demonstrate that although biological invasions are driven by propagule pressure across different ecoregions, these processes interact strongly with biotic factors. Intriguingly, our results suggest that propagule pressure may become less important than biotic interactions as invasions proceed. Multi-region studies including both the native and introduced ranges provide unparalleled opportunities for understanding how these interactions change among regions as invasions proceed.

Introduction

Biological invasions generally, and non-native tree species in particular, are rapidly increasing components of global change that can have profound impacts on ecosystems (Richardson *et al.*, 2014). Pines (genus *Pinus*) have been widely introduced across the Southern Hemisphere, where several species have become highly invasive (Richardson *et al.*, 1994; Simberloff *et al.*, 2010) and strongly alter native biodiversity (Ledgard & Paul, 2008; Pawson *et al.*, 2010; Urrutia *et al.*, 2013), belowground communities (Dehlin *et al.*, 2008; Dickie *et al.*, 2011, 2014), and hydrological processes (Simberloff *et al.*, 2010). The widespread introduction of pines to diverse regions of the Southern Hemisphere is an ideal 'natural experiment' for determining which processes drive pine invasions and whether these processes are globally consistent or context-dependent (Gundale *et al.*, 2014b). Some species also invade open habitats in their native range (Simberloff *et al.*, 2012), thus enabling direct comparisons of invasions in both the native and introduced ranges and generating insights into the processes and mechanisms underlying invasions that are not possible from more biogeographically constrained approaches (Pauchard *et al.*, 2004; Hierro *et al.*, 2005; Leishman *et al.*, 2014). Multi-

region studies are also essential to determine if results found at individual sites depend on local land use history, biotic and abiotic conditions, and disturbance or are more generalizable (Kueffer *et al.*, 2013; Moodley *et al.*, 2014).

Comparing invasion patterns across regions provides insights into the environmental and ecological processes and filters that operate at different stages of invasion (Dietz & Edwards, 2006; Theoharides & Dukes, 2007; Catford *et al.*, 2009). Early in invasion, propagule pressure (i.e. the supply and frequency of plant propagule introductions) is widely thought to drive invasion success (Lockwood *et al.*, 2005; Theoharides & Dukes, 2007; Catford *et al.*, 2009; Simberloff, 2009). The role of propagule pressure later in invasion is less certain; evidence both for continued (Rouget & Richardson, 2003; Lockwood *et al.*, 2005; Simberloff, 2009) or diminished importance relative to abiotic factors and biotic resistance (Theoharides & Dukes, 2007; Catford *et al.*, 2009) suggests that interactions among these drivers are likely. Therefore, studies that determine how propagule pressure, biological, and environmental factors interact to determine invasion success are needed (Rouget & Richardson, 2003).

Pine invasions are an ideal system to determine the relative importance of habitat, disturbance, and propagule pressure during the spread phase of invasion. Deliberately established plantations have created similar source populations for invasions across the Southern Hemisphere (Gundale *et al.*, 2014b). Although pine species used in forestry are often more invasive than non-forestry species (Essl *et al.*, 2010), invasion away from plantations does not always occur (Zenni & Nuñez, 2013). A given pine species is more likely to be broadly invasive if it has relatively small seeds, rapid onset of reproduction

and more frequent large seed crops (Richardson *et al.*, 1994). Studies of specific pine species invasions can also resolve the role of changing invasion drivers at the intraspecific level (Dietz & Edwards, 2006) because of the known introduction history.

Pinus contorta, Dougl. (lodgepole pine), native to western North America, is one of the most invasive pine species introduced to the Southern Hemisphere (Richardson *et al.*, 1994). *P. contorta* has recently encroached into grasslands, shrublands, and subalpine meadows in its native range (e.g. Jakubos & Romme, 1993; Widenmaier & Strong, 2010). Hereafter, we refer to this encroachment as invasion (Jakubos & Romme, 1993; Boulant *et al.*, 2009). *P. contorta* is a 'model species' to compare hypotheses of invasion success because it has a known introduction history, it can be aged providing an invasion history, and has been planted across different biotic and abiotic conditions (Gundale *et al.*, 2014b). There have been several studies describing patterns of, and limitations to, *P. contorta* invasion in Chile (Peña *et al.*, 2008; Langdon *et al.*, 2010), Argentina (Simberloff *et al.*, 2002; Sarasola *et al.*, 2006; Nuñez *et al.*, 2008; Nuñez *et al.*, 2009), and New Zealand (Allen & Lee, 1989; Ledgard, 2001; Ledgard, 2006); however, no study has compared invasion patterns among ecoregions and the relative importance of propagule pressure, native vegetation, topography, and climate in determining invasion patterns across ecoregions. These factors are consistently important in determining the distribution of invasive species (e.g. Rouget & Richardson, 2003; Catford *et al*., 2009). Additionally, understanding if invasive species behave or grow differently in their introduced range than in their native range is a central question in invasion biology (e.g. Willis *et al.*, 1999; Parker *et al.*, 2013).

We evaluated differences in the patterns and processes that drive *P. contorta* invasion across nine sites in six ecoregions in Argentina, Chile, New Zealand, and the native range in western USA. Specifically, we predicted that (1) propagule pressure would be more important in explaining *P. contorta* invasion patterns than biotic or abiotic factors across all ecoregions; (2) *P. contorta* invasion success, measured by invasion density, would be higher in the introduced than the native range; and (3) that ecoregions with the highest invasion densities would also have the highest *P. contorta* growth rates and fecundity.

Methods

Study Species

Pinus contorta is a shade-intolerant fast growing tree species that first reproduces at 3 to 15 years and has small seeds capable of long-distance wind dispersal (Richardson et al., 1994; Despain, 2001; Ledgard, 2001). *P. contorta* is native to North America where it has a wide distribution ranging from South Dakota (103°W) to the Pacific coast (134°W) and from Baja California, Mexico (31°N) to the Yukon Territory, Canada (64°N) (Lotan & Critchfield, 1990).

Study Sites

Sampling occurred at nine sites in six ecoregions (based on Olson *et al.*, 2001) in Argentina, Chile, New Zealand (all introduced), and the USA (native; Table 2.1; Fig. A1, Tables A1 & A2 in Appendix A). The first site in Bariloche, Argentina (AR1a) was a shrub steppe community (*Mulinum spinosum*, *Acaena* spp.) with patches of the small tree

Nothofagus antarctica. Fires have burned through this area in the past 15 years. Three km away was site AR1b which was dominated by the same shrub community but had a younger source population (Table 2.1). Coyhaique Alto, Chile (CL1) was a grass steppe community (*Festuca* spp.) with several large *N. antarctica* patches and small areas of *Pinus ponderosa* plantation and *Nothofagus pumilio* forest (Langdon *et al.*, 2010). The second Chilean site was located in Reserva Nacional Malalcahuello (CL2) and was dominated by *Araucaria araucana* woodland, had areas of *N. antarctica* and an understory comprised mainly of *Chusquea culeou* (Peña *et al.*, 2008; Urrutia *et al.*, 2013). The sites in New Zealand were all in the Canterbury Region on the South Island. NZ1 was dominated by a mixture of native and non-native grasses and forbs (*Agrostis capillaris, Hieracium* spp., *Festuca novae-zelandiae*). The more diverse Craigieburn Forest Park site (NZ2a) had a similar mixture of grasses and forbs, but also contained the tall shrub *Leptospermum scoparium*, shorter shrubs, and *Fuscospora cliffortioides* forest. NZ2b was a grass-dominated community similar to NZ1. NZ2a and NZ2b were located 10 km apart and differed in the age and size of source populations (Table 2.1). The sites in the USA were located in the Greater Yellowstone Ecosystem, Montana and Wyoming, and included unburned (USA1a) and burned (1988; USA1b) sagebrush steppe (*Artemisia tridentata, Festuca idahoensis*). The oldest invading trees at USA1 were older than 100 years; however, most of the encroachment has occurred in the last 50 years. We tried to minimize differences between sites (grazing, management) but inevitably some differences in land use history may have contributed to variation in our data.

Table 2.1. Descriptions of all study regions (AR1, CL1, CL2, NZ1, NZ2, USA1) and sites within regions. Abbreviations include longitude (long.), latitude (lat.), annual (ann.), temperature (temp.), and precipitation (precip.). Introduced range regions included AR1 in Argentina; CL1 and CL2 in Chile; and NZ1 and NZ2 in New Zealand. The native range region USA1 was in Montana and Wyoming, United States of America. For more site details see Fig. A1, Tables A1 & A2 in Appendix A.

Site	Long.	Lat.	Ecoregion	Density plots	Source type	Source Age (years)	Ann. temp. (°C)	Ann. precip. (mm)
AR1a	-71.2	-41.2	Patagonian shrub-steppe	786	Plantation	34	8.2	846
AR1b	-71.2	-41.2		153	Planted shelter	25	8.2	846
CL1	-71.7	-45.5	Patagonian grass steppe	434	Plantation	23	5.8	715
CL2	-71.5	-38.4	Valdivian temperate forests	54	Forestry trial plots	43	6.7	1586
NZ1	170.2	-44.1	Canterbury-Otago tussock grasslands	402	Plantation	45	9.3	658
NZ2a	171.7	-43.2	South Island montane grasslands	247	Plantation	53	7.3	2241
NZ2b	171.7	-43.2		84	Planted shelter	46	8.3	1652
USA1a	-111.1	45.1	South Central Rockies forest - shrub steppe	1024	Native Forest	>100	1.4	643
USA1b	-111.0	44.7		827	Native Forest	25	1.6	587

Field Sampling within Each Ecoregion

Within each study site, random points along the *P. contorta* source population were selected as starting points for 10 m wide transects. Transects were located

perpendicularly away from the source until they: a) entered another *P. contorta* stand, b) reached 2 km from the source, or c) were unpassable due to topographic barriers. At NZ1 the invasion spread farther from the source requiring longer (3.5 km) transects. Tree density in 100 m^2 plots was collected continuously along each transect except in NZ1 and CL2 where density was collected in randomly-selected plots (n = 1-5 every 100 m). Along all transects, height, basal diameter, age, and current year cone production for all *P. contorta* individuals were measured within complete sample plots (n = 1-5 every 100 m). No serotinous cones were observed in the introduced range, but occasionally observed in the native range.

Statistical Analysis

All statistical analyses were conducted using R version 3.1.1 (R Core Team, 2014).

Importance of Propagule Pressure, Biotic Factors, and Abiotic Factors within Ecoregions.

To determine the relative importance of drivers for invasion success, we created negative binomial mixed models of *P. contorta* density for each ecoregion (AR1, CL1, CL2, NZ1, NZ2, USA1); this accounts for both overdispersion (Ver Hoef & Boveng, 2007) and spatial autocorrelation (Fournier *et al.*, 2012; Skaug *et al.*, 2013). AR1, NZ2, and USA1 had two sites within the ecoregion (e.g. AR1a and AR1b) so site was included in models for those ecoregions. Fixed effects in all models included: distance from source edge (nearest *P. contorta* plantation or forest), slope, cosine of aspect, sine of aspect, elevation, vegetation type (grass, *Araucaria araucana*, *Fuscospora cliffortioides*, *Nothofagus* spp., *Pinus ponderosa*

plantation, short shrub (<1 m), tall shrub (>1 m)), and the interaction between vegetation type and distance from source (Table A2 in Appendix A). Where the interaction was not significant (P>0.05) it was removed from the model. In AR1, fire (if burned in last 15 years) was also included as a fixed effect. Correlograms suggested that the maximum distance of density correlation was around 50 m and that including 50 m clusters as a random effect in the model significantly reduced the spatial autocorrelation. A post-hoc Markov chain (MCMC) run for 10 000 simulations was used to estimate model coefficients. Likelihood ratio tests were also used to test fixed effects.

The relative importance of propagule pressure (at the local scale, represented by distance from source edge), biotic (vegetation type), and abiotic (slope, sine and cosine of aspect, elevation, fire) factors (*sensu* Catford *et al.*, 2009) in explaining *P. contorta* density in each region was determined by assessing the improvement in model fit (AICc) over the null model (random cluster effect, and where necessary, site) due to each predictor group (propagule pressure, biotic, abiotic). Only the native region (USA) had a large temperature and precipitation range within the region so a second mixed effect negative binomial model for the USA data only was created to assess the role of climate with the fixed effects of vegetation type, distance to forest edge, mean annual temperature, and mean annual precipitation. The random effects included site and cluster. We recognize that each of these factors do not represent all components of propagule pressure, biotic factors, and abiotic factors that affect invasions. For example, soil nutrients, texture and biota likely differed between plots and could also affect invasion density. However, given the broad scale of our study, we selected factors that are directly

comparable amongst contrasting sites, are well known to determine plant growth or performance, and that have been used in other studies examining species distributions (e.g. Brummer *et al*., 2013). Although additional abiotic (e.g. soil variables) and biotic (e.g. soil biota) factors can also contribute to variation in invasion success, these were beyond the scope of our study, and would contribute to unexplained sources of variation in our models.

Comparing Densities between Sites. A mixed negative binomial model of tree density was constructed using data from all sites. The fixed effects were site, distance from source, vegetation type, the interaction between vegetation type and distance from source, and the interaction between site and distance from source. The random effect was cluster. In this global model, site was significant, so to further determine what factors explained the site effect, we also constructed models with climate variables and plantation age. We explored the potential for climate to explain differences between sites using 19 bioclimatic variables (Hijmans *et al.,* 2005). Many bioclimatic variables were collinear so we first created models with the fixed effects of one bioclimatic variable, vegetation type, and distance from source. Site and cluster were included as random effects. We used the most explanatory climate variable, based on AICc from these models, in the final model. This process was then repeated for data from just the introduced range. With data from the introduced range we also explored the possibility that differences in plantation age contributed to different invasion patterns between sites by including source age (young, <30 years; old, >30 years) and its interaction with distance from plantation (instead of climate, due to collinearity) in a separate model.

Finally, to estimate invasion potential in each site regardless of source age, we compared invasion densities next to the source edge at all sites by modelling density of the plots within 200 m of the source with a mixed negative binomial model with site and vegetation type as fixed effects and cluster as a random effect.

Differences in Growth and Reproduction between Ecoregions. Data for tree size and reproduction from all ecoregions were combined. Only trees aged ≤20 years (4784 total) were used for this analysis since several sites did not contain trees older than 20 years. A mixed linear model of log-transformed basal diameter was run with tree age, ecoregion, vegetation type, distance from source, and the interaction between age and ecoregion as fixed effects and plot as a random effect (Bates *et al.*, 2014). *P*-values were calculated with Satterthwaite 's approximations (Kuznetsova *et al.*, 2014). The number of cones per tree was modeled as a response to the fixed effects tree age, ecoregion, vegetation type, distance from source, and the interaction between age and ecoregion, as well as the random effect of plot, with a Poisson model fit with quasi-likelihood (Venables & Ripley, 2002). Some sites had low *P. contorta* densities so ecoregion (AR1, CL1, CL2, NZ1, NZ2, USA1) rather than site was used in these models.

Results

Importance of Propagule Pressure, Biotic Factors, and Abiotic Factors within Ecoregions

Across all regions there was a negative relationship between tree density and distance from source (see Table A3 in Appendix A for detailed model results). In the introduced range, *P. contorta* density variation was best accounted for by distance from

source at CL1, CL2, and NZ1, whereas vegetation type was the most explanatory variable at AR1 and NZ2, and also important at CL1 (Table 2.2). Areas dominated by southern beech (*Nothofagus* spp. and *Fuscospora cliffortioides*) in all ecoregions, and by tall shrubs at NZ2, had low *P. contorta* densities (Fig. 2.1; Table A3). The relationship between distance from source and density differed between vegetation types at AR1 and CL1 (Table A3), because density was consistently near zero for vegetation dominated by *N. antarctica* but not other vegetation types. Abiotic factors were never the strongest predictor of *P. contorta* density (Table 2.2), although some topographic factors were significant at some sites (Table A3). Recently burned areas had lower *P. contorta* densities at AR1 (Table A3). The sites AR1a and NZ2a had higher densities than AR1b and NZ2b respectively (Tables 2.1 & A3).

Table 2.2. The improvement in the AICc of each model over the null model (random cluster effect, and where necessary, site) within each ecoregion (the more negative, the more improvement over the null model). Definitions of the region codes and further region descriptions can be found in Table 2.1 and Appendix A. P stands for the model containing the propagule pressure (distance from source) covariate, B for the model containing the biotic covariate (vegetation type), A for the model containing abiotic covariates (elevation, slope, aspect (sine and cosine), and fire), and PAB for the model containing all covariates. See Table A4 Appendix A for more detailed results.

	Improvement in AICc			
Region	P	A	B	PAB
AR1	-14.8	-8.3	-98.7	-137.7
CL1	-48.8	4.9	-37.9	-107.5
CL2	-11.5	-2.6	2.7	-14.8
NZ1	-12.8	-8.4	2.1	-12.8
NZ2	1.8	-12.6	-48.3	-78.0
USA1	-14.5	-2.7	-0.2	-37.9

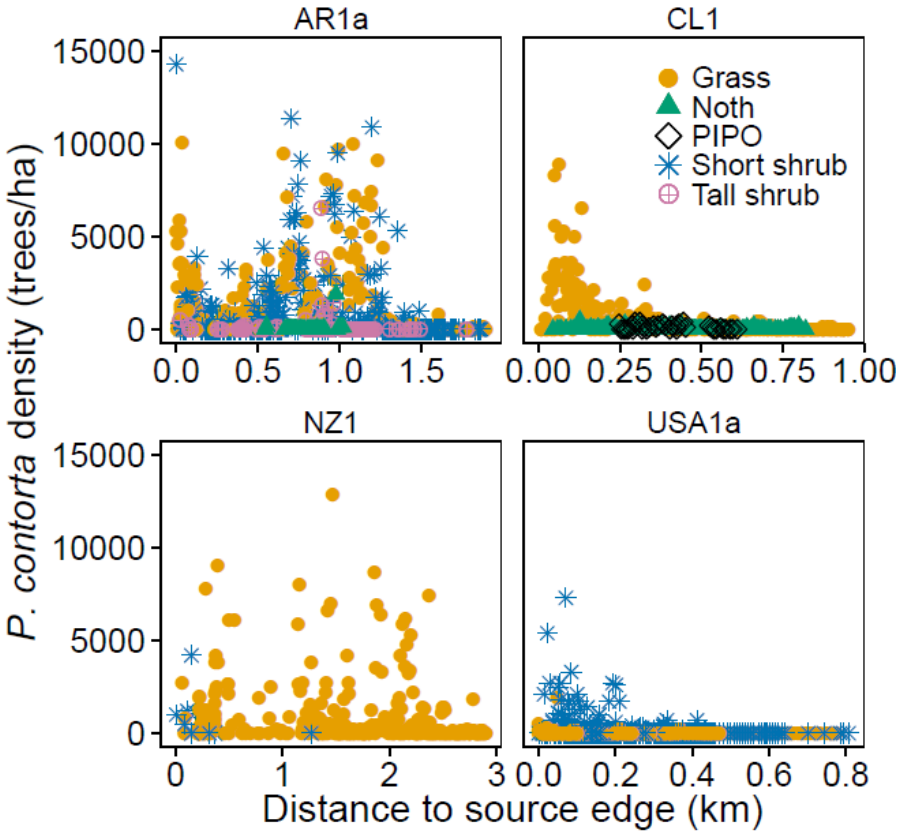

Figure 2.1. Relationship between tree density (*P. contorta* trees/ha) and distance from source populations (km) for four sites (AR1a, CL1, NZ1, USA1a) representing different ecoregions (Table 1 and Appendix A). *P. contorta* is native to sites in the USA, but not to other ecoregions. Vegetation (biotic) differences within individual sites are shown using contrasting symbols for data points representing plot vegetation type. "Noth" represents native *Nothofagus* spp. trees and "PIPO" represents *Pinus ponderosa* plantation.

In the native range (USA1), distance from source was the most important explanatory variable (Table 2.2). Higher *P. contorta* densities were associated with short shrub compared to grass dominated areas close to the forest edge (significant vegetation by distance to source interaction) and there was a negative relationship between elevation and *P. contorta* density (Fig. 2.1; Table A3). Higher *P. contorta* densities were observed in USA1a (unburned) than USA1b (burned in 1988; Table A3). The climate model for USA1 showed that both mean annual temperature and precipitation were positively

associated with *P. contorta* density (χ^2=23.3, d.f.=1, *P*<0.0001; and χ^2=11.0, d.f.=1, *P*=0.0009, respectively; Fig. A2 in Appendix A).

Comparing Densities between Sites

Density, in the global model, was explained by distance from source (χ^2=61.5, d.f.=1, *P*<0.001), vegetation type (χ^2=136.9, d.f.=3, *P*<0.001), site (χ^2=2906.6, d.f.=8, *P*<0.001), distance from source by vegetation interaction (χ^2=7.6, d.f.=3, *P*=0.054; Fig. 2.1), and distance from source by site interaction (χ^2=272.1, d.f.=8, *P*<0.001; Fig. 2.2; Table A5 in Appendix A). Average *P. contorta* density decreased with increasing distance from the source. Forested areas and areas dominated by tall shrubs had lower *P. contorta* densities than grasslands, while areas dominated by short shrubs had higher densities than grasslands. NZ1, NZ2a, and AR1a had a smaller decline in density with distance from source than the native unburned site (USA1a; Table A5). The two native sites had lower mean *P. contorta* densities in the first 200 m of invasion than all introduced sites (*P*<0.001 for all pairwise comparisons). Invasion density was positively correlated with mean temperature of the coldest quarter when using data from all sites (χ^2=356.7, d.f.=1, *P*<0.001; Table A6 in Appendix A) and, in just the introduced range density was positively correlated with mean temperature of the wettest quarter (χ^2=4.25, d.f.=1, *P*=0.039). Introduced sites with source plantations younger than 30 years had a significantly steeper decline in density with increasing distance from plantations than sites with older source plantations (χ^2=39.5, d.f.=1, *P*<0.001).

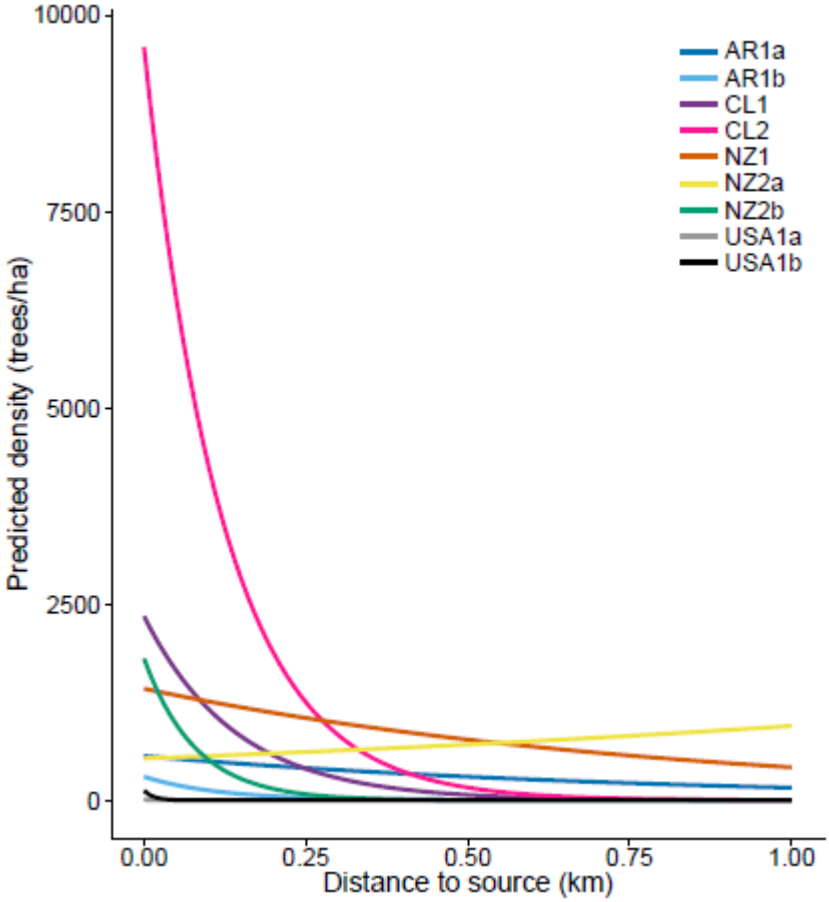

Figure 2.2. Fitted relationships between *P. contorta* density (trees/ha) and distance from source population (km) for grass-dominated areas from the global model which contained distance from source, vegetation type, site, distance from source by vegetation interaction, and distance from source by site interaction as explanatory variables (Table A5 in Appendix A). Introduced range sites included AR1a and AR1b in Argentina; CL1 and CL2 in Chile; and NZ1, NZ2a and NZ2b in New Zealand. Native range sites included USA1a and USA1b in Montana and Wyoming, United States of America (Table 2.1; Appendix A).

Differences in Growth and Reproduction between Ecoregions

Pinus contorta grew fastest and produced more cones at the youngest ages at the New Zealand sites; CL2 and USA1 had the slowest growth rates and lowest cone production, and AR1 and CL1 were intermediate. Ecoregion, tree age and their interaction best predicted variation in *P. contorta* basal diameter (χ^2=251.6, d.f.=5,

P<0.001; χ^2=12591.1, d.f.=1, P<0.001; χ^2=1491.2, d.f.=5, P<0.001, respectively). Vegetation type was also a significant predictor of basal diameter (χ^2=16.7, d.f.=5, P=0.005) with higher growth rates in *Pinus ponderosa* plantations (t=3.23, d.f.=747, P=0.001) and short shrublands (t=2.28, d.f.=266, P=0.023) compared to grasslands. The relationship between basal diameter and tree age differed between the native ecoregion and all introduced ecoregions (P<0.001 for all pairwise comparisons; Figure 2.3).

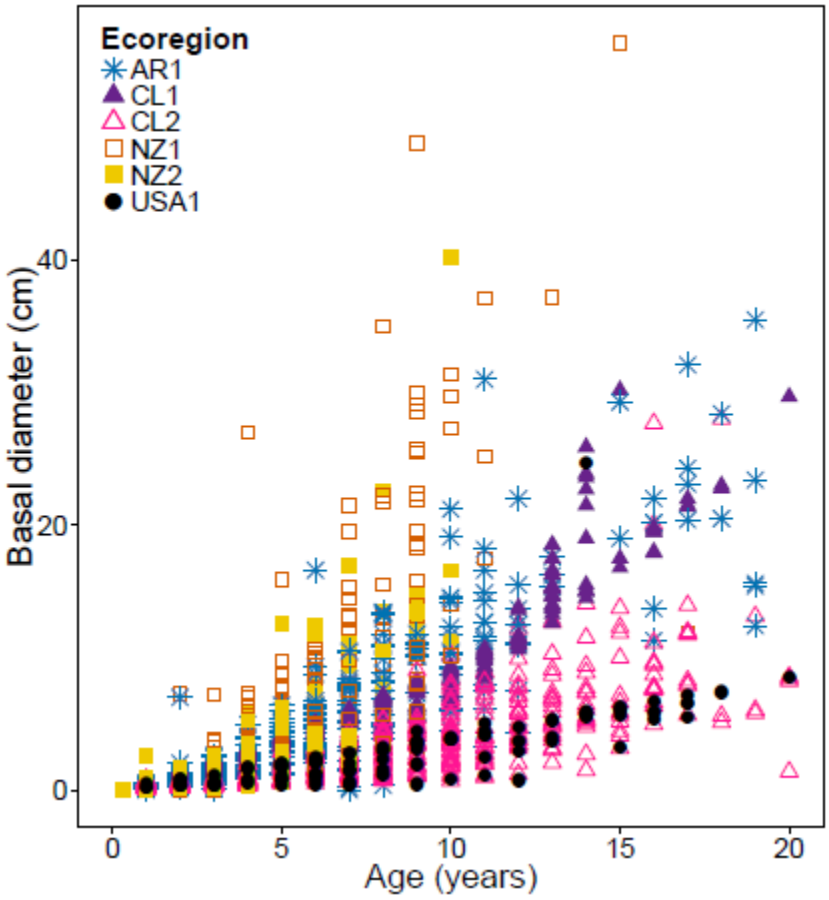

Figure 2.3. Relationships between *P. contorta* tree size (basal diameter (cm)) and age (years) among ecoregions. Data shown are coloured by ecoregion and shaped by country (but filled or hollow based on ecoregion). Descriptions of the ecoregions can be found in Table 2.1 and Appendix A.

Ecoregion, tree age and their interaction were also all highly significant predictors of cones per tree (χ^2=107.9, d.f.=5, P<0.001; χ^2=13385.4, d.f.=1, P<0.001; χ^2=164.5, d.f.=5, P<0.001, respectively). Trees in all introduced ecoregions produced, on average, more cones at a younger age than trees in the native ecoregion (P<0.05 for all pairwise comparisons; Figure 2.4).

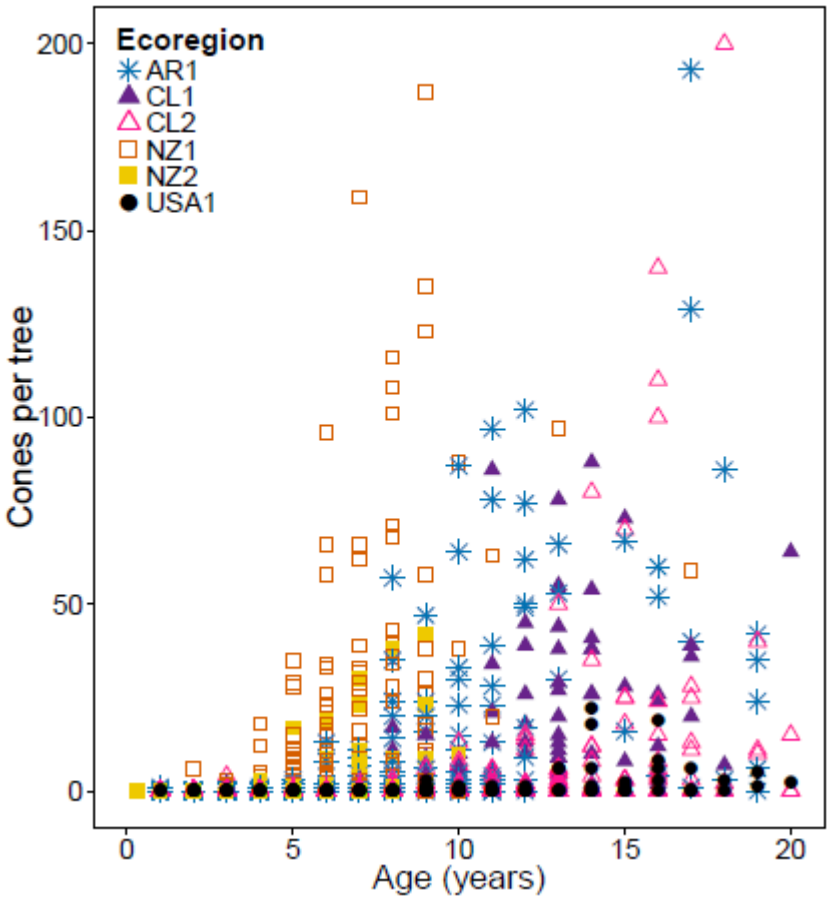

Figure 2.4. Relationships between *P. contorta* reproductive effort or fecundity (number of cones produced in sampling year per tree) and tree age (years) among ecoregions. Data shown are coloured by ecoregion and shaped by country (but filled or hollow based on ecoregion). Descriptions of the ecoregions can be found in Table 2.1 and Appendix A.

Discussion

We provide empirical evidence that the relative importance of widely accepted drivers of invasion (propagule pressure, biotic factors, and abiotic factors) varied strongly amongst six ecoregions for a widespread invasive tree species. This variation in factors driving invasion was due to plantation age, local vegetation, and climate, but also a consistent shift in demographic properties of the invasive tree towards faster growth, greater reproductive effort and higher rates of establishment in the introduced than in the native range. Biological resistance at the introduced sites altered invasion patterns and became more important than propagule pressure as the invasion proceeded. These findings provide a better understanding of variation in major drivers of biological invasions across biogeographic regions as outlined below.

Propagule Pressure

Propagule pressure is thought to be the major driver of biological invasions (Lockwood *et al.*, 2005; Simberloff, 2009). Consistent with this view, we observed negative relationships between *P. contorta* density and distance from source (Fig. 2.2) as have previous studies at individual sites (Ledgard, 2001; Sarasola *et al.*, 2006; Peña *et al.*, 2008; Langdon *et al.*, 2010). However, we additionally show that the relative importance of propagule pressure differed among regions. In the introduced range the sharpest decrease in density with increasing distance from the source population occurred at sites with recent invasions (AR1b, CL1) whereas older invasions (AR1a, NZ1, NZ2a) maintained high densities farther from the source (Fig. 2.1). One explanation for this is that habitat characteristics or biotic factors may become increasingly important relative to

propagule pressure as invasion proceeds (Dietz & Edwards, 2006). This idea is supported by our finding that vegetation type was more important than propagule pressure for older invasions at AR1a and NZ2. Similarly, Donaldson *et al.* (2014) also report that source population was most important in explaining invasion abundance early in a tree invasion, but that the invader's reproduction rate was more important for later stages. In the native range, distance to source was the most important variable despite the older source age, potentially due to the harsh abiotic conditions (Theoharides & Dukes, 2007). However, we could not disentangle fully the effects of propagule pressure from the source population or plantation, from propagules supplied by previously invading trees (Fig. A3 in Appendix A). Overall, our results show that biotic effects outweighed propagule pressure at some stages of invasion, and therefore strongly suggest that understanding the long-term biotic interactions that occur during biological invasions are important, even though these interactions are not typically considered by, for example, climate matching models (e.g. Nuñez & Medley, 2011).

Biotic Factors

There was little invasion by *P. contorta* into areas dominated by either tall shrubs or southern beech across our study sites, suggesting that biological regulation of tree invasion may be a common feature and should occur in other introduced ranges. More generally, it has been suggested that forests and shrublands are less likely than grasslands to be invaded by pines (Richardson *et al.*, 1994). Consistent with this idea, a previous study also found a negative relationship between *P. contorta* invasion success and presence of the native tree *Nothofagus antarctica* (Peña *et al.*, 2008). In contrast, native

Araucaria araucana forests were easily invaded (our study and Peña *et al*., 2008), suggesting that biological regulation of tree invasions can be context-dependent, in this case likely related to overall canopy cover in the different forest types (Peña *et al.*, 2008) or due to associated biological interactions not considered here such as the availability and efficacy of mutualistic species (e.g. Dickie *et al.*, 2010; Hayward *et al.*, 2015). Our global model incorporating data across all sites demonstrates that short shrublands had higher tree invasion densities than grasslands. Although we did not investigate the potential mechanisms involved, such as resource competition between grasses and *P. contorta* seedlings (Ledgard, 2001; Ledgard, 2006), our results suggest that areas with higher soil moisture and greater plant cover were consistently more resistant to *P. contorta* invasion. Such biological mediation of invasion success is likely widespread. For example, in Chile (near CL1), native grass steppe communities were more easily invaded than European forage grass communities (Langdon *et al.*, 2010). Boulant *et al.* (2009) found that the effect of shrub cover on pine invasion rate depended on grazing intensity. Therefore, our results coupled with previous studies demonstrate that generalizations about whether forests, shrublands, or grasslands may be more easily invaded are not warranted, but rather that biological factors *per se* (e.g. vegetation type, herbivory, presence of mutualists or pathogens) determine differences in invasion success and thus invasion rate and extent is context-dependent (e.g. Wood *et al.*, 2015).

High propagule pressure is thought to overwhelm the effect of biotic resistance to invasions (Von Holle & Simberloff, 2005). However, we observed little *P. contorta* invasion from plantations into adjacent areas dominated by tall shrubs or southern beech

despite relatively long-term (decadal) high propagule pressure (Fig. 2.1). For example, in Chile (site CL1), there was little *P. contorta* invasion into adjacent savannah-like vegetation dominated by the native tree *N. antarctica* despite available bareground and low canopy cover, factors typically thought to promote establishment and invasion by conifers (Lotan & Critchfield, 1990; Ledgard, 2001). This highlights the difference between propagule pressure and establishment success, and there are a range of likely biotic mechanisms mediating between propagule pressure and establishment success such as missing mutualists (Nuñez *et al.*, 2009), herbivory or granivory by animals (Buckley *et al.*, 2005; Nuñez *et al.*, 2008; Boulant *et al.*, 2009), or accumulated pathogens and disease (Diez *et al.*, 2010). This highlights the importance of considering site-specific interactions between individual drivers (propagule pressure, biotic factors, abiotic factors) when explaining invasion patterns (Catford *et al.*, 2009).

Differences in density and growth between sites could also be a result of biotic interactions. Although, climate differs between the native and introduced ranges (Table 2.1), the importance of winter temperature in the global density model may represent differences between the USA and other sites generally, including climate factors but also other differences not included in the model. For example, there could be native pathogens or herbivores that are more abundant in the USA than in introduced ranges. Seed predation could cause reduced establishment in the native range, where it is higher than in all other sites (Taylor, unpublished). Soil feedbacks on *P. contorta* have been found to be more negative in native soil than soil from the introduced range (Gundale *et al.*, 2014a), which could also contribute to the observed differences in growth. Finally,

ectomycorrhizae could contribute to differences in growth rates as evidenced by the higher growth rate of *P. contorta* invading *Pinus ponderosa* plantations than the grass steppe (where pine-specific ectomycorrhizae are likely less abundant) and higher growth rates at NZ2 where *P. contorta* associates with 14 ectomycorrhizal species (Dickie *et al.*, 2010) compared to CL1 where it often associates with just one ectomycorrhizal species (Hayward *et al.*, 2015).

Abiotic Factors

We did not find strong or consistent effects of topographic variables on *P. contorta* density; however, climate had a more important role. The ability of *P. contorta* to grow on most slopes, aspects, and elevations likely reflects its broad fundamental niche (Rehfeldt *et al.*, 1999). Where topographic factors were important, elevation was most likely to show a relationship with density, however, the direction of the relationship was not consistent among locations. In the USA the relationship between elevation and density may be largely explained by the positive correlation between mean annual temperature and *P. contorta* invasion density. Within the warmer low elevation areas, those that received higher precipitation had higher densities. Similarly, in the introduced range the most important climate variable in explaining invasion density was temperature during the wettest quarter of the year. This suggests that *P. contorta* establishes and survives better in areas with high precipitation during warmer months. The importance of abiotic factors in explaining invasion density may have been higher if we had been able to include other abiotic factors, such as detailed soil data.

At AR1 and USA1 there were lower levels of invasion in recently burned areas than in unburned areas. While at USA1 the difference in fire history is confounded with site, the sites' vegetation and abiotic settings are extremely similar, so fire is likely partially responsible for differences found in invasion density. Thus, fire through low density invasion fronts may reduce invasion rates where native plants are adapted to regenerate following fire (Widenmaier & Strong, 2010), contrary to concerns that a positive feedback could form between pine invasions and fire (Simberloff *et al*., 2010). Our results suggest that prescribed fire in low density invasions could be explored as a management option. In contrast, fire through higher density invasions or plantations in the introduced range may have different outcomes because dense invasions alter fuel structure (Cóbar-Carranza *et al.*, 2014) and therefore may alter fire behavior and the post-fire plant community.

Global Differences in Density, Size, and Reproduction

Pinus contorta invasion density was consistently higher in the introduced range than the native range. Several other plant species also have higher densities in their introduced than native ranges; however, for some species densities do not vary across ranges (Parker *et al.*, 2013). Therefore it is important to recognize that *P. contorta* does behave differently when invading open areas in its native and introduced ranges, which could reflect differences in the underlying processes causing invasion between the native and introduced ranges. Although *P. contorta* can form extremely dense stands in forested areas in its native range, particularly after fire, our results suggest that these densities are not reached in situations where *P. contorta* encroaches from forest edges into shrubland

steppe in its native range, even after fire. It is possible that invasion from plantations (introduced range) may proceed differently than from forest edges (native range), where the surrounding vegetation has evolved in proximity to pines. Plantations often are highly disturbed during the planting process and post-planting management (such as removing lower limbs) may alter wind dynamics and seed dispersal. Additional differences between the native and introduced range that could affect the invasion process include different seed predators, herbivores, and pathogens, as well as climatic differences that may result in a longer photosynthetic period in the warmer introduced ranges.

Pinus contorta trees grew faster and reproduced more prolifically and at a younger age in the introduced than the native range. Other plant species also have increased growth or seed production in their introduced range, although the underlying mechanisms are unresolved (Willis *et al.*, 1999; Parker *et al.*, 2013). The observed difference in *P. contorta* cone production could result in significantly higher propagule pressure in the introduced range than the native range, and this could explain the difference in invasion densities between ranges. Given the relatively long generation time of *P. contorta* and the young age of the plantations in most areas, it is more likely that the differences in density, growth, and reproduction are phenotypic responses to differences in climate or pathogens and herbivores rather than the result of rapid evolution in the introduced range (Buswell *et al.*, 2011). Our results suggest that higher temperatures are correlated with higher invasion densities, especially when sufficient moisture is present. In its native range in British Columbia, Canada, *P. contorta* occurs in climates that are colder and more continental than those in which optimal growth occurs (Rehfeldt *et al.*,

1999). The warmer, more maritime climates found at the Southern Hemisphere study sites may thus be more optimal for *P. contorta* growth. More detailed investigation of the mechanisms involved (e.g. climatic effects), and differences in fundamental traits (e.g. variability in seed number and quality among individuals (Coutts *et al.*, 2012)) is thus warranted. Overall, our data suggest that a co-ordinated demographic shift towards faster growth and earlier, greater reproductive effort in the introduced range has occurred, however the underpinning mechanisms involved and the persistence of these demographic shifts remains to be determined.

Management Implications

The best management approach for tree invasions depends on both habitat heterogeneity and tree demography (Caplat *et al.*, 2014). We found that invasion success was driven by propagule pressure but that certain habitats, such as closed canopy forests or tall shrublands, resisted pine invasions regardless of propagule pressure. Therefore, low density *P. contorta* invasions in these habitats should be a low priority for management. Low-lying areas with dense herbaceous cover also may provide resistance to pine invasion (Ledgard, 2006), especially if herbivory is common (Buckley *et al*., 2005). Additionally, we found that *P. contorta* demography varied between sites, suggesting that invasion spread rates will likely differ between sites even within a management jurisdiction. Therefore, monitoring invasions and response to management will help prioritize populations to manage (Rew *et al*., 2007; Wilson *et al*., 2014).

Acknowledgements

We would like to thank Hannah Funke, Jeff Patriache, and Sam Wall for field assistance. Nick Ledgard provided valuable assistance and knowledge regarding pine invasions in New Zealand. KTT and BDM funded by NSF-WildFIRE PIRE, OISE 09667472. AP funded by Fondecyt grants 1100792 & 1140485, ICM P05-002, CONICYT PFB-23. DAP acknowledges financial support provided by Core funding for Crown Research Institutes from the New Zealand Ministry of Business, Innovation and Employment's Science and Innovation Group.

References

Allen, R.B. & Lee, W.G. (1989) Seedling establishment microsites of exotic conifers in *Chionochloa rigida* tussock grassland, Otago, New Zealand. *New Zealand Journal of Botany*, **27**, 491-498.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) lme4: Linear mixed-effects models using Eigen and S4. http://CRAN.R-project.org/package=lme4.

Boulant, N., Garnier, A., Curt, T. & Lepart, J. (2009) Disentangling the effects of land use, shrub cover and climate on the invasion speed of native and introduced pines in grasslands. *Diversity and Distributions*, **15**, 1047-1059.

Brummer, T.J., Maxwell, B.D., Higgs, M.D. & Rew, L.J. (2013) Implementing and interpreting local-scale invasive species distribution models. *Diversity and Distributions*, **19**, 919-932.

Buckley, Y.M., Brockerhoff, E., Langer, L., Ledgard, N., North, H. & Rees, M. (2005) Slowing down a pine invasion despite uncertainty in demography and dispersal. *Journal of Applied Ecology*, **42**, 1020-1030.

Buswell, J.M., Moles, A.T. & Hartley, S. (2011) Is rapid evolution common in introduced plant species? *Journal of Ecology*, **99**, 214-224.

Caplat, P., Hui, C., Maxwell, B.D. & Peltzer, D.A. (2014) Cross-scale management strategies for optimal control of trees invading from source plantations. *Biological Invasions*, **16**, 677-690.

Catford, J.A., Jansson, R. & Nilsson, C. (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, **15**, 22-40.

Cóbar-Carranza, A.J., García, R.A., Pauchard, A. & Peña, E. (2014) Effect of *Pinus contorta* invasion on forest fuel properties and its potential implications on the fire regime of *Araucaria araucana* and *Nothofagus antarctica* forests. *Biological Invasions*, **16**, 2273-2291.

Coutts, S.R., Caplat, P., Cousins, K., Ledgard, N. & Buckley, Y.M. (2012) Reproductive ecology of *Pinus nigra* in an invasive population: individual- and population-level variation in seed production and timing of seed release. *Annals of Forest Science*, **69**, 467-476.

Dehlin, H., Peltzer, D.A., Allison, V.J., Yeates, G.W., Nilsson, M.-C. & Wardle, D.A. (2008) Tree seedling performance and below-ground properties in stands of invasive and native tree species. *New Zealand Journal of Ecology*, **32**, 67-79.

Despain, D.G. (2001) Dispersal ecology of lodgepole pine (*Pinus contorta* Dougl.) in its native environment as related to Swedish forestry. *Forest Ecology and Management*, **141**, 59-68.

Dickie, I.A., Bolstridge, N., Cooper, J.A. & Peltzer, D.A. (2010) Co-invasion by *Pinus* and its mycorrhizal fungi. *New Phytologist*, **187**, 475-484.

Dickie, I. A., Burrows, L.E., Yeates, G.W., St. John, M.G., Hunt, J.E., Peltzer**,** D.A., Scott, J.T., Orwin, K.H., Stevenson, B., Rillig, M.C., Aislabie, J., Barbour, M.M., & Kirschbaum, M.U.F. (2011) Ecosystem service and biodiversity tradeoffs in two woody successions. *Journal of Applied Ecology*, **48**, 926–934.

Dickie, I.A., St John, M.G., Yeates, G.W., Morse, C.W., Bonner, K.I., Orwin, K. & Peltzer, D.A. (2014) Belowground legacies of *Pinus contorta* invasion and removal result in multiple mechanisms of invasional meltdown. *AoB Plants*, **6,** plu056.

Dietz, H. & Edwards, P.J. (2006) Recognition that causal processes change during plant invasion helps explain conflicts in evidence. *Ecology*, **87**, 1359-1367.

Diez, J.M., Dickie, I., Edwards, G., Hulme, P.E., Sullivan, J.J. & Duncan, R.P. (2010) Negative soil feedbacks accumulate over time for non-native plant species. *Ecology Letters*, **13**, 803-809.

Donaldson, J.E., Hui, C., Richardson, D.M., Robertson, M.P., Webber, B.L. & Wilson, J.R.U. (2014) Invasion trajectory of alien trees: the role of introduction pathway and planting history. *Global Change Biology*, **20**, 1527-1537.

Essl, F., Moser, D., Dullinger, S., Mang, T. & Hulme, P.E. (2010) Selection for commercial forestry determines global patterns of alien conifer invasions. *Diversity and Distributions*, **16**, 911-921.

Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N., Nielsen, A. & Sibert, J. (2012) AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods & Software*, **27**, 233-249.

Gundale, M., Kardol, P., Nilsson, M.C., Nilsson, U., Lucas, R.W. & Wardle, D.A. (2014a) Interactions with soil biota shift from negative to positive when a tree species is moved outside its native range. *New Phytologist*, **2**, 415-421.

Gundale, M.J., Pauchard, A., Langdon, B., Peltzer, D.A., Maxwell, B.D. & Nuñez, M.A. (2014b) Can model species be used to advance the field of invasion ecology? *Biological Invasions*, **16**, 591-607.

Hayward, J., Horton, T.R., Pauchard, A. & Nuñez, M.A. (2015) A single ectomycorrhizal fungal species can enable a *Pinus* invasion. *Ecology*, **96**:1438–1444.

Hierro, J.L., Maron, J.L. & Callaway, R.M. (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology*, **93**, 5-15.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965-1978.

Jakubos, B. & Romme, W.H. (1993) Invasion of sub-alpine meadows by lodgepole pine in Yellowstone National Park, Wyoming, USA. *Arctic and Alpine Research*, **25**, 382-390.

Kueffer, C., Pyšek, P. & Richardson, D.M. (2013) Integrative invasion science: model systems, multi-site studies, focused meta-analysis and invasion syndromes. *New Phytologist*, **200**, 615-633.

Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B. (2014) lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 2.0-11. http://CRAN.R-project.org/package=lmerTest.

Langdon, B., Pauchard, A. & Aguayo, M. (2010) *Pinus contorta* invasion in the Chilean Patagonia: local patterns in a global context. *Biological Invasions*, **12**, 3961-3971.

Ledgard, N. (2001) The spread of lodgepole pine (*Pinus contorta*, Dougl.) in New Zealand. *Forest Ecology and Management*, **141**, 43-57.

Ledgard, N.J. (2006) Determining the effect of increasing vegetation competition through fertiliser use on the establishment of wildings in unimproved high country grassland. *New Zealand Journal of Forestry*, **51**, 29-34.

Ledgard, N.J. & Paul, T.S.H. (2008) Vegetation successions over 30 years of high country grassland invasion by *Pinus contorta*. *New Zealand Plant Protection*, **61**, 98-104.

Leishman, M. R., Cooke, J., & Richardson, D. M. (2014). Evidence for shifts to faster growth strategies in the new ranges of invasive alien plants. *Journal of Ecology*, ***102***, 1451-1461.

Lockwood, J.L., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution*, **20**, 223-228.

Lotan, J.E. & Critchfield, W.B. (1990) *Pinus contorta* Dougl. ex. Loud. lodgepole pine. *Silvics of North America. Volume 1. Conifers. Agric. Handb. 654* (ed. by R.M. Burns and B.H. Honkala), pp. 302-315. U.S. Department of Agriculture, Forest Service, Washington, DC.

Moodley, D., Geerts, S., Rebelo, T., Richardson, D.M. & Wilson, J.R.U. (2014) Site-specific conditions influence plant naturalization: The case of alien Proteaceae in South Africa. *Acta Oecologica-International Journal of Ecology*, **59**, 62-71.

Nuñez, M.A. & Medley, K.A. (2011) Pine invasions: climate predicts invasion success; something else predicts failure. *Diversity and Distributions*, **17**, 703-713.

Nuñez, M.A., Simberloff, D. & Relva, M.A. (2008) Seed predation as a barrier to alien conifer invasions. *Biological Invasions*, **10**, 1389-1398.

Nuñez, M.A., Horton, T.R. & Simberloff, D. (2009) Lack of belowground mutualisms hinders Pinaceae invasions. *Ecology*, **90**, 2352-2359.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the worlds: A new map of life on Earth. *Bioscience*, **51**, 933-938.

Parker, J.D., Torchin, M.E., Hufbauer, R.A., Lemoine, N.P., Alba, C., Blumenthal, D.M., Bossdorf, O., Byers, J.E., Dunn, A.M., Heckman, R.W., Hejda, M., Jarosik, V., Kanarek, A.R., Martin, L.B., Perkins, S.E., Pyšek, P., Schierenbeck, K., Schloeder, C., van Klinken, R., Vaughn, K.J., Williams, W. & Wolfe, L.M. (2013) Do invasive species perform better in their new ranges? *Ecology*, **94**, 985-994.

Pauchard, A., Cavieres, L.A. & Bustamante, R.O. (2004) Comparing alien plant invasions among regions with similar climates: where to from here? *Diversity and Distributions*, **10**, 371-375.

Pawson, S.M., McCarthy, J.K., Ledgard, N.J. & Didham, R.K. (2010) Density-dependent impacts of exotic conifer invasion on grassland invertebrate assemblages. *Journal of Applied Ecology*, **47**, 1053-1062.

Peña, E., Hidalgo, M., Langdon, B. & Pauchard, A. (2008) Patterns of spread of *Pinus contorta* Dougl. ex Loud. invasion in a Natural Reserve in southern South America. *Forest Ecology and Management*, **256**, 1049-1054.

R Core Team. (2014) R: A language and environment for statistical computing version 3.1.1. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Rehfeldt, G.E., Ying, C.C., Spittlehouse, D.L. & Hamilton, D.A. (1999) Genetic responses to climate in *Pinus contorta*: Niche breadth, climate change, and reforestation. *Ecological Monographs*, **69**, 375-407.

Rew, L.J., Lehnhoff, E.A. & Maxwell, B.D. (2007) Non-indigenous species management using a population prioritization framework. *Canadian Journal of Plant Science*, **87**, 1029-1036.

Richardson, D.M. & Pyšek, P. (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography*, **30**, 409-431.

Richardson, D.M., Williams, P.A. & Hobbs, R.J. (1994) Pine invasion in the Southern Hemisphere: determinants of spread and invadability. *Journal of Biogeography*, **21**, 511-527.

Richardson, D.M., Hui, C., Nuñez, M.A. & Pauchard, A. (2014) Tree invasions: patterns, processes, challenges and opportunities. *Biological Invasions*, **16**, 473-481.

Rouget, M. & Richardson, D.M. (2003) Inferring process from pattern in plant invasions: A semimechanistic model incorporating propagule pressure and environmental factors. *American Naturalist*, **162**, 713-724.

Sarasola, M.M., Rusch, V.E., Schlichter, T.M. & Ghersa, C.M. (2006) Tree conifers invasion in steppe areas and *Austrocedus chilensis* forests in NW Patagonia. *Ecologia Austral*, **16**, 143-156.

Simberloff, D. (2009) The Role of Propagule Pressure in Biological Invasions. *Annual Review of Ecology Evolution and Systematics*, pp. 81-102. Annual Reviews, Palo Alto.

Simberloff, D., Relva, M.A. & Nuñez, M. (2002) Gringos en el Bosque: Introduced tree invasion in a *Nothofagus*/*Austrocedrus* forest. *Biological Invasions*, **4**, 35-53.

Simberloff, D., Souza, L., Nuñez, M.A., Barrios-Garcia, M.N. & Bunn, W. (2012) The natives are restless, but not often and mostly when disturbed. *Ecology*, **93**, 598-607.

Simberloff, D., Nuñez, M.A., Ledgard, N.J., Pauchard, A., Richardson, D.M., Sarasola, M., Van Wilgen, B.W., Zalba, S.M., Zenni, R.D., Bustamante, R., Peña, E. & Ziller, S.R. (2010) Spread and impact of introduced conifers in South America: Lessons from other southern hemisphere regions. *Austral Ecology*, **35**, 489-504.

Skaug, H., Fournier, D., Nielsen, A., Magnusson, A. & Bolker, B. (2013) Generalized Linear Mixed Models using AD Model Builder. R package version 0.7.7.

Theoharides, K.A. & Dukes, J.S. (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist*, **176**, 256-273.

Urrutia, J., Pauchard, A. & García, R.A. (2013) Differences in plant composition in an *Araucaria araucana* (Molina) K.Koch and *Nothofagus antarctica* (G. Forst.) Oerst. forest in a *Pinus contorta* Douglas ex Loudon invasion gradient. *Gayana Botanica*, **70**, 92-100.

Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*, Fourth Edition. edn. Springer, New York.

Ver Hoef, J.M. & Boveng, P.L. (2007) Quasi-poisson vs. negative binomial regression: how should we model overdispersed count data? *Ecology*, **88**, 2766-2772.

Von Holle, B. & Simberloff, D. (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology*, **86**, 3212-3218.

Widenmaier, K.J. & Strong, W.L. (2010) Tree and forest encroachment into fescue grasslands on the Cypress Hills plateau, southeast Alberta, Canada. *Forest Ecology and Management*, **259**, 1870-1879.

Willis, A.J., Thomas, M.B. & Lawton, J.H. (1999) Is the increased vigour of invasive weeds explained by a trade-off between growth and herbivore resistance? *Oecologia*, **120**, 632-640.

Wilson, J.R.U., Caplat, P., Dickie, I.A., Hui, C., Maxwell, B.D., Nuñez, M.A., Pauchard, A., Rejmánek, M., Richardson, D.M., Robertson, M. P., Spear, D., Webber, B.L.,

van Wilgen, B.W. & Zenni, R.D. (2014) A standardized set of metrics to assess and monitor tree invasions. *Biological Invasions*, **16,** 535-551.

Wood, J.R., Dickie, I.A., Moeller, H.V., Peltzer, D.A., Bonner, K.I., Rattray, G. & Wilmshurst, J.M. (2015) Novel interactions between non-native mammals and fungi facilitate establishment of invasive pines. *Journal of Ecology*, **103**, 121-129.

Zenni, R.D. & Nuñez, M.A. (2013) The elephant in the room: the role of failed invasions in understanding invasion biology. *Oikos*, **122**, 801-815.

CHAPTER THREE

NATIVE VERSUS NONNATIVE INVASIONS: SIMILARITIES AND DIFFERENCES IN THE BIODIVERSITY IMPACTS OF *PINUS CONTORTA* IN INTRODUCED AND NATIVE RANGES

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

Author: Kimberley T. Taylor

Contributions: Conceived the study and methodology, collected field data, executed statistical analysis and wrote initial manuscript.

Co-Author: Bruce D. Maxwell

Contributions: Assisted in study design, field data collection, analysis and manuscript preparation.

Co-Author: Aníbal Pauchard

Contributions: Provided guidance interpreting results and edited manuscript.

Co-Author: Martin Nuñez

Contributions: Provided guidance interpreting results and edited manuscript.

Co-Author: Lisa J. Rew

Contributions: Provided guidance in analysis and interpreting results and edited manuscript.

Manuscript Information Page

Kimberley T. Taylor, Bruce D. Maxwell, Aníbal Pauchard, Martin Nuñez, and Lisa J. Rew
Journal Name: Diversity and Distributions
Status of Manuscript:
____ Prepared for submission to a peer-reviewed journal
____ Officially submitted to a peer-review journal
____ Accepted by a peer-reviewed journal
__x_ Published in a peer-reviewed journal

John Wiley & Sons Ltd
Early View online 10 January 2016

The following chapter has been published in the journal *Diversity and Distributions* and appears in this dissertation with the journal's permission.

Abstract

Aim: To determine if one of the most invasive pine species introduced to the Southern Hemisphere, *Pinus contorta*, has changed plant species richness, composition, diversity, and litter depth where it has invaded into native open forest, shrub-steppe and grassland communities and to assess if changes were similar in its native and introduced range.

Location: Río Negro Province, Argentina; Aysén and Araucanía Regions, Chile; Greater Yellowstone Ecosystem, USA.

Methods: We measured changes in plant species richness, species composition and cover, diversity, and litter depth associated with increasing *P. contorta* tree cover along the invasion front at three sites in the introduced range (Argentina and Chile) and one in the native range (Montana, USA).

Results: Plant species richness and cover generally declined with increasing *P. contorta* canopy cover, at similar rates in both the introduced and native range. However, plant cover was not affected by *P. contorta* in a forested setting in the introduced range. *P. contorta* invasion explained more of the decline in species richness in the introduced than native range. Native species composition changed more strongly across the invasion gradient in the introduced than native range. Litter depth increased more rapidly with *P. contorta* cover in the native than introduced range.

Main conclusions: Our results highlight the potential of pines to alter plant communities whether encroaching from forests in the native range or from plantations in the introduced range. Species richness and plant cover declined in both settings; however, individual species abundance and species composition were more impacted in the

introduced range than in the native range. We suggest that invading trees have a greater capacity to cause ecological impacts in their introduced than in their native range, particularly where they represent a novel life form.

Introduction

Invasive plants, particularly invasive trees, are well known to have significant impacts on native biodiversity (e.g. Gaertner *et al*., 2009; Camarillo *et al*., 2015; Constán-Nava *et al*., 2015; Lazzaro *et al*., 2015; Shackleton *et al*., 2015). Less known, however, is whether the impact differs depending on whether the invasion occurs in an introduced range or in the species' native range. Many plant species grow larger and more densely in their introduced than in their native range (Parker *et al.*, 2013), which would suggest that the potential for negative impacts through competition would be greater in the introduced range (Blossey & Notzold, 1995). Invasive species can also alter ecosystems through the introduction of novel traits or life forms (Levine *et al.*, 2003). When the introduction of a novel trait to the new system causes invader impacts, similar impacts would not be expected in the native range where the trait was not novel. Generally, native species are less likely to spread into adjacent habitats than introduced species (Simberloff *et al.*, 2012). However, few studies have compared the impacts of a species invading new areas in both its native and introduced range. Here, we examine the influence of *Pinus contorta* invasion on plant biodiversity in both its native and introduced ranges when it encroaches into adjacent habitat.

Biogeographic studies that have examined invasive plant impacts on biodiversity have found that the presence of the invader is negatively correlated with native plant

species richness or biomass in the introduced range, but neutral or positive correlations were noted in the native range (Inderjit *et al.*, 2011; Callaway *et al.*, 2012; Kaur *et al.*, 2012; Shah *et al.*, 2014). With one exception (Shah *et al.*, 2014), these studies examined plants that were not actively invading adjacent communities in their native range. They also did not measure species richness along an abundance gradient of the study species, but instead compared areas with and without the species present.

Several mechanisms have been suggested to explain differences in invader impacts between the native and introduced ranges. These mechanisms include: stronger competitive effects of invading species in the introduced range than in the native range (Callaway & Aschehoug, 2000; Ni *et al.*, 2010); evolution of increased growth rates in the introduced range (Blossey & Notzold, 1995; Siemann & Rogers, 2001); differences in plant-soil feedbacks between ranges (Klironomos, 2002); allelopathy in the litter and soil (Callaway *et al.*, 2008; Thorpe *et al.*, 2009; Ni *et al.*, 2010; Kaur *et al.*, 2012); differences in volatile organic compounds that affect neighbouring plant mortality between ranges (Inderjit *et al.*, 2011); and altered soil nitrogen cycling (Thorpe & Callaway, 2011). Many invader impacts are caused by alteration of the microenvironment, changes in litter abundance or composition, or changes in soil microbial communities (Skurski *et al.*, 2014), although it is unclear how these processes differ between invasions of new habitat in the native versus in the introduced ranges. Other studies have suggested that invader impacts can increase when multiple invasive species facilitate each other (e.g. exotic fungus promoting growth of exotic pines), creating an “invasional meltdown” (Simberloff & Von Holle, 1999; Nuñez *et al.*, 2013; Dickie *et al.*, 2014).

Pines (genus *Pinus*) are an ideal group to examine whether invasion impacts are similar in the native and introduced ranges. Pines are widely distributed across the Northern Hemisphere but there are no native pines in the Southern Hemisphere outside of a small area in Indonesia (Rundel et al., 2014). In the 19th and 20th centuries pines were introduced throughout the Southern Hemisphere for forestry (Richardson & Higgins, 1998). Currently, in both the introduced and native ranges, pines are encroaching into grasslands and shrublands (Richardson & Bond, 1991; Jakubos & Romme, 1993; Simberloff *et al.*, 2010). Generally, pine seeds are widely dispersed by wind and the seedlings are good colonizers of grasslands and shrublands (Richardson, 1998). In areas where they have been introduced and escaped, pines have had measurable impacts on native biodiversity (Ledgard & Paul, 2008; Pawson *et al.*, 2010; Urrutia *et al.*, 2013), nutrient cycling and soil microbial communities (Dehlin *et al.*, 2008; Dickie *et al.*, 2011; Dickie *et al.*, 2014), and hydrological cycles (Farley *et al.*, 2005; Fernandez *et al.*, 2009). *Pinus contorta* Dougl. (lodgepole pine), which is native to western North America, has traits that lead to high invasive potential (low seed mass, short juvenile period, and short interval between large seed crops; Rejmánek & Richardson, 1996) and only three pine species introduced to the Southern Hemisphere have been found to invade more regions than *P. contorta* (of 24 species; Rejmánek & Richardson, 2013). *Pinus contorta* was initially introduced for soil erosion control in New Zealand and Patagonia and has since been planted for forestry purposes.

Pinus contorta and other exotic pine species have been associated with biodiversity declines in their introduced ranges both within plantations (Nilsson *et al.*,

2008; Paritsis & Aizen, 2008) and where they have invaded into surrounding natural habitat (Ledgard & Paul, 2008; Dickie *et al.*, 2011; Steers *et al.*, 2013; Urrutia *et al.*, 2013). Impacts have also been observed in the native range where conifer encroachment (hereafter called invasion) into meadows in western North America has altered soil biogeochemical cycles and microbial communities (Griffiths *et al.*, 2005) and lowered meadow plant species diversity (Haugo & Halpern, 2007). Increased density of native slash pines (*Pinus elliottii*) due to fire suppression in the Southeast US was also correlated with lower understorey plant diversity (Brewer, 1998).

Thus, examining *P. contorta* invasions into grassland and shrubland plant communities provides a unique opportunity to compare their impacts on plant diversity between the native and introduced ranges. While impacts have been observed in both ranges, *P. contorta* invades more densely and grows faster in the introduced than native range (Taylor *et al.*, 2015). In addition, Southern Hemisphere plants have no evolutionary history of interacting with species in the Pinaceae. Therefore, we expected that *P. contorta* invasions would have a greater impact on plant communities in the introduced than native range, especially where pines add new functional traits (deep litter with slow decay, continuous tree canopy, and unique mycorrhizal associations) to the community (Rundel *et al.*, 2014).

The consequences that invasive species have on communities vary (Hulme *et al.*, 2013) as a function of the existing species composition and environmental conditions (Ehrenfeld, 2003). Therefore, it is important to study invasion across various sites with different environmental characteristics (Hulme *et al.*, 2013; Kumschick *et al.*, 2015).

Previous studies have not compared the biodiversity of plant communities across a gradient of pine invasion in both the native and introduced range, and few have examined how the influence of an invader relates to its abundance (Vilà *et al.*, 2011). In this paper we examine changes in plant communities and litter depth across a range of invasion intensities (as measured by *P. contorta* cover) at three sites in Patagonia (Argentina and Chile) and one site in the native range (Montana, USA). The specific objectives of this study were: 1) to determine the relationship between changes in *P. contorta* cover and plant species richness, cover, composition, and diversity in native and introduced regions; 2) to assess if certain life forms within the native communities were correlated with *P. contorta* invasion; 3) to determine if litter depth (a potentially important transformative trait) differs across the *P. contorta* invasion gradients; and 4) to assess the relative importance of litter abundance versus *P. contorta* cover in explaining variation in species richness and plant cover. We hypothesized that species richness, plant cover, and diversity would decline with increasing *P. contorta* cover at a faster rate in the introduced range than in the native range. We also expected that litter depth would increase with increasing *P. contorta* cover at all sites and would additionally contribute to reduced native species cover.

Methods

Study Sites

Study sites included locations in Bariloche and El Bolsón, Argentina (AR); Coyhaique Alto, Chile (CL1); Malalcahuello, Chile (CL2; all introduced range); and southwestern Montana, United States America (USA; native range; see Fig. B1 and Table

B1 in Appendix B for climate and other environmental characteristics of all sites). The sites in Argentina (AR) were combined because they had similar shrub steppe communities, dominated by *Festuca pallescens*, *Mulinum spinosum*, and *Acaena* spp. (see Table B2 in Appendix B for full species lists). Adjacent *P. contorta* plantations were established between 20 and 35 years ago. Coyhaique Alto, Chile (CL1) was a grass steppe community dominated by *Festuca pallescens, Baccharis magellanicum* and *Acaena intergerrima*. The source *P. contorta* plantations at CL1 were 17 to 26 years old. The second site in Chile was located in the Reserva Nacional Malalcahuello (CL2) and was dominated by sparse *Araucaria araucana* forest with areas of *Nothofagus antarctica* and an understorey composed of *Festuca scabriuscula, Chusquea culeou* and *Gaultheria* species. Here the source populations were trial forestry plots planted 43 years ago (Peña *et al.*, 2008; Urrutia *et al.*, 2013). The site in Montana (USA) included sagebrush steppe dominated by *Artemisia tridentata*, *Festuca idahoensis*, and *Stipa* species. Most of the *P. contorta* encroachment into the sagebrush steppe at this site has occurred in the last 50 years (Patten, 1969). *Pinus contorta* encroachment into nearby grasslands has been attributed to long term climatic change (Jakubos & Romme, 1993), although encroachment is generally rare in this region. There was no evidence of recent fire in any site. Nomenclature follows Lesica (2012) for USA and Zuloaga *et al*. (2008) for Argentina and Chile.

Field Sampling

Plots were randomly located within sites and stratified by *P. contorta* canopy cover. The *P. contorta* cover gradient was positively correlated with the age of invading

trees and their distance from the seed source plantation or native forest. Non-invaded plots were constrained to areas dominated by vegetation types known to be invaded by *P. contorta* at these same sites (Peña *et al.*, 2008; Langdon *et al.*, 2010; Taylor *et al.*, 2016).

Ocular canopy cover data were collected for every vascular plant species in each plot (five by five meters); every species had the potential to account for 100 percent cover. In the only site with native trees (CL2), we did not include cover of overstorey tree species (mainly *Araucaria araucana*) in the analyses. At each plot we estimated mean litter depth from five depth measurements. *P. contorta* canopy cover was recorded in the centre of each plot with a spherical densiometer. Sample sizes were 13 in AR, 20 in CL1, 19 in CL2, and 21 in USA, across a *P. contorta* canopy cover gradient from zero to nearly 100 percent.

Studies that experimentally add an invasive plant and record impacts on plant communities over time are superior to the chronosequence approach that we took, but the years required for this type of experiment made it logistically unfeasible. Our sites were relatively homogenous and the invasions progressed uniformly from the plantations (Fig. B1 in Appendix B), so we are confident that the main difference between invaded and non-invaded plots in any study site was largely a result of *P. contorta* presence. The continuous wave of invasion, as demonstrated by the decreasing age of trees with increasing distance from the plantation/forest edge (rather than patchy invasion) suggests that *P. contorta* establishment was not influenced by minor differences in local species composition or abundance (Pauchard *et al*., pers. comm.).

Statistical Analysis

We used *P. contorta* percent cover as the explanatory variable in all analyses (Pawson *et al*., 2010). Relative species richness (percent of maximum at that site) was modelled with linear regression as a function of *P. contorta* cover for each site individually. We used relative species richness to account for overall differences in richness between sites. Shannon diversity was calculated for each plot (Oksanen *et al.*, 2013) and then modelled with linear regression as a function of *P. contorta* cover for each site individually. Additionally, data from all sites were combined and relative species richness and diversity were modelled as a function of *P. contorta* cover, site, and their interaction to determine if the rate of change of richness and diversity differed between sites.

Species composition at each site was examined by calculating the Bray-Curtis distance between plots based on all species cover (excluding *P. contorta*). Permutational multivariate analysis of variance (PERMANOVA) was used to determine if *P. contorta* cover was significantly related to species composition as represented by the Bray Curtis distances. Linear regression was used to model total plant cover, plant cover by life form (cushion, grass, forb, shrub), exotic plant cover, and cover of each species individually in response to *P. contorta* cover for each site separately. A Poisson regression was used to model exotic species richness as a function of *P. contorta* cover for each site. Finally, total plant cover data from all sites was combined to test for differences in the relationship between *P. contorta* cover and total cover between sites. To control for differences between sites in overall productivity, relative total plant cover (cover of each

plot divided by maximum plant cover at that site) was modelled with linear regression as a function of *P. contorta* cover, site, and their interaction.

Two potential mechanisms by which *P. contorta* could influence plant communities are through an increase in shade (measured here as canopy cover) and an increase in persistent litter (measured as litter depth). To explore these possibilities, we first modelled litter depth as a function of *P. contorta* cover at each site individually and then in a model that combined data from all sites to determine differences in litter accumulation rates with *P. contorta* invasion between sites. We then modelled relative species richness (percent of maximum), total plant cover and plant cover by life form (grass, forb, shrub) as a function of both *P. contorta* cover and litter depth. We used commonality analysis (Ray-Mukherjee *et al.*, 2014) to improve our interpretation of the multiple regression results, given the collinearity between *P. contorta* cover and litter depth (R^2 between 0.16 and 0.62, Table 3.1). Commonality analysis separates the variance of the model R^2 into unique and shared effects of the predictors (Ray-Mukherjee *et al.*, 2014). Commonality analysis allowed us to determine how much of the variance in the responses was explained by only *P. contorta* cover, only litter depth, or both due to collinearity. All statistical analysis was performed in R (R Core Team, 2014).

Results

Species Richness and Diversity

Relative species richness declined with increasing *P. contorta* cover at all sites but *P. contorta* cover explained more than twice the variance in species richness at the introduced sites than at the native site (Table 3.1; Fig. 3.1(a**)**). In the combined model,

the rate of decline in relative species richness with increasing *P. contorta* cover did not differ between the USA (native range) and introduced range sites ($F_{3,65}$ = 1.33, P = 0.272). There was a significant negative relationship between Shannon diversity and *P. contorta* cover at CL2 (t = -2.4, d.f. = 17, P = 0.028) but no relationship at other sites.

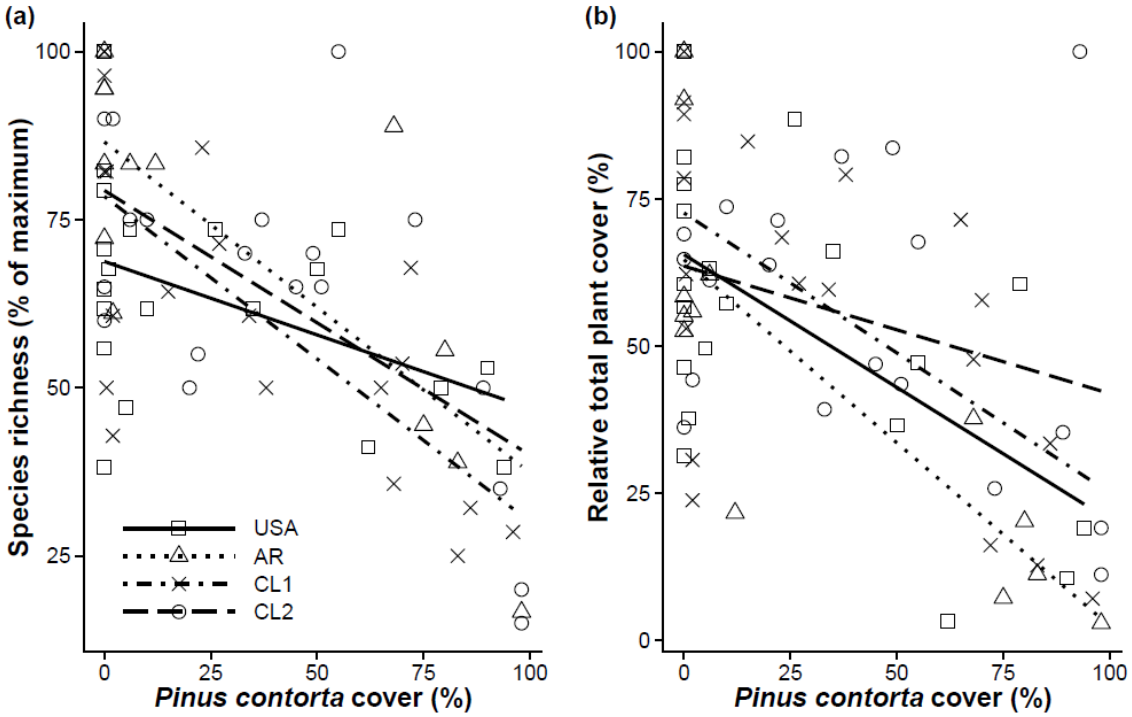

Figure 3.1. Relative species richness (a) and relative total plant cover (b) plotted against *Pinus contorta* cover (%) for each site with the fitted line from the combined models containing all data from all sites. Statistically the slope of the lines do not differ between the native site (USA) and any introduced site (AR, CL1, CL2) for both relative species richness and relative total plant cover (p>0.05). Solid line and squares represent USA, dotted line and triangles represent AR, dot-dashed line and x's represent CL1, and long dashed line and circles represent CL2. See Fig. B1 and Table B1 in Appendix B for full site descriptions (AR, CL1, CL2, USA).

Table 3.1. Results from models from each site of species richness, grass cover, forb cover, shrub cover, total plant cover, and litter depth as a function of *Pinus contorta* cover. – indicates that that life form was not present at the given site. R^2 is adjusted R^2. Results from cushion plants were not shown because there was no significant relationship with *Pinus contorta* cover at any site ($P > 0.05$). See Fig. B1 and Table B1 in Appendix B for full site descriptions (AR, CL1, CL2, USA).

		AR	CL1	CL2	USA
Relative species richness	Cover	-0.492	-0.484	-0.394	-0.219
	SE	0.119	0.11	0.118	0.094
	t-value	-4.145	-4.4	-3.325	-2.317
	P-value	0.002	<0.001	0.004	0.032
	R^2	0.57	0.49	0.359	0.18
Litter depth	Cover	0.012	0.021	0.011	0.029
	SE	0.007	0.004	0.004	0.007
	t-value	1.823	5.696	2.840	4.385
	P-value	0.096	<0.001	0.011	<0.001
	R^2	-	0.623	0.282	0.477
Grass cover	Cover	-0.042	-0.176	-0.201	-0.061
	SE	0.013	0.069	0.063	0.105
	t-value	-3.159	-2.555	-3.185	-0.577
	P-value	0.009	0.02	0.005	0.571
	R^2	0.428	0.225	0.337	-
Forb cover	Cover	-0.003	-0.019	-0.014	-0.185
	SE	0.01	0.005	0.007	0.078
	t-value	-0.316	-3.993	-1.997	-2.376
	P-value	0.758	0.001	0.062	0.028
	R^2	-	0.440	-	0.189
Shrub cover	Cover	-0.421	-	0.071	-0.297
	SE	0.09	-	0.137	0.104
	t-value	-4.668	-	-0.514	-2.859
	P-value	<0.001	-	0.614	0.01
	R^2	0.634	-	-	0.264
Total cover	Cover	-0.435	-0.236	-0.177	-0.543
	SE	0.095	0.075	0.126	0.169
	t-value	-4.571	-3.158	-1.406	-3.208
	P-value	<0.001	0.006	0.178	0.005
	R^2	0.624	0.321	-	0.317

Plant Composition

Pinus contorta cover was significantly related to differences in species composition between plots within sites in both introduced and native ranges (Table 3.2). However, *P. contorta* cover explained twice as much of the similarity in species composition between steppe plots in the introduced range (AR and CL1) than in the native range (USA; Table 3.2).

Table 3.2. Results from the PERMANOVA (permutational multivariate analysis of variance) for each site that models Bray-Curtis distance between plot species composition as a function of *Pinus contorta* cover. AR (shrubland), CL1 (grassland), and CL2 (open forest) are introduced range sites and USA (shrubland) is the native range site. See Fig. B1 and Table B1 in Appendix B for full site descriptions.

	P. contorta cover	
Site	R^2	*P*-value
AR	0.31	0.001
CL1	0.21	0.003
CL2	0.12	0.023
USA	0.11	0.023

When examining relationships between *P. contorta* cover and individual species cover we found that at all introduced sites most of the significant relationships ($P < 0.05$) were negative (Fig. 3.2; Table B3 in Appendix B). In contrast, in the native range the only species (*Poa palustris*) that had a significant relationship with *P. contorta* cover had higher abundance in more highly invaded plots (Fig. 3.2; Table B3). At AR, *P. contorta* cover had a significant negative relationship with the cover of three native species (14% of the species present in at least three sampled plots), including the most frequently occurring shrub species (*Mulinum spinosum*). At CL1, *P. contorta* cover had a significant negative relationship with cover of fourteen species (37% of the species

present in at least three sampled plots), including the most common grass species *Festuca pallescens* (Fig. B2 in Appendix B). Only the native *Viola reichei* had a significant positive relationship with *P. contorta* cover at CL1 (Fig. 3.2; Table B3). At CL2, *P. contorta* cover had a significant negative relationship with two species (7% of species present in at least three plots), including the most common grass species (*Festuca scabriuscula*; Fig. B2).

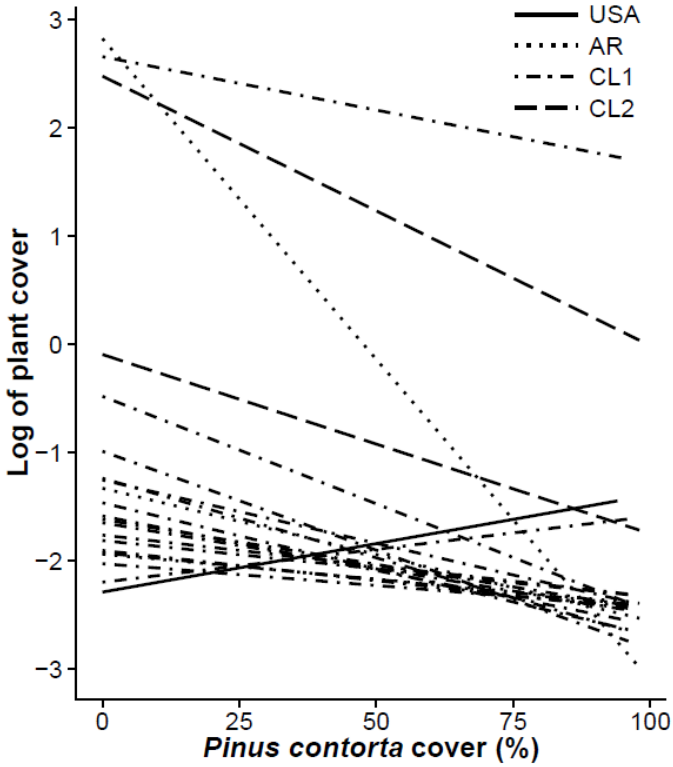

Figure 3.2. Fitted lines from linear models of the natural log of cover for all individual species as a function of *Pinus contorta* cover. Each line represents one species and lines are only shown for species that had a significant relationship with *Pinus contorta* cover ($P<0.05$). All species, their slopes, model p-values, and sample sizes are reported in Table B3 in Appendix B. Solid lines represent species found in the USA, dotted lines represent species found in AR, dot-dashed lines represent species found in CL1, and long dashed lines represent species found at CL2. See Fig. B1 and Table B1 in Appendix B for full site descriptions (AR, CL1, CL2, USA).

Changes in Plant Cover by Life Form and Origin

Pinus contorta cover was negatively correlated with total plant cover at all sites except CL2 (Fig. 3.3; Table 3.1). In the combined model, the relationship between *P. contorta* cover and relative total cover did not differ between the native site (USA) and introduced sites ($F_{3,65} = 1.27$, $P = 0.293$; Fig. 3.1). Analysis of the sites separately showed *P. contorta* cover was negatively correlated with, grass cover at AR, CL1, and CL2 (Table 3.1), forb cover at CL1 and USA (Table 3.1), and shrub cover at USA and AR (Table 3.1).

Exotic species cover other than *P. contorta* was low (<2%), although some exotic species were frequently present in sampled plots (e.g. *Rumex acetosella* in introduced range sites; Table B2). Seven exotic species were found at AR and CL1, three at CL2, and six at USA. Exotic plant cover decreased with increasing *P. contorta* cover at CL1 ($F_{1,18} = 8.43$, $P = 0.010$). Exotic cover at all other sites and exotic richness at all sites were not correlated with *P. contorta* cover ($P > 0.05$ for all comparisons).

Relationship between *P. contorta* Cover and Litter Depth

Pinus contorta cover was positively correlated with litter depth at CL1, CL2, and USA but not at AR (Table 3.1; Fig. 3.4). The relationship between litter depth and *P. contorta* cover did not differ between USA and CL1 ($t = -1.02$, d.f. = 65, $P = 0.312$), but litter depth increased more slowly with invasion at CL2 than at USA ($t = -2.33$, d.f. = 65, $P = 0.023$; Fig. 3.4). Litter included pine needles, but also dead material from native grasses and shrubs.

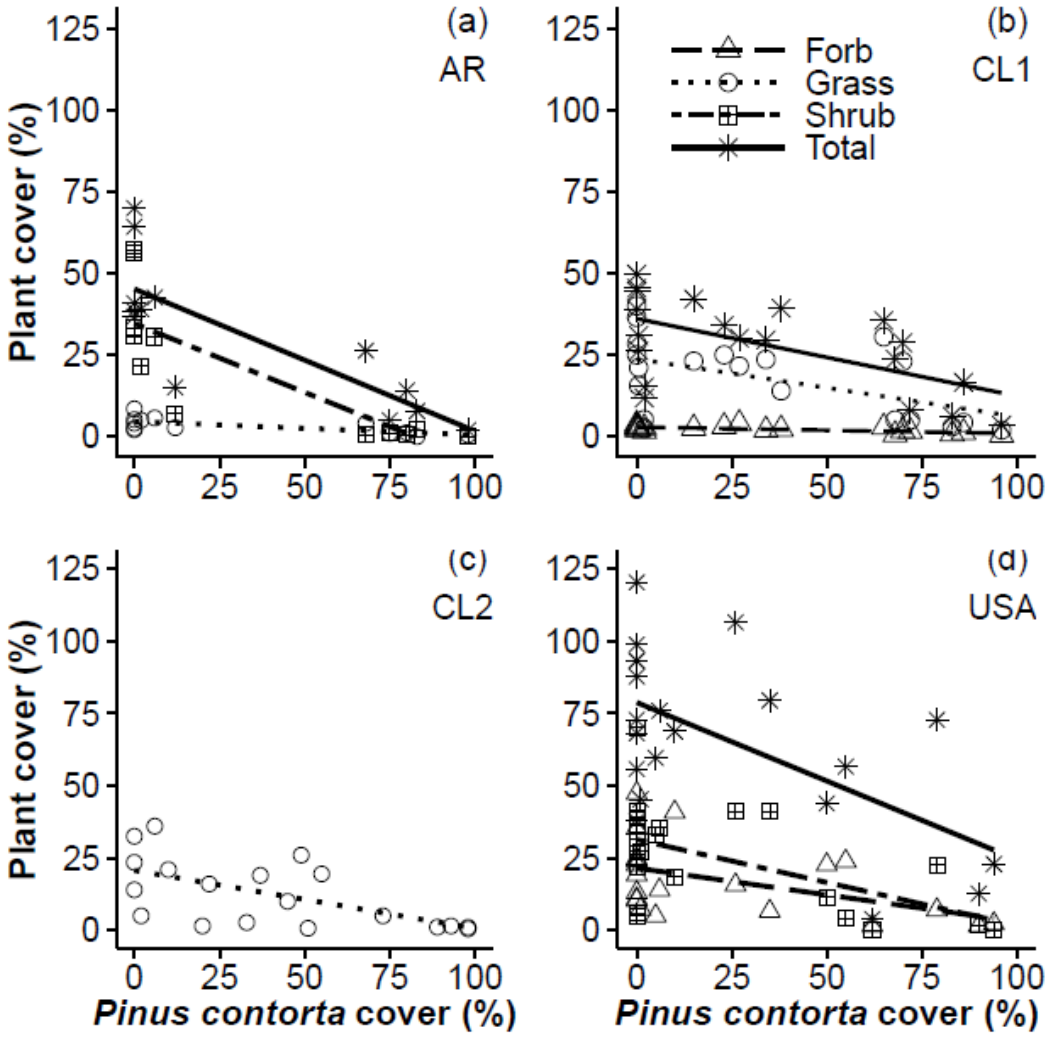

Figure 3.3 Relationship between *Pinus contorta* cover and plant cover by life form and total plant cover at introduced (AR (a), CL1 (b), CL2 (c)), and native (USA (d)) sites. Only lines for relationships between *Pinus contorta* cover and life forms that were significant at the *P*=0.05 level (Table 3.1) are shown. Dashed lines and triangles represent forb cover, dotted lines and circles represent grass cover, dot-dashed lines and squares represent shrub cover, and solid lines and asterisks represent total plant cover. See Fig. B1 and Table B1 in Appendix B for full site descriptions (AR, CL1, CL2, USA).

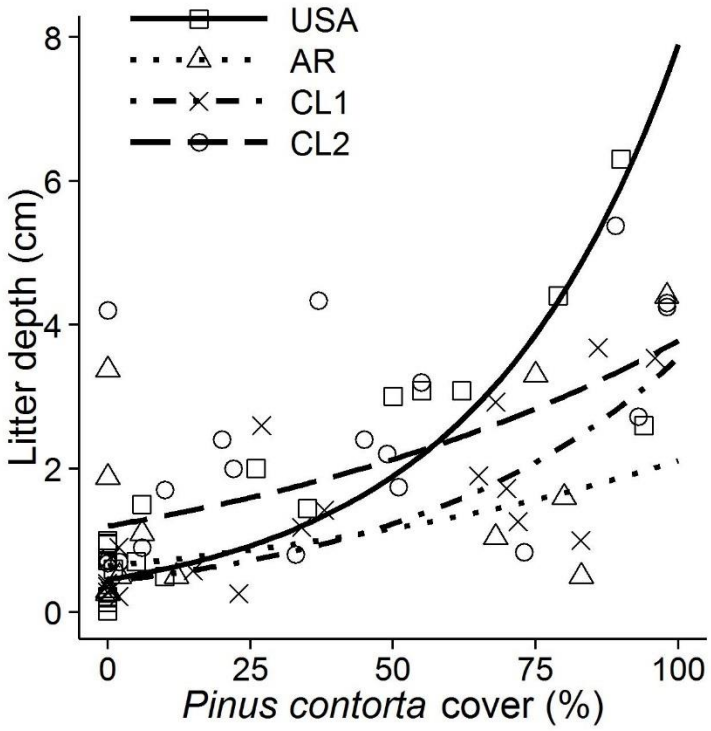

Figure 3.4. Litter depth and cover of *Pinus contorta* at the three introduced (AR, CL1, CL2) and one native (USA) sites, with the fitted lines from the linear model of the natural log of litter depth (back transformed to original scale). Solid line and squares represent USA, dotted line and triangles represent AR, dot-dashed line and x's represent CL1, and long dashed line and circles represent CL2. See Fig. B1 and Table B1 in Appendix B for full site descriptions (AR, CL1, CL2, USA).

Mechanism of Impact

Pinus contorta cover alone explained more of the variance in relative species richness and plant cover than did litter depth alone (Fig. 3.5). The only case where litter depth explained more variance than *P. contorta* cover was for forb cover at CL2 (*Araucaria araucana* forest). In all cases, a significant amount of variance was explained jointly by *P. contorta* cover and litter depth (Fig. 3.5).

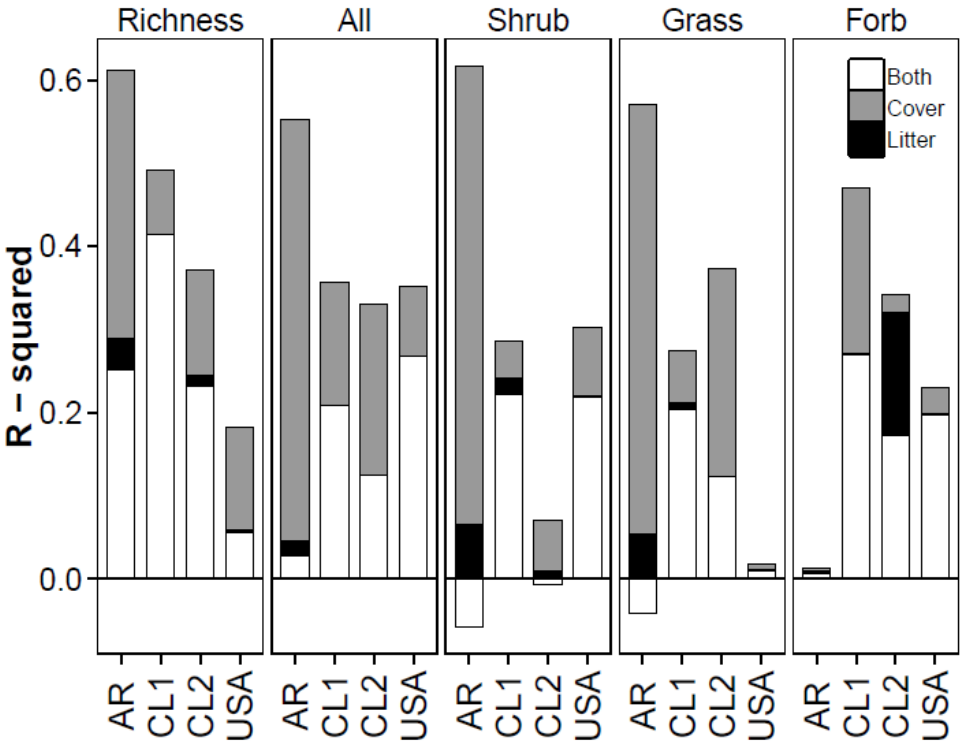

Figure 3.5. Results from the commonality analysis showing the percent of the variance explained (R-squared, also known as the coefficient of determination) by either *Pinus contorta* cover or litter depth, or shared explanatory power due to collinearity, in the full model for each site. The responses include relative species richness (richness), all plant cover (All), shrub cover, grass cover, and forb cover for each site. See Fig. B1 and Table B1 in Appendix B for full site descriptions (AR, CL1, CL2, USA).

Discussion

Pinus contorta cover was negatively correlated with plant species richness and cover at every study site (except plant cover at CL2), suggesting that pine invasion impacts on species richness and cover are similar in native and introduced ranges. However, species composition and individual species cover were more affected by *P. contorta* invasion in the introduced than native range. Additionally, invasions reach high levels of *P. contorta* cover more quickly in the introduced range than in the native range due to higher growth rates (Taylor *et al.*, 2016). Therefore, although the relationship

between *P. contorta* cover and plant species richness and cover were similar between sites, the declines in these properties may occur faster in the introduced than native range.

The negative correlation between *P. contorta* cover and species richness agrees with previous studies in New Zealand (Ledgard & Paul, 2008) and Chile (Urrutia *et al.*, 2013; Franzese *et al*., pers. comm.). Thus, there is mounting evidence that pine invasions into adjacent habitats will lead to declines in native plant species richness. *Pinus contorta* cover explained more of the decline in richness at the introduced steppe sites dominated by grass and shrubs where trees are likely a novel life form (AR; CL1) than at the introduced forested site (CL2) or in the native range (USA). Species in the steppe are likely less tolerant of shade and litter accumulation than those in the *A. araucana* forest. We saw a consistent decline in richness with increases in *P. contorta* cover, unlike the hump-shaped response observed with *Pinus nigra* invasions in New Zealand (Dickie *et al*., 2011). Neither ours nor the New Zealand study identified a threshold at which species richness changed rapidly, suggesting that pine's influence on species richness scales with invader abundance and tipping points are unlikely. Although species richness declined with increasing *P. contorta* cover, at most sites we did not see a significant decrease in Shannon diversity. This finding contradicts other studies, with a broader range of species, that found lower diversity in invaded plots than in non-invaded plots (Hejda *et al.*, 2009; Vilà *et al.*, 2011).

Contrary to expectations, the rate of species loss associated with increasing *P. contorta* cover was the same in the native and introduced ranges. Other studies examining species richness associated with invasive species in their introduced and native ranges

found a neutral or positive relationship between the invader and species richness in the native range (Inderjit *et al.*, 2011; Kaur *et al.*, 2012; Shah *et al.*, 2014). Our results may differ because we assessed species richness associated with an active *P. contorta* invasion in the native range, whereas in other studies, the target species was invading in the introduced but not native range. Similar decreases in species richness in native plant communities following *P. contorta* invasion, and native woody encroachment in general, have also been observed (Haugo & Halpern, 2007; Ratajczak *et al.*, 2012). Therefore, results from this study and previous work suggest that conifer invasion of treeless areas is likely to decrease species richness, even in the native range.

Relative total plant cover decreased significantly with increasing *P. contorta* cover at the same rate in all sites. At all the grassland or shrubland sites the dominant life form (grass in CL1 and shrubs in AR and USA) declined significantly with higher *P. contorta* cover. Additionally, at all introduced sites, cover of dominant species had negative relationships with *P. contorta* cover. Changes in the dominant life forms and species, as a result of invasion, likely alter litter quantity and quality, which could result in cascading effects on belowground communities (Bardgett & Wardle, 2010; Dickie *et al.*, 2011). The switch from grasslands or shrublands to areas with high tree cover and little shrub or grass cover in AR, CL1, and USA, may also affect animal communities that depend on grass and shrubs for habitat (Pawson *et al.*, 2010). The only site with native forest (CL2) showed no significant decline in total plant cover with increasing *P. contorta* cover, potentially because many native species growing in this forested site are shade tolerant. Another study also found less impact of *P. contorta* invasion on plant

communities in an *A. araucana* forest than in a Patagonian steppe site (Franzese *et al*., pers. comm.). A trend of greater invader impact on species richness in shrublands than forests has been observed in Mediterranean-type ecosystems as well (Gaertner *et al.*, 2009). Our results support the concept that impacts on plant communities depend on the traits of both the invader and the native communities (Levine *et al.*, 2003; Maron & Marler, 2008; Kumschick *et al*., 2015).

Impacts on species composition and individual species differed between the native and introduced range, suggesting that species richness alone is not the best metric to understand plant community change following non-native plant invasions (Parker *et al.*, 1999). The most pronounced differences in plant species composition across the invasion gradient in our study were observed in the introduced range (Table 3.2). Cover of 19 individual species declined as *P. contorta* cover increased in the introduced range, while in the native range no individual species had a significant negative relationship with *P. contorta* cover (Fig. 3.2; Table B3 in Appendix B). This difference between native and introduced ranges is exemplified by the grass genus *Festuca*, which was the most abundant grass genus at all sites, but only declined in abundance with increasing *P. contorta* cover in the introduced range (Fig. B2 in Appendix B). Although species with high or intermediate abundance were more likely to decline with *P. contorta* invasion in the introduced than native range, there were locally rare species at the USA site that were sensitive to invasion (Table B2 in Appendix B). Overall, differences in the impacts on species composition and individual species cover between native and introduced ranges suggest that Rocky Mountain grassland and shrubland communities, which have a long

history of coevolution with pines, may be less fundamentally altered by pine invasions. While invaded areas will likely experience a decline in species richness, species composition is expected to remain similar between invaded and uninvaded areas, at least for the first 50 years of invasion.

We saw little colonization by forest understorey species in *P. contorta* invaded plots in the native range. This observation differs from a study in Oregon, USA in which native conifer invasion into subalpine meadows was associated with colonization of forest understorey species within two decades of tree establishment (Haugo & Halpern, 2007). Perhaps such spread of forest understorey species at our USA site requires more than 50 years. Given that the Pinaceae is a novel family in Patagonia, it is unclear whether understorey species from native *Nothofagus* forest will colonize pine-dominated forest, especially in the steppe (AR and CL1) where dispersal distances to the nearest forest may be long.

Several studies have found increased exotic species richness correlated with the presence of an invasive species in the introduced range (Kaur *et al.*, 2012; Shah *et al.*, 2014). We saw no support for this type of "invasional meltdown" (Simberloff & Von Holle, 1999; Dickie *et al.*, 2014). However, a study in New Zealand found only exotic species persisting in the understorey of a *P. contorta* invasion thirty years after introduction (Ledgard & Paul, 2008). Another study in New Zealand found that legacy impacts from pine invasions on soil processes promoted exotic grasses and forbs (Dickie *et al.*, 2014). Therefore, the potential for *P. contorta* to promote invasion by herbaceous exotic species is not consistent between sites.

Often native communities are altered as a result of the different litter quantity or quality from exotic plants (Skurski *et al.*, 2014). The sharpest increase in litter depth with increasing *P. contorta* cover was seen in the native range (USA; Fig. 3.4), potentially because invasions in the USA are at least fifteen years older than invasions in the introduced range so there has been more time for litter to accumulate. Alternatively, the deeper litter could be due to differences in decomposition rates related to the colder conditions in Montana (USA) than the Southern Hemisphere sites (Table B1 in Appendix B). The changes in litter depth and quality may result in changes to soil processes or biotic communities (Dehlin *et al.*, 2008; de Oliveira *et al.*, 2014; Dickie *et al.*, 2014). Increased litter abundance may also create a more continuous wildfire fuel bed in the steppe ecosystems where traditionally bareground patches have limited fire size (Baker, 2009; Paritsis *et al.*, 2013).

Although litter accumulation is likely a mechanism driving impact, the results of our commonality analysis show that *P. contorta* cover alone explains more of the variance in species richness and plant cover than does litter depth alone. Therefore, increased shade is a strong mechanism causing changes in the plant community; although as litter accumulates over time, as these young pine trees age, litter depth and influence on biogeochemical processes could become more important in explaining native plant response. At the forested site (CL2), a decline in forb cover was more related to litter depth than *P. contorta* cover, potentially because forb species at this site may be adapted to low light situations, whereas pine litter chemistry likely differs from native species litter. In fact, *Pinus ponderosa* litter limited germination of several native Patagonian

grass species (Raffaele & Schlichter, 2000). At all sites, a large amount of variability in species richness and plant cover was jointly explained by *P. contorta* cover and litter depth. The overlap in explanatory power between litter depth and canopy cover is likely because litter is a measure of leaf area index which also represents shade. Therefore, these results highlight the need for manipulative experiments to separate the mechanisms of invader impacts.

Our results, along with those of previous studies, suggest that pine invasions will likely have significant impacts on plant communities in native and introduced ranges. We found that high *P. contorta* cover led to a decline in species richness whether it occurred in its native or introduced range. Impacts on native communities scaled with *P. contorta* abundance and no thresholds were found beyond which rapid declines in species richness or cover occurred. Contrary to previous biogeographic studies of plant invasion impacts, trends in species richness and plant cover were similar in the introduced and native ranges. Thus, biogeographic novelty alone does not govern all aspects of invader impact. Presence of a novel life form and specific species traits may determine invader impact on recipient plant communities. Nonetheless, fundamental components of the plant communities, such as species composition, were more altered by pine invasions in the introduced than native range. Therefore, for some characteristics, native invaders may have less capacity than exotic invaders to cause significant impacts. These results highlight the need to examine multiple metrics of plant communities in order to fully understand invader impacts. In addition, to elucidate the importance of specific mechanisms of pine invasion impact on native ecosystems, management of pine

invasions could be integrated with experimentation by designing treatments and follow-up monitoring.

Acknowledgements

We thank David McWethy, Hannah Funke, Maria Theresa Jessen and Sam Wall for field assistance and Pablo Bravo, Jonathan Urrutia and Jorgelina Franzese for help with species identification. We thank Cathy Whitlock, David McWethy, and three anonymous reviewers for helpful comments on the manuscript. KTT and BDM were funded by NSF-WildFIRE PIRE, OISE 09667472. AP was funded by Fondecyt grants 1100792 and 1140485, and the Institute of Ecology and Biodiversity with the grants by the Ministry of the Economy ICM P05-002 and CONICYT PFB-23. MAN was funded by Biosilva #5 from MAGyP of Argentina.

References

Baker, W.L. (2009) *Fire Ecology in Rocky Mountain Landscapes*. Island Press, Washington D.C.

Bardgett, R.D. & Wardle, D.A. (2010) *Aboveground - Belowground Linkages*. Oxford University Press, Oxford.

Blossey, B. & Notzold, R. (1995) Evolution of increased competitive ability in invasive nonindigenous plants - A hypothesis. *Journal of Ecology*, **83**, 887-889.

Brewer, J.S. (1998) Patterns of plant species richness in a wet slash-pine (*Pinus elliottii*) savanna. *Journal of the Torrey Botanical Society*, **125**, 216-224.

Callaway, R.M. & Aschehoug, E.T. (2000) Invasive plants versus their new and old neighbors: A mechanism for exotic invasion. *Science*, **290**, 521-523.

Callaway, R.M., Schaffner, U., Thelen, G.C., Khamraev, A., Juginisov, T. & Maron, J.L. (2012) Impact of *Acroptilon repens* on co-occurring native plants is greater in the invader's non-native range. *Biological Invasions*, **14**, 1143-1155.

Callaway, R.M., Cipollini, D., Barto, K., Thelen, G.C., Hallett, S.G., Prati, D., Stinson, K. & Klironomos, J. (2008) Novel weapons: Invasive plant suppresses fungal mutualists in America but not in its native Europe. *Ecology*, **89**, 1043-1055.

Camarillo, S.A., Stovall, J.P. & Sunda, C.J. (2015) The impact of Chinese tallow (*Triadica sebifera*) on stand dynamics in bottomland hardwood forests. *Forest Ecology and Management*, **344**, 10-19.

Constán-Nava, S., Soliveres, S., Torices, R., Serra, L. & Bonet, A. (2015) Direct and indirect effects of invasion by the alien tree *Ailanthus altissima* on riparian plant communities and ecosystem multifunctionality. *Biological Invasions*, **17**, 1095-1108.

de Oliveira, S.M., Boll, P.K., Baptista, V.D. & Leal-Zanchet, A.M. (2014) Effects of pine invasion on land planarian communities in an area covered by *Araucaria* moist forest. *Zoological Studies*, **53**, 19.

Dehlin, H., Peltzer, D.A., Allison, V.J., Yeates, G.W., Nilsson, M.-C. & Wardle, D.A. (2008) Tree seedling performance and below-ground properties in stands of invasive and native tree species. *New Zealand Journal of Ecology*, **32**, 67-79.

Dickie, I.A., St John, M.G., Yeates, G.W., Morse, C.W., Bonner, K.I., Orwin, K. & Peltzer, D.A. (2014) Belowground legacies of *Pinus contorta* invasion and

removal result in multiple mechanisms of invasional meltdown. *AoB Plants*, **6**, plu056.

Dickie, I.A., Yeates, G.W., St John, M.G., Stevenson, B.A., Scott, J.T., Rillig, M.C., Peltzer, D.A., Orwin, K.H., Kirschbaum, M.U.F., Hunt, J.E., Burrows, L.E., Barbour, M.M. & Aislabie, J. (2011) Ecosystem service and biodiversity trade-offs in two woody successions. *Journal of Applied Ecology*, **48**, 926-934.

Ehrenfeld, J.G. (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, **6**, 503-523.

Farley, K.A., Jobbagy, E.G. & Jackson, R.B. (2005) Effects of afforestation on water yield: a global synthesis with implications for policy. *Global Change Biology*, **11**, 1565-1576.

Fernandez, M.E., Gyenge, J. & Schlichter, T. (2009) Water flux and canopy conductance of natural versus planted forests in Patagonia, South America. *Trees-Structure and Function*, **23**, 415-427.

Gaertner, M., Den Breeyen, A., Hui, C. & Richardson, D.M. (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. *Progress in Physical Geography*, **33**, 319-338.

Griffiths, R., Madritch, M. & Swanson, A. (2005) Conifer invasion of forest meadows transforms soil characteristics in the Pacific Northwest. *Forest Ecology and Management*, **208**, 347-358.

Haugo, R.D. & Halpern, C.B. (2007) Vegetation responses to conifer encroachment in a western Cascade meadow: a chronosequence approach. *Canadian Journal of Botany-Revue Canadienne De Botanique*, **85**, 285-298.

Hejda, M., Pyšek, P. & Jarosik, V. (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology*, **97**, 393-403.

Hulme, P.E., Pyšek, P., Jarošík, V., Pergl, J., Schaffner, U. & Vilà, M. (2013) Bias and error in understanding plant invasion impacts. *Trends in Ecology & Evolution*, **28**, 212-218.

Inderjit, Evans, H., Crocoll, C., Bajpai, D., Kaur, R., Feng, Y.-L., Silva, C., Treviño Carreón, J., Valiente-Banuet, A., Gershenzon, J. & Callaway, R.M. (2011) Volatile chemicals from leaf litter are associated with invasiveness of a Neotropical weed in Asia. *Ecology*, **92**, 316-324.

Jakubos, B. & Romme, W.H. (1993) Invasion of sub-alpine meadows by lodgepole pine in Yellowstone National Park, Wyoming, USA. *Arctic and Alpine Research*, **25**, 382-390.

Kaur, R., Gonzales, W.L., Daniel Llambi, L., Soriano, P.J., Callaway, R.M., Rout, M.E., Gallaher, T.J. & Inderjit (2012) Community impacts of *Prosopis juliflora* invasion: biogeographic and congeneric comparisons. *Plos One*, **7**, e44966.

Klironomos, J.N. (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature*, **417**, 67-70.

Kumschick, S., Gaertner, M., Vilà, M., Essl, F., Jeschke, J.M., Pyšek, P., Ricciardi, A., Bacher, S., Blackburn, T.M., Dick, J.T.A., Evans, T., Hulme, P.E., Kühn, I., Mrugała, A., Pergl, J., Rabitsch, W., Richardson, D.M., Sendek, A. & Winter, M. (2015) Ecological Impacts of Alien Species: Quantification, Scope, Caveats, and Recommendations. *Bioscience*, **65**, 55-63.

Langdon, B., Pauchard, A. & Aguayo, M. (2010) *Pinus contorta* invasion in the Chilean Patagonia: local patterns in a global context. *Biological Invasions*, **12**, 3961-3971.

Lazzaro, L., Giuliani, C., Benesperi, R., Calamassi, R. & Foggi, B. (2015) Plant species loss and community nestedness after leguminous tree *Acacia pycnantha* invasion in a Mediterranean ecosystem. *Folia Geobotanica*, **50**, 229-238.

Ledgard, N.J. & Paul, T.S.H. (2008) Vegetation successions over 30 years of high country grassland invasion by *Pinus contorta*. *New Zealand Plant Protection*, **61**, 98-104.

Lesica, P. (2012) *Manual of Montana Vascular Plants*. Brit Press, Fort Worth.

Levine, J.M., Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society B*, **270**, 775-781.

Maron, J.L. & Marler, M. (2008) Effects of native species diversity and resource additions on invader impact. *American Naturalist*, **172**, S18-S33.

Ni, G.-Y., Schaffner, U., Peng, S.-L. & Callaway, R.M. (2010) *Acroptilon repens*, an Asian invader, has stronger competitive effects on species from America than species from its native range. *Biological Invasions*, **12**, 3653-3663.

Nilsson, C., Engelmark, O., Cory, J., Forsslund, A. & Carlborg, E. (2008) Differences in litter cover and understory flora between stands of introduced lodgepole pine and native scots pine in Sweden. *Forest Ecology and Management*, **255**, 1900-1905.

Nuñez, M.A., Hayward, J., Horton, T.R., Amico, G.C., Dimarco, R.D., Barrios-Garcia, M.N. & Simberloff, D. (2013) Exotic Mammals Disperse Exotic Fungi That Promote Invasion by Exotic Trees. *Plos One*, **8**, e66832.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2013) vegan: Community Ecology Package. R package version 2.0-10. http://CRAN.R-project.org/package=vegan

Paritsis, J. & Aizen, M.A. (2008) Effects of exotic conifer plantations on the biodiversity of understory plants, epigeal beetles and birds in *Nothofagus dombeyi* forests. *Forest Ecology and Management*, **255**, 1575-1583.

Paritsis, J., Holz, A., Veblen, T.T. & Kitzberger, T. (2013) Habitat distribution modeling reveals vegetation flammability and land use as drivers of wildfire in SW Patagonia. *Ecosphere*, **4**, art53.

Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E. & Goldwasser, L. (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, **1**, 3-19.

Parker, J.D., Torchin, M.E., Hufbauer, R.A., Lemoine, N.P., Alba, C., Blumenthal, D.M., Bossdorf, O., Byers, J.E., Dunn, A.M., Heckman, R.W., Hejda, M., Jarošík, V., Kanarek, A.R., Martin, L.B., Perkins, S.E., Pyšek, P., Schierenbeck, K., Schlöeder, C., van Klinken, R., Vaughn, K.J., Williams, W. & Wolfe, L.M. (2013) Do invasive species perform better in their new ranges? *Ecology*, **94**, 985-994.

Patten, D.T. (1969) Succession from sagebrush to mixed conifer forest in Northern Rocky Mountains. *American Midland Naturalist*, **82**, 229-240.

Pawson, S.M., McCarthy, J.K., Ledgard, N.J. & Didham, R.K. (2010) Density-dependent impacts of exotic conifer invasion on grassland invertebrate assemblages. *Journal of Applied Ecology*, **47**, 1053-1062.

Peña, E., Hidalgo, M., Langdon, B. & Pauchard, A. (2008) Patterns of spread of *Pinus contorta* Dougl. ex Loud. invasion in a Natural Reserve in southern South America. *Forest Ecology and Management*, **256**, 1049-1054.

R Core Team. (2014) R: A language and environment for statistical computing version 3.1.1. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Raffaele, E. & Schlichter, T. (2000) Efectos de las plantaciones de pino ponderosa sobre la heterogeneidad de micrositios en estepas del noroeste patagónico. *Ecología Austral*, **10**, 151-158.

Ratajczak, Z., Nippert, J.B. & Collins, S.L. (2012) Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology*, **93**, 697-703.

Ray-Mukherjee, J., Nimon, K., Mukherjee, S., Morris, D.W., Slotow, R. & Hamer, M. (2014) Using commonality analysis in multiple regressions: a tool to decompose regression effects in the face of multicollinearity. *Methods in Ecology and Evolution*, **5**, 320-328.

Rejmánek, M. & Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology*, **77**, 1655-1661.

Rejmánek, M. & Richardson, D.M. (2013) Trees and shrubs as invasive alien species - 2013 update of the global database. *Diversity and Distributions*, **19**, 1093-1094.

Richardson, D.M. (ed.). (1998) *Ecology and Biogeography of Pinus*. Cambridge University Press, Cambridge.

Richardson, D.M. & Bond, W.J. (1991). Determinants of plant distribution: Evidence from pine invasions. *American Naturalist*, **137**, 639-668.

Richardson, D.M. & Higgins, S.I. (1998) Pines as invaders in the southern hemisphere. *Ecology and Biogeography of Pinus* (ed. by D.M. Richardson), pp. 450-473. Cambridge University Press, Cambridge.

Rundel, P.W., Dickie, I.A. & Richardson, D.M. (2014) Tree invasions into treeless areas: mechanisms and ecosystem processes. *Biological Invasions*, **16**, 663-675.

Shackleton, R.T., Le Maitre, D.C., Van Wilgen, B.W. & Richardson, D.M. (2015) The impact of invasive alien *Prosopis species* (mesquite) on native plants in different environments in South Africa. *South African Journal of Botany*, **97**, 25-31.

Shah, M.A., Callaway, R.M., Shah, T., Houseman, G.R., Pal, R.W., Xiao, S., Luo, W., Rosche, C., Reshi, Z.A., Khasa, D.P. & Chen, S. (2014) *Conyza canadensis* suppresses plant diversity in its nonnative ranges but not at home: a transcontinental comparison *New Phytologist*, **202**, 1286–1296.

Siemann, E. & Rogers, W.E. (2001) Genetic differences in growth of an invasive tree species. *Ecology Letters*, **4**, 514-518.

Simberloff, D. & Von Holle, B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, **1**, 21-32.

Simberloff, D., Souza, L., Nuñez, M.A., Barrios-Garcia, M.N. & Bunn, W. (2012) The natives are restless, but not often and mostly when disturbed. *Ecology*, **93**, 598-607.

Simberloff, D., Nuñez, M.A., Ledgard, N.J., Pauchard, A., Richardson, D.M., Sarasola, M., Van Wilgen, B.W., Zalba, S.M., Zenni, R.D., Bustamante, R., Peña, E. & Ziller, S.R. (2010) Spread and impact of introduced conifers in South America: Lessons from other southern hemisphere regions. *Austral Ecology*, **35**, 489-504.

Skurski, T.C., Rew, L.J. & Maxwell, B.D. (2014) Mechanisms Underlying Nonindigenous Plant Impacts: A Review of Recent Experimental Research. *Invasive Plant Science and Management*, **7**, 432-444.

Steers, R.J., Fritzke, S.L., Rogers, J.J., Cartan, J. & Hacker, K. (2013) Invasive Pine Tree Effects on Northern Coastal Scrub Structure and Composition. *Invasive Plant Science and Management*, **6**, 231-242.

Taylor, K.T., Maxwell, B.D., Pauchard, A., Nuñez, M.A., Peltzer, D.A., Terwei, A. & Rew, L.J. (2016) Drivers of plant invasion vary globally: evidence from pine invasions within six ecoregions. *Global Ecology and Biogeography*, **25**, 96-106.

Thorpe, A.S. & Callaway, R.M. (2011) Biogeographic differences in the effects of *Centaurea stoebe* on the soil nitrogen cycle: novel weapons and soil microbes. *Biological Invasions*, **13**, 1435-1445.

Thorpe, A.S., Thelen, G.C., Diaconu, A. & Callaway, R.M. (2009) Root exudate is allelopathic in invaded community but not in native community: field evidence for the novel weapons hypothesis *Journal of Ecology*, **97**, 641-645.

Urrutia, J., Pauchard, A. & Garcia, R.A. (2013) Differences in plant composition in an *Araucaria araucana* (Molina) K.Koch and *Nothofagus antarctica* (G. Forst.) Oerst. forest in a *Pinus contorta* Douglas ex Loudon invasion gradient. *Gayana Botanica*, **70**, 92-100.

Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y. & Pyšek, P. (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, **14**, 702-708.

Zuloaga, F.O., Morrone, O. & Belgrano, M.J. (2008) *Catálogo de las Plantas Vasculares del Conosur (Argentina, Sur de Brasil, Chile, Paraguay y Uruguay)*. Missouri Botanical Garden Press, St. Louis.

CHAPTER FOUR

POSITIVE FEEDBACK BETWEEN *PINUS CONTORTA* INVASION AND FIRE LIKELY ABOVE AN INVASION DENSITY THRESHOLD

Contribution of Authors and Co-Authors

Manuscript in Chapter 4

Author: Kimberley T Taylor

Contributions: Conceived the study and methodology, collected field data, executed statistical analysis and wrote initial manuscript.

Co-Author: Bruce D. Maxwell

Contributions: Assisted in study design, field data collection, analysis and manuscript preparation.

Co-Author: David B. McWethy

Contributions: Assisted in field data collection, provided guidance in analysis and interpreting results, and edited manuscript.

Co-Author: Cathy Whitlock

Contributions: Provided guidance in interpreting results and edited manuscript.

Co-Author: Aníbal Pauchard

Contributions: Provided guidance interpreting results and edited manuscript.

Co-Author: Martin Nuñez

Contributions: Provided guidance interpreting results and edited manuscript.

Manuscript Information Page

Kimberley T. Taylor, Bruce D. Maxwell, David B. McWethy, Cathy Whitlock, Aníbal Pauchard, Martín Nuñez
Journal Name: Ecology
Status of Manuscript:
__x_ Prepared for submission to a peer-reviewed journal
____ Officially submitted to a peer-review journal
____ Accepted by a peer-reviewed journal
____ Published in a peer-reviewed journal

Ecological Society of America

Abstract

Invasive plant species that have the potential to alter fire regimes have significant impacts on native ecosystems. Concern that pine invasions in the Southern Hemisphere will increase fire activity and severity and subsequently promote further pine invasion prompted us to examine the potential for feedbacks between *Pinus contorta* invasions and fire in Patagonia and New Zealand. We determined how fuel loads and fire effects were altered by *P. contorta* invasion. We also examined post-fire plant communities across invasion gradients to assess how invasion alters the post-fire vegetation trajectory. We found that fuel loads and soil heating during simulated fire increase with increasing *P. contorta* invasion age or density. However, *P. contorta* density only increased significantly post-fire where the pre-fire *P. contorta* density was above an invasion threshold. Below this threshold, *P. contorta* did not dominate after fire and plant communities responded to fire in a similar manner as uninvaded communities. The positive feedback observed at high densities is caused by the accumulation of fuel that in turn results in greater soil heating during fires and high *P. contorta* density post-fire. Therefore, a positive feedback may form between *P. contorta* invasions and fire, but only above an invasion density threshold. These results suggest that management of pine invasions before they reach the invasion density threshold is important for reducing fire risk and preventing a transition to an alternate ecosystem state dominated by pines and novel understory plant communities.

Introduction

Invasive plants can lead to abrupt shifts in fire regimes that increase the potential for invasions to impact native ecosystems (Brooks et al. 2004, Pausas and Keeley 2014). Invasions that alter fire regimes may endanger native plants that are well adapted to one fire regime but may be threatened in another (Keeley et al. 2011). Invasive plants can influence fire regimes by altering fuel loads (Dibble and Rees 2005, Pauchard et al. 2008), fire frequency (Brooks 1999, Balch et al. 2013), fire spread (Lonsdale and Miller 1993, Vila et al. 2001, Balch et al. 2013), fire intensity (van Wilgen and Richardson 1985, Rossiter et al. 2003, Stevens and Beckage 2009, Setterfield et al. 2010), and flammability (Dibble et al. 2007). Impacts of woody invasive plants on vegetation structure, composition and fuel loads are highly variable (Mandle et al. 2011, Taylor et al. 2016b) suggesting that it is necessary to examine each species or group of species on a case-by-case basis to fully understand the potential effects of woody invasions on fire regimes.

Invasion impacts on native communities can be exacerbated when invasive plants create positive feedbacks with fire, altering fire regimes in ways that promote their own success over native plants. Positive feedbacks can cause rapid shifts in the frequency and severity of fire activity. Hence, identifying invasive species capable of causing positive feedbacks is essential to predict which species will be high impact invaders and to prioritize management efforts (Gaertner et al. 2014). For example, the grass-fire cycle is a well described phenomenon (D'Antonio and Vitousek 1992) in which non-native grasses increase fine fuel loads and/or fine fuel continuity thus promoting more frequent (Balch

et al. 2013), larger (Vila et al. 2001, Balch et al. 2013), or more intense fires (Vila et al. 2001, Rossiter et al. 2003, Setterfield et al. 2010, Flory et al. 2015, Wagner and Fraterrigo 2015), which in turn promote their own dominance over native plants in these systems, leading to alternative ecosystem states. Feedbacks between woody invasive plants and fire are less well studied and can either promote or discourage fire (Pauchard et al. 2008, Stevens and Beckage 2009).

There is concern that invasions by fire-adapted pine species (genus *Pinus*) may increase fuel loads and overall landscape flammability, promoting a more fire-prone plant community to the detriment of native species (Jaffré et al. 1998, Veblen et al. 2008, Simberloff et al. 2010, Veblen et al. 2011). However, even though pine invasions are widespread across the Southern Hemisphere due to pine introduction for forestry (Richardson and Higgins 1998, Rejmanek and Richardson 2013), few studies have examined direct evidence for the formation of a positive feedback between pines and fire. *Pinus contorta* (lodgepole pine) is one of the most invasive pine species (Rejmanek and Richardson 1996), and it is rapidly invading the Patagonian steppe (Sarasola et al. 2006, Langdon et al. 2010, Taylor et al. 2016a), Chilean Araucaria forests (Peña et al. 2008, Taylor et al. 2016a), and both North and South Island, New Zealand (Ledgard 2001, Taylor et al. 2016a). While *P. contorta* is known to accumulate high fuel loads in its native range (Brown 1975, Baker 2009), it grows faster in its introduced than native range (Taylor et al. 2016a) thus potentially resulting in even greater fuel accumulation. Furthermore, fire is widely considered to enhance *P. contorta* regeneration in the western

USA and Canada by causing prolific and rapid recolonization of burned areas, even in non-serotinous populations (Brown 1975, Agee 1998, Pierce and Taylor 2011).

Although evidence suggests a positive feedback between fire and pine invasions, this idea has not been well tested with empirical data. To our knowledge, only one study has examined changes in fuel loads due to pine invasions. Cóbar-Carranza et al. (2014) found that in a forested ecosystem overall fuel quantities did not change with *P. contorta* invasion but fuel structure was altered. *P. contorta* acted as a ladder fuel that connected the understory to the native *Araucaria araucana* canopy causing a potential switch from a surface- to canopy-fire dominated regime (Cóbar-Carranza et al. 2014). Several studies have looked at regeneration and other post-fire effects in areas with and without exotic pine species. In South Africa, soil properties under burned pine canopies and native fynbos suggested that fire severity was higher in pine plantations than in fynbos (Scott and Van Wyk 1990). In Patagonia, post-fire *Pinus ponderosa* plantations created novel conditions that prevented regrowth of native matorral (shrubland), despite the fact that matorral is well adapted to surface fire (Nuñez and Raffaele 2007). Whether the post-fire vegetation trajectories differed due to pre-fire species composition or changes in fire severity in this study is not clear. In the Argentine pampas and the South African fynbos, fire caused a rapid expansion of introduced *Pinus halepensis* (Richardson 1988, Zalba et al. 2008).

Post-fire successional trajectories can be altered by pine plantations and invasions yet, the mechanisms causing the observed changes in community structure and function are still poorly understood. The goal of this study is to better understand the relationship

between *P. contorta* invasions and fire activity in locations where *P. contorta* has invaded open habitat (grasslands and shrublands) in the Southern Hemisphere. We addressed this objective by first, assessing changes in fuel loads across a *P. contorta* invasion gradient at four in the introduced range (Argentina, Chile and New Zealand). Specifically, we determined if the abundance of each type of fuel was related to pine invasion age or invasion density. Second, we used our fuel data from across the invasion gradient to model soil heating during a simulated fire. Third, we assessed the response of the vegetation and, in particular, *P. contorta* to fire in a subset of sites that had recent fires. We expected that increasing pine density would be associated with increasing fuel loads and thus greater soil heating during fire, which in turn may reduce recovery of some native species. We hypothesized that pines would dominate burned areas, especially those that were invaded prior to burning. The results of our study provide new information about the mechanisms that may cause changes in fire regimes as a result of pine invasions in Southern Hemisphere plant communities.

Methods

Study Sites

Sampling occurred at four sites in Argentina (AR) (1), Chile (CL) (1), and New Zealand (NZ) (2) (Table 4.1). Each of these sites has been invaded by *P. contorta* over the past 24 to 53 years, with the younger invasions in Argentina and Chile where pine plantations are fairly recent. The sites were either dominated by native and introduced grasses (CL, first NZ site) or native shrubs (AR, second NZ site). The site in Bariloche, Argentina (AR) was a shrub steppe community (dominated by *Mulinum spinosum*,

Acaena spp., and *Stipa* spp.) with patches of the disturbance-adapted small tree *Nothofagus antarctica.* Various fires have burned through this area in the past 11 years. The *P. contorta* plantations at AR are on average 34 years old. The Chilean site, located in Coyhaique Alto, was a grass steppe community (*Festuca* spp.; Langdon et al. 2010). *Pinus contorta* plantations at CL were an average of 24 years old.

Table 4.1. Descriptions of all study sites (AR, CL, NZ1, NZ2). Abbreviations include longitude (long.), latitude (lat.), temperature (temp.), precipitation (precip.), elevation (elev.), minimum (min.) and maximum (max.).

Site	Long.	Lat.	Dominant vegetation	Fuel plots	Plantation Age (years)	Elev. range (M.S.L)	Annual mean temp. (°C)	Annual precip. (mm)
AR	-71.2	-41.1	Shrubland	44	34	845-892	8.2	846
CL	-71.7	-45.5	Grassland	35	23	703-823	5.8	715
NZ1	170.2	-44.1	Grassland	73	45	544-655	9.3	658
NZ2	171.7	-43.2	Shrubland	138	53	785-1040	7.3	2241

The two NZ sites were in the Canterbury region on the South Island. NZ1, located on the edge of Lake Pukaki, was dominated by introduced grasses and forbs (e.g. *Agrostis capillaris*, *Hieracium* spp.) and native *Festuca novae-zelandiae*. The more diverse Craigieburn Forest Park site (NZ2) contained areas dominated by introduced grasses and forbs, native grasses, the tall shrub manuka (*Leptospermum scoparium*), and shorter shrubs (*Discaria toumatou*, *Dracophyllum* spp.). Plantations were originally

planted 45 years ago at NZ1 and 53 years ago at NZ2. New Zealand sites were sampled in January and February 2013 and Patagonian sites in January and February 2014.

Fuel Loads

To collect fuel data across the gradient of invasion levels, ten meter-wide transects were placed perpendicular to the edge of *P. contorta* plantations. The transects continued until they reached the distance of two kilometers or were unpassable due to topographic or anthropogenic barriers (e.g. cliffs, highways, private land). At NZ1, the invasion spread farther from the source requiring longer (3.5 km) transects. Fuel sample plots were randomly selected (n = 1-5 every 100 m) for a total of 44 plots at AR, 35 at CL, 73 at NZ1 and 138 at NZ2. Within each plot, basal diameter, diameter at breast height, height to crown base, and height were measured for each *P. contorta* individual. Age of each tree was recorded based on whorl counts or tree cores. One thousand-hour fuel loads were also collected within the entire 100 m^2 plot. In four one-m^2 subplots (one in each corner of the large plot), one hour, ten hour, 100 hour, herbaceous, and shrub fuels were recorded using the Photoload method and averaged for each plot (Keane and Dickinson 2007). All of the biomass in 12 subplots at AR and 17 subplots at NZ2 was clipped, sorted into fuel type, dried, and weighed to calibrate field Photoload estimates. The species composition at the two New Zealand sites and the two Patagonian sites was very similar (with the exception of the greater dominance of shrubs at AR and NZ2) so the calibration from NZ2 and AR were also applied to NZ1 and CL, respectively. Two measurements of litter and duff depth were taken in each subplot. Percent litter cover and litter type (e.g. grass, pine, shrub, *Nothofagus* spp.) were also recorded. Samples of each

type of litter were collected, dried, and weighed to determine the bulk density of each litter type. Depth, cover and bulk density values were used to determine litter fuel loads in each subplot. Duff was very rare and so the same process was not repeated for duff. *Pinus contorta* biomass was calculated for each plot using separate allometric equations for trees with heights > 1.37 m (Jenkins et al. 2004) and < 1.37 m (Turner et al. 2004). *P. contorta* biomass < 2 m in height was added to the shrub stratum fuel loads (hereafter referred to as shrub fuel loads – which includes all live woody biomass < 2 m in height).

To examine the relationship between *P. contorta* and fuel loads, total fuel and fuel of each fuel type were modelled with multiple linear regression as a function of time since invasion (TSI; age of oldest tree in plot) and *P. contorta* density. At CL2, the model included management as a predictor because some plots were in areas where pines had been cut or hand pulled and left on the site in the past year.

Fire Effects

The impact of *P. contorta* invasion on first-order fire effects was determined with the First Order Fire Effects Model (FOFEM; Reinhardt 2003). FOFEM assumes that all herbaceous and litter fuels will be consumed but it models duff consumption as a function of duff moisture and depth (Brown et al. 1985, Reinhardt et al. 1991). FOFEM uses the Burnup model to consume all woody fuels in each plot (Albini et al. 1995, Albini and Reinhardt 1997). Soil heating is modeled as a function of fire intensity, duration, and soil properties under both smoldering duff fires and flaming surface fires (Hungerford et al. 1991, Campbell et al. 1993, Campbell et al. 1995). Fuel data for each plot were input

into the batch processing function of FOFEM. Log-transformed soil temperature was modeled using multiple linear regression as a function of TSI and *P. contorta* density.

Plant Community Response to Fire

We examined both the response of *P. contorta* to fire (e.g., regeneration density) and the effect of invasion on the response of the rest of the vegetation community to fire (e.g., composition, abundance) at a subset of sites with recent fire activity (AR, CL, NZ2). We determined *P. contorta* density continuously in 10 x 10 m plots along the transects described above at AR, CL, and NZ2 where the transects passed through recent burns (CL burned in 2011; AR multiple fires in past 11 years; NZ2 burned in the 1980's). Where the plots were burned at AR and CL, we recorded the density of trees pre-fire, most of which died during the fire, as well as live regeneration density. We only recorded live regeneration density at NZ2 because the fire was older (>25 yrs) and we could not reliably count trees killed by the fire. We used the densities from these burned plots and all unburned plots on the transects that were within 100 m of the fire edge in order to control for environmental variability in the comparison of *P. contorta* invasion density in burned versus unburned plots (n=347 at AR; n=68 at CL; n=27 at NZ2). We modeled density in the selected plots as a function of fire, plot vegetation type (e.g., shrub or grass dominated), and their interaction using a negative binomial mixed model to account for both overdispersion (Ver Hoef and Boveng 2007) and spatial autocorrelation (Fournier et al. 2012, Skaug et al. 2013). Where vegetation type was not significant ($P>0.05$) it was not included in the final model. Correlograms suggested that

the maximum distance of density correlation was about 50 m and that including 50 m clusters as a random effect in the model significantly reduced the spatial autocorrelation.

At AR, we also plotted the density of *P. contorta* that had colonized burned plots as a function of the number of dead, burned *P. contorta* in each plot to determine the invasion level at which *P. contorta* density is higher after fire than before. We used the pre-fire density at which the post-fire density in a given plot was always higher than pre-fire (Fig. 4.1; 1000 trees/ha) to divide the pre-fire invasion level for each density plot into categories (low invasion burned, high invasion burned). We then modeled the density data from AR as a function of the fire-invasion category (unburned, uninvaded burned, low invasion burned, high invasion burned) using a negative binomial mixed model as described above. We could not repeat this process at CL because only two plots were invaded by *P. contorta* prior to burning.

In order to further examine *P. contorta* and understory plant community response to fire at AR, we surveyed the species composition of burned and unburned plots located in plantations, invaded areas (invaded pre-fire), and uninvaded areas. Hereafter, we refer to these different areas of sampling as "conditions" which include the six categories: uninvaded unburned, uninvaded burned, invaded unburned, invaded burned, plantation unburned, and plantation burned. We randomly placed five plots in each category except the plantation burned category, which had 7 plots (32 plots total). The plots were all 5 x 5 m and in each we recorded the aerial percent cover of all species and the number of *P. contorta* individuals, their aerial cover (using a spherical densiometer in plots with trees taller than 1.37 m), and their age. We used principal coordinates analysis based on

Morista-Horn distances between plots to examine differences in species composition (excluding *P. contorta*) between plots. We used permutational multivariate analysis of variance (PERMANOVA) to determine if plot condition affected plot level species composition (Oksanen et al. 2013). We also modeled total native plant cover and log transformed exotic plant cover as a function of condition with linear regression.

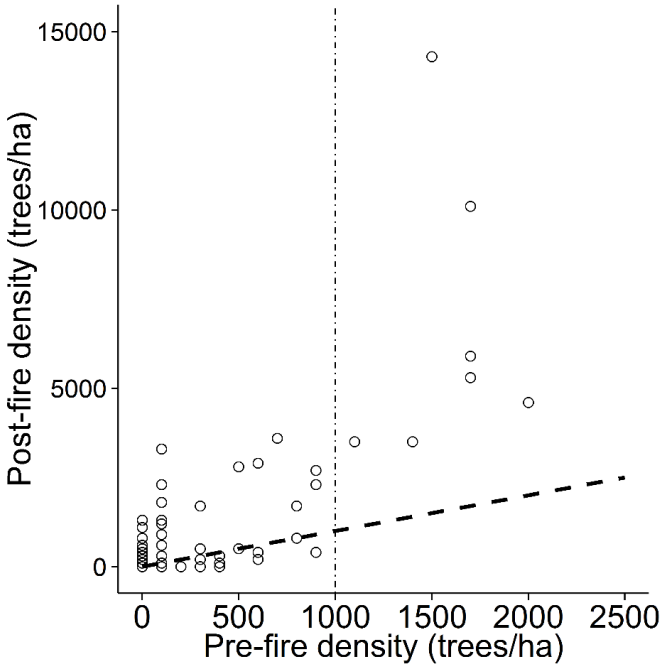

Figure 4.1. Post-fire *Pinus contorta* density (trees/ha) versus pre-fire *P. contorta* density (trees/ha) at the AR sites for all burned 100 m^2 plots sampled. The dashed line shows the 1:1 line where post-fire density equals density pre-fire. The vertical line shows the threshold of 1,000 trees/ha above which post-fire *P. contorta* density was higher than pre-fire *P. contorta* density for all plots measured.

Finally, to examine post-fire regeneration at NZ2 and determine if *P. contorta* or native plants dominated, we set up four 1 m^2 subplots in 20 of the 100 m^2 plots (12 burned, 8 unburned) on the transects through the burned area and surrounding unburned area described above (80 subplots total). Within each subplot, we recorded aerial cover

of *P. contorta*, grasses, and all other species in the plots. We modeled cover in each subplot as a function of vegetation type, fire, and the random effect plot to determine if *P. contorta* dominated after fire.

Results

Changes in Fuel Loads

P. contorta invasion was associated with increased overall fuels at all sites (Figs. 4.2 & C1 in Appendix C; Table 4.2). Metrics of *P. contorta* invasion explained more of the variation in fuel loads at the grassland sites (CL, NZ1) than the shrubland sites (AR, NZ2; Table 4.2). Time since invasion (TSI; oldest tree in plot) was generally more important than *P. contorta* density in explaining fuel loads at CL, NZ1 and NZ2, while invasion density was more important than TSI at AR (Table 4.2). In all cases except one, the significant relationships between invasion age or density and fuel loads were positive. At the two grassland sites, *P. contorta* invasion had opposing effects on herbaceous fuel loads, with a positive relationship between TSI and herbaceous fuel loads at NZ1 and a negative relationship at CL (Table 4.2).

Changes in Fire Effects

Overall, simulated soil heating increased most with invasion into grass-dominated sites CL and NZ1, and TSI and/or *P. contorta* invasion density generally explained more of variation in these responses than at the shrub-dominated AR and NZ2 sites (Table 4.2). TSI was generally the best predictor of simulated soil temperatures, although there was some variation by site and response (Table 4.2). Management to cut down *P. contorta* at

NZ2 generally resulted in a steeper increase in soil heating with increasing TSI (Fig. 4.3D). At CL1, soil heating appears to have a threshold (around age 10 for oldest tree in plot) below which soil temperature does not change with increasing invasion age and after which there is a rapid increase in soil temperatures (Fig. 4.3A).

Table 4.2. Coefficients, *P*-values and the variation explained by the best model (either *P. contorta* density and time since invasion (TSI) or only one explanatory variable where the other is not significant) for fuel overall, each fuel class, and simulated soil temperatures at each site. TSI signifies the coefficient for time since invasion, Den for total *P. contorta* density, and "-" signifies no significant relationship between that predictor and the response variable (fuel loads or fire effects). Dead woody fuels are not shown for CL and AR because there were no significant relationships between dead woody fuels and *P. contorta* density or TSI at these sites.

	CL - grassland					AR - shrubland				
Response	Den	*P*	TSI	*P*	R^2	Den	*P*	TSI	*P*	R^2
All fuel	-	-	0.20	<0.01	0.55	0.01	0.02	-	-	0.12
Shrub fuel	-	-	0.32	<0.01	0.66	0.02	<0.01	-	-	0.17
Herb fuel	-0.001	0.02	-	-	0.15	-	-	-	-	-
Litter fuel	-	-	0.18	<0.01	0.30	0.07	0.06	-	-	0.09
Surface soil heating	-	-	0.13	<0.01	0.47	-	-	-	-	-
2 cm soil heating	-	-	0.07	<0.01	0.53	-	-	-	-	-

Table 2. continued

	NZ1 - grassland					NZ2 - shrubland				
Response	Den	*P*	TSI	*P*	R^2	Den	*P*	TSI	*P*	R^2
All fuel	-	-	0.26	<0.01	0.49	-	-	0.19	<0.01	0.28
Shrub fuel	-	-	0.38	<0.01	0.34	-	-	0.63	<0.01	0.26
Herb fuel	-	-	0.13	<0.01	0.29	-	-	-	-	-
Litter fuel	-	-	0.24	<0.01	0.29	-	-	0.09	<0.01	0.06
Dead woody fuel	-	-	-	-	-	-0.03	0.04	0.58	<0.01	0.47
Surface soil heating	-	-	0.11	<0.01	0.28	-0.02	0.02	0.09	<0.01	0.08
2 cm soil heating	0.004	0.03	0.07	<0.01	0.65	-	-	0.07	<0.01	0.19

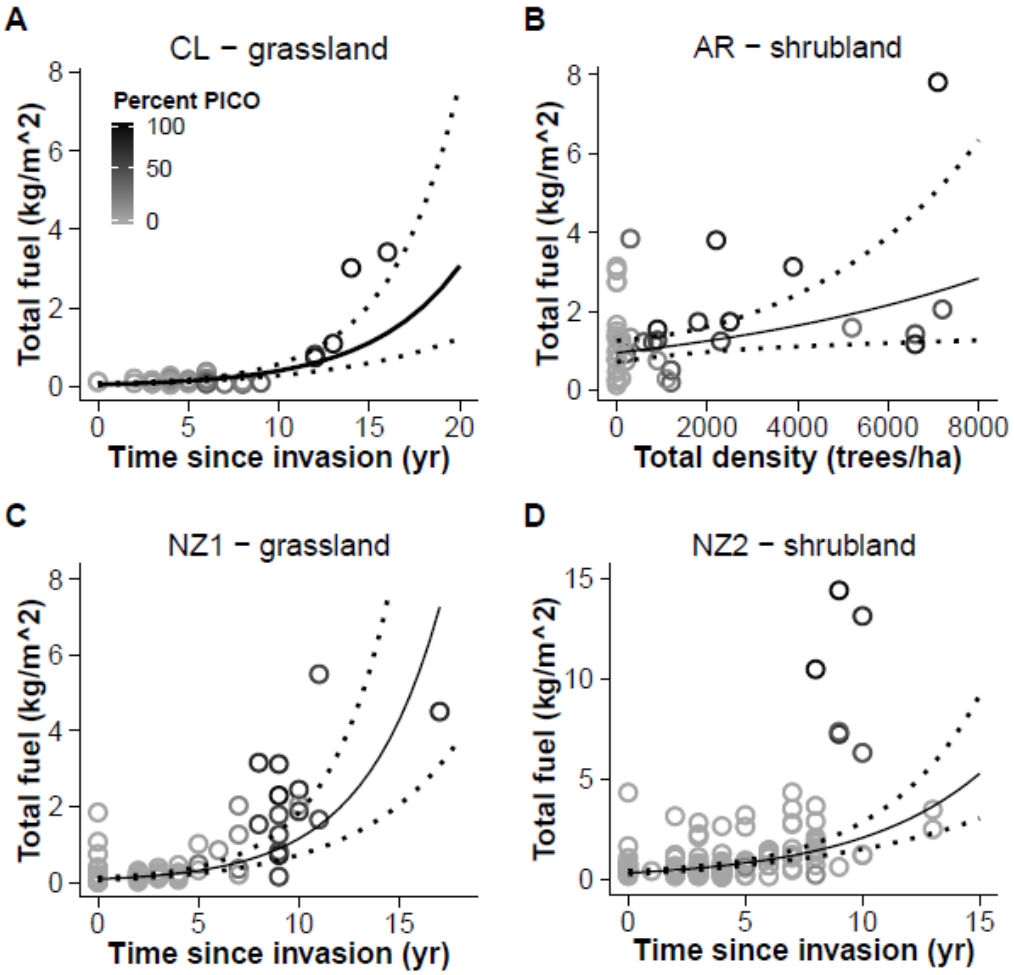

Figure 4.2. Total fuel (kg/m^2) as a function of time since invasion (CL, A; NZ2, D; NZ1, C) and *Pinus contorta* (PICO) density (AR, B) with the fitted line from the models of each site and the 95% confidence interval shown. The grayscale of the points represents the percent of the total fuel load that was accounted for by *P. contorta* biomass (Percent PICO), with darker points having a higher percent of *P. contorta* biomass relative to other types of fuels.

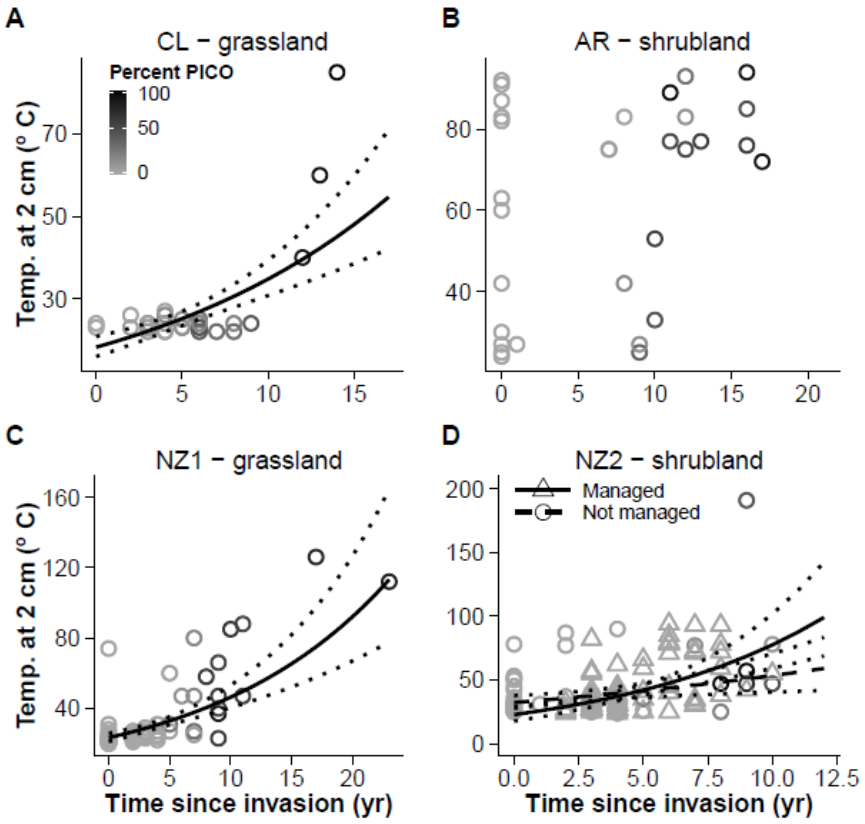

Figure 4.3. Simulated soil temperature at 2 cm depth as a function of time since invasion (yr) with the fitted line from the models of each site and the 95% confidence interval shown. The color of the points represents the percent of the total fuel load that was accounted for by *P. contorta* biomass (Percent PICO), with darker points having a higher percent of *P. contorta* biomass relative to other types of fuels.

Pinus contorta Response to Fire

In the 100 m^2 plots at AR, the density of *P. contorta* depended on fire-invasion class (high invasion pre-fire, low invasion pre-fire, no invasion pre-fire, unburned; χ^2 = 32.2, df = 3, P<0.0001). Density was highest in plots with high pre-fire invasion, followed by unburned plots, low-invasion pre-fire plots, and finally plots that had not been invaded pre-fire, with statistically significant differences (P<0.05 for pairwise comparisons) between all groups except the unburned and low-invasion pre-fire plots

(Fig. 4.4A). In the 25 m^2 plots that were sampled for plant species composition at AR, uninvaded burned and uninvaded unburned plots had no *P. contorta* individuals (Fig. 4.4B). The invaded burned plots had significantly lower density than invaded unburned plots (df = 21, z = 4.3, $P<0.0001$) and burned plantation plots (df = 21, z = 3.9, $P<0.0001$). Burned plantation plots had significantly higher *P. contorta* density than unburned plantation plots (df = 21, z = 2.6, $P = 0.0096$).

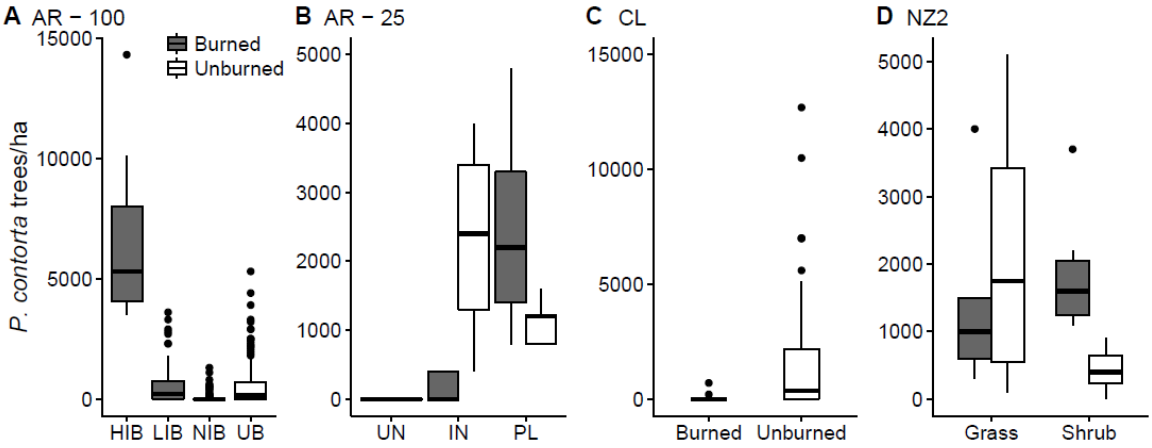

Figure 4.4. *Pinus contorta* density (trees/ha) in burned (gray fill) and unburned (white fill) 100 m^2 plots at AR (A), CL (C), and NZ2 (D). Also shown is the density of *P. contorta* in the 25 m^2 vegetation sampling plots at AR (B). HIB = high invasion burned, LIB = low invasion burned, NIB = not invaded burned, UN = uninvaded, IN = invaded, PL = plantation. "Grass" and "shrub" in (D) refer to whether the plot was dominated by grass or shrub pre-fire.

At CL, we sampled 32 plots in the 2011 burn, of which only two had *P. contorta* trees growing in the plot. Both plots had been invaded prior to the fire and were on the edge of the burn so the *P. contorta* that were present had survived the fire and were not newly established. No other plots in the burned area had been invaded prior to the fire.

Consequently, plots in the burned area had significantly lower *P. contorta* density than unburned plots at this site (χ^2 = 15.7, df = 1, P<0.0001; Fig. 4.4C).

At NZ2, there was a significant vegetation x fire interaction (χ^2 = 8.7, df = 1, P = 0.0031) whereby there was no difference in *P. contorta* density between burned and unburned 100 m^2 plots in grasslands; however, unburned shrublands had significantly lower *P. contorta* density than burned shrublands (Fig. 4.4D). In all areas, *P. contorta* cover in the 1 m^2 subplots was significantly lower than cover of grass, native cushion plants, and native shrubs after accounting for fire and the random effect plot (P<0.05 for all pairwise comparisons; Fig. C2 in Appendix C). All vegetation types had lower cover in the unburned than in burned plots (df = 310.98, t = -2.986, P = 0.0031); however, cover was highly variable and some unburned plots had extremely high native shrub cover (Fig. C2).

Plant Community Response to Fire

At AR, we found that fire altered plant species composition in uninvaded and lightly invaded sites but that in plantations and highly invaded sites (greater than 50% pre-fire *P. contorta* cover or 800 trees/ha), plant composition changed little with fire (Fig. 4.5). The principal coordinates analysis identified three main groups of plots: (1) plots that had high cover of *P. contorta* before or after fire (Fig. 4.5, dash-dot line circle), (2) plots that burned and were either uninvaded or had low densities of *P. contorta* (a maximum of 200 individuals per hectare pre-fire as judged by dead stems and aerial photos; Fig. 4.5, dashed line circle), and (3) plots that were unburned and either uninvaded or very lightly invaded (*P. contorta* cover 6 to 12%; Fig. 4.5, solid line circle).

Condition (uninvaded unburned, uninvaded burned, invaded unburned, invaded burned, plantation unburned, plantation burned) was a significant predictor of species composition (judged by Morista Horn distances between plots; $F_{5,31} = 3.5$, $P = 0.001$) with an R^2 of 0.40.

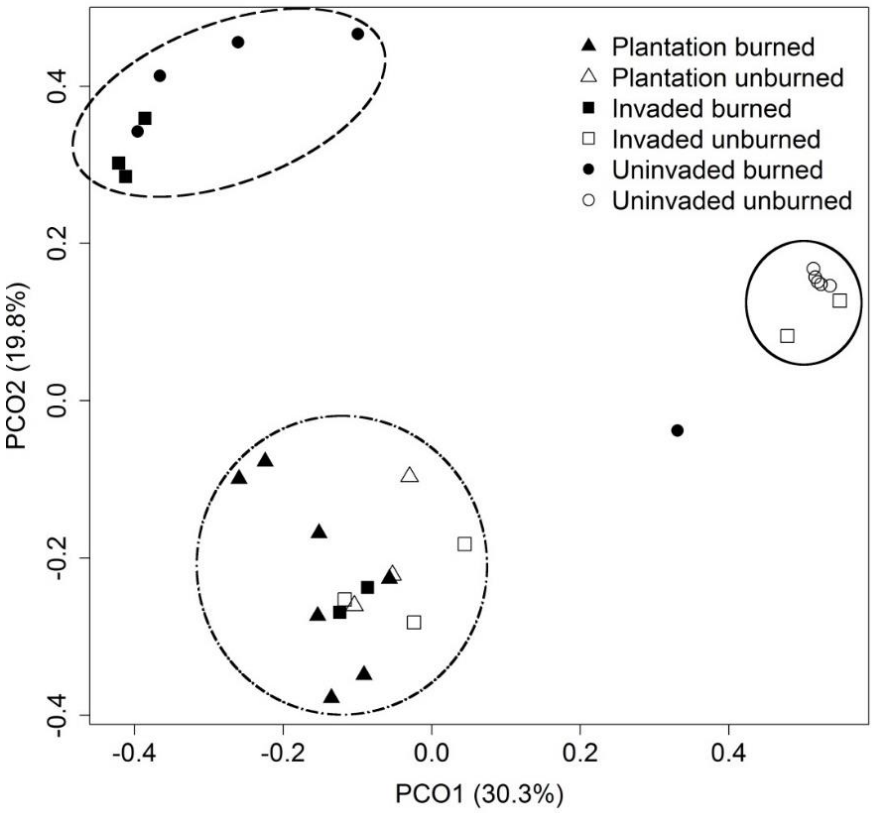

Figure 4.5. Principal coordinates analysis of understory plant communities based on the Morista-Horn distance between species compositions of each plot. Filled points represent burned plots and hollow points represent unburned plots. Triangles are plantation plots, squares are invaded plots, and circles are uninvaded plots. Dash-dot line encircles plots that had high cover of *P. contorta* before or after fire, dashed line encircles plots that burned and were either uninvaded or had low P. densities (a maximum of 200 *P. contorta* individuals per hectare pre-fire as judged by dead stems and aerial photos), and the solid line encircles plots that were unburned and either uninvaded or very lightly invaded (*P. contorta* cover 6 to 12%). The point not in a circle was uninvaded and burned and still had no *P. contorta* when sampled after fire.

Condition was also a significant predictor of total native plant cover ($F_{5,26} = 9.6$, $P<0.001$, $R^2 = 0.65$) and total exotic plant cover (not including *P. contorta*; $F_{5,26} = 5.6$, $P = 0.001$, $R^2 = 0.52$). There was no difference in native plant cover between uninvaded unburned and uninvaded burned plots ($t = -1.0$, d.f. = 26, $P = 0.31$); however, plots in all other conditions had significantly lower native plant cover ($P<0.05$ for all pairwise comparisons) than uninvaded unburned plots. Exotic cover was higher in invaded burned plots (mean = 11.14%, $t = 2.4$, d.f. = 26, $P = 0.03$) and lower in plantation unburned plots (mean = 0.02%, $t = -2.4$, d.f.= 26, $P = 0.02$) than in the uninvaded unburned plots (mean = 0.66%).

Discussion

Our results demonstrate that invasive plant impacts can have nonlinear threshold responses that result in regime shifts. Once *P. contorta* invasions cross a density threshold a positive feedback with fire is likely to develop (Fig. 4.6). The positive feedback at high *P. contorta* densities is created by the accumulation of high fuel loads that in turn result in greater soil heating during the fire and consequently altered plant communities and high *P. contorta* density post-fire. Once communities cross the threshold it is unlikely that they will return to a native-dominated state without significant management intervention (Cuevas and Zalba 2010). Understanding the ability of an invader to cause a regime shift is essential for determining management priorities (Gaertner et al. 2014). Our results suggest that a shift to an alternative state is likely after a pine invasion threshold is crossed and therefore management of pine invasions before

they reach this threshold is necessary to prevent a new fire regime and vegetation state that may be undesirable.

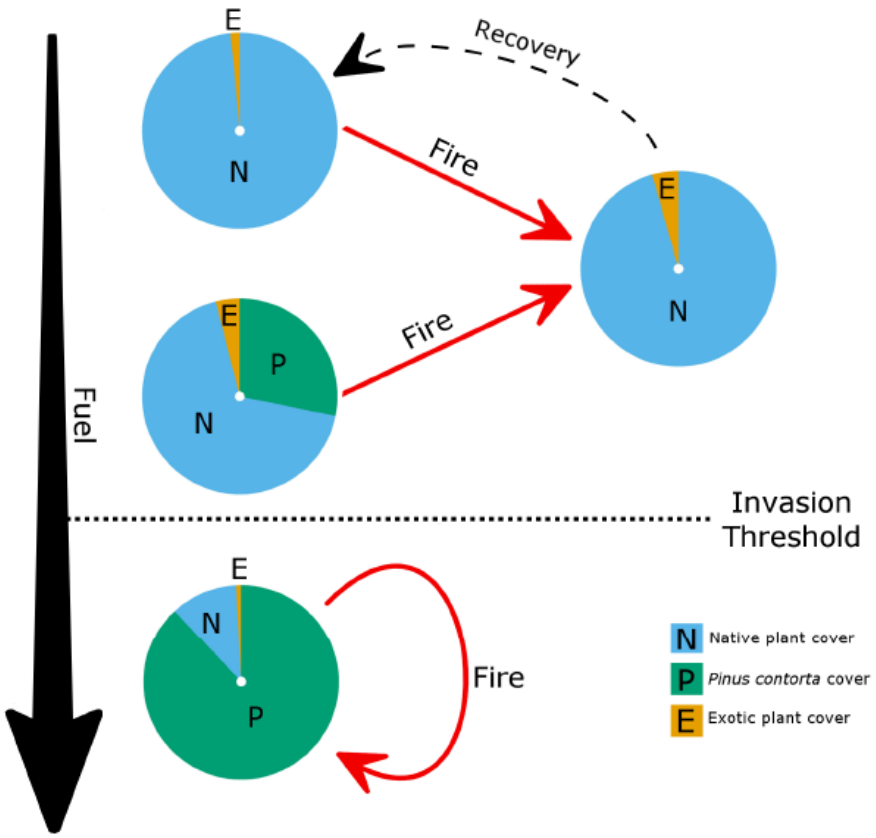

Figure 4.6. Conceptual diagram demonstrating the effects of *P. contorta* invasion and fire on native plant communities, based on data collected in Bariloche, Argentina (AR). The percent cover of each plant type in each ecosystem state is shown in the pie charts (data are means from plots). Invasion level increases going down through the diagram and the dotted line represents the invasion threshold. As *P. contorta* invasion increases, fuel loads also increase.

As expected, overall fuel loads increased with increasing *P. contorta* invasion age or density at all sites. This increase in fuels likely has serious consequences for fire activity and behavior, particularly in older invasions. Other studies have also found fuel

loads to increase with woody invaders (Dibble and Rees 2005, Pauchard et al. 2008), which can lead to increased fire intensity (van Wilgen and Richardson 1985). The amount of variability explained by *P. contorta* invasion varied by fuel type and site (Table 4.2). Generally, TSI was more important than total density because it takes time for woody fuels and litter to accumulate enough to have a significant impact. We saw the fastest accumulation of fuels at NZ1, likely because *P. contorta* grows faster there than at any other site (Taylor et al. 2016a). Dead woody fuels and duff did not make up a significant amount of the fuel loads because the young invading trees are healthy and have not yet started to self-thin. As *P. contorta* die off due to increasing stand density, we expect that dead woody fuels will become a more significant contribution to overall fuel loads.

Our results suggest that changes in fire behavior, and not just changes in pre-fire plant composition, likely contribute to differences in post-fire regeneration success. Simulated soil heating during fires significantly increased with increasing *P. contorta* invasion age or density. More severe soil heating may explain the different post-fire trajectories seen in sites dominated by pines compared to native-dominated sites in our study and others (Holmes et al. 2000, Nuñez and Raffaele 2007, Zalba et al. 2008). If seedbanks and resprouting plants are destroyed by fire, then native regeneration is more dependent on distance to nearest seed source. In invaded shrublands and grasslands, pines may have the advantage in seed dispersal over native shrubs and forbs because their greater height and winged seeds readily allow for long-distance dispersal (Ledgard 2001). We expect that soil heating will be more intense in older invasions, even if density stays constant or declines, as a duff layer and 1000-hour fuel loads develop. Areas with the

most soil heating tend to be where duff or large downed logs smolder for longer periods of time (Baker 2009). None of our sites yet support a duff layer or large downed logs and these characteristics were not present at the time of our study, but are likely to develop in the future.

Another factor that contributes significantly to increased soil heating is management practices that cut trees but leaves them on site. As seen at NZ2, this practice leads to a more rapid increase in soil heating with increasing invasion age than at sites without management. Similarly, in South Africa cutting and leaving invasive pines on site followed by burning led to more negative impacts on native plant communities compared with strategies that burned standing pine trees (Holmes et al. 2000). That study suggests that high fire severity in "fell and burn" treatments likely sterilized the upper layers of the soil harming reproductive organs, mycorrhizae, and seeds of many species (Holmes et al. 2000). Other types of management, such as herbicide treatments that kill entire stands, may lead to pulse increases in litter and fine fuel loads, as seen in pine stands experiencing high mortality from mountain pine beetle (Hicke et al. 2012). Therefore, managers should consider the impact of control actions on potential fire behavior to avoid undesirable vegetation trajectories post-fire.

Overall, we saw more impact on fuel loads and fire effects in grasslands than shrublands, and *P. contorta* invasion into grassland regularly explained more variation in fuel loads and fire effects. Shrublands had higher live woody and litter biomass and higher variability in fuel loads prior to invasion. Impacts of *P. contorta* invasions on the fire regimes in grasslands thus should be more extreme than in shrublands. It is likely

that some shrublands already have enough fuel present to burn at moderate to high severities without *P. contorta* invasion, such as manuka in NZ (Perry et al. 2014) and tall shrublands and *N. antarctica* stands in Patagonia (Veblen et al. 2003, Mermoz et al. 2005). Identifying combinations of plant life-forms and ecosystems most likely to result in a regime shift is important to predict high-impact invaders (Gaertner et al. 2014). We suggest that trees invading into grasslands are most likely to significantly alter fire severity and post-fire vegetation communities. These results support the hypothesis that invaders are most likely to have significant impacts where they add new functional traits or life forms to a system (Levine 2003) and fundamentally alter fuel structure and continuity.

The changes that we observed in fuel loads and simulated fire effects likely contribute to the different post-fire trajectories of plant communities in areas with different levels of *P. contorta* invasion. *P. contorta* density only increased after fires in areas that were highly invaded or plantations prior to fire; conversely, in some sites, fire in low-density invaded plots actually resulted in lower *P. contorta* density than in their pre-fire condition or in invaded unburned plots. This threshold effect could result from the ability of natives to recolonize after fire when *P. contorta* seed trees are at low densities and/or because of differences in fire behavior caused by high fuels in older and denser invasions. Densities of *P. contorta* regeneration were higher in plots that experienced severe surface burns than in those with light surface burns in *P. contorta*'s native range as well (Turner et al. 1997). The more severe fires could hamper herbaceous or shrub regeneration by harming native plant seeds or reproductive organs (Holmes et al.

2000, Zalba et al. 2008, Baker 2009), whereas *P. contorta* seeds have been found to resist higher temperatures than two native tree species (*Araucaria araucana* and *Nothofagus antarctica*) present in our Patagonian sites (Cóbar-Carranza et al. 2015). Additionally, *P. contorta* seedlings do not compete well with grass or herbaceous species (Despain 2001, Ledgard 2006) and thus more severe fires may create favorable conditions for seed germination and seedling growth by increasing post-fire soil-surface temperatures and reducing herbaceous competition (Coates et al. 1991, Page-Dumroese et al. 2002). Furthermore, highly invaded areas have lower native plant cover and species richness than uninvaded areas pre-fire (Ledgard and Paul 2008, Urrutia et al. 2013, Taylor et al. 2016b). As a result, sites of dense invasion have fewer native plants to contribute to the seedbank or to resprout after fire.

The threshold response that we observed supports the theoretical model of Buckley *et al.* (2007) who posit that there is a tension between disturbance promoting invasion and disturbance killing the seed source necessary for invasion. They suggest that disturbance in an invaded area actually increases the introduced plant density necessary to initiate invasion. Our results support this idea because fire in pine-invaded areas promoted further invasion only when the initial invasion density was high. This finding is consistent with other studies that suggest that frequent fires prevent *P. contorta* invasion into grasslands (Widenmaier and Strong 2010).

We also found that the ability of fire to promote pine invasions depends on specific site characteristics. In sites where edaphic conditions are poorly suited to *P. contorta* establishment, fire will not necessarily promote invasion. At CL, fire burned an

area adjacent to a *P. contorta* plantation that had not been invaded prior to the fire, likely due to high soil moisture and competition from herbaceous species (Taylor et al. 2016a). After the fire there was still no invasion of this area despite significant propagule pressure. Conversely, at NZ2, areas that had been dominated by shrubs prior to burning (mainly *Leptospermum scoparium*) had higher *P. contorta* densities than similar adjacent and unburned shrub-dominated plots (Fig. C2 in Appendix C). Thus, fire seems to promote more invasion in places where shrub cover or shade limit pre-fire *P. contorta* establishment. However, fire has little effect where soil moisture or other edaphic features limit pre-fire *P. contorta* invasion.

Native plant communities also appeared to have a threshold response to fire based on the level of *P. contorta* invasion. Plant community composition in areas without dense *P. contorta* invasion at AR shifted after fire compared with the composition in unburned plots; however, post-fire plant communities were still dominated by native species in uninvaded as well as in lightly invaded plots. Many shrubs at AR resprouted after fire (Nuñez and Raffaele 2007). However, highly invaded plots at AR had a different species composition than uninvaded burned or unburned plots, and this composition did not shift after fire (Fig. 4.5). The maintenance of similar species composition in burned and unburned highly invaded plots, as well as the creation of high *P. contorta* densities post-fire, suggest that dense invasions lead to a new and relatively stable state that is resistant to disturbances such as fire. The same is true of plantations where the density is also high. In fact, fire may perpetuate this state by leading to even higher invasion densities

than pre-fire, which will likely lead to even lower native species richness and cover (Taylor et al. 2016b).

At AR we found an invasion threshold between 800 and 1000 trees ha^{-1}, above which the plant composition is altered and *P. contorta* regenerates prolifically after fire. Below the threshold plant composition was similar to uninvaded plots and native plants dominated after fire. Invasion densities above the 1000 trees ha^{-1} threshold were common in all the study sites (Fig. C3 in Appendix C; Taylor et al. 2016a), suggesting that the potential for the development of a positive pine-fire feedback is already high. The exact value of this threshold likely varies between sites depending on the fire adaptations of the native plants and climate. The threshold may be higher in the shrublands at AR which have naturally higher fuel loads, higher probability of fire, and many shrub species capable of resprouting (Mermoz et al. 2005, Nuñez and Raffaele 2007, Paritsis et al. 2013) than in low productivity areas, such as the Patagonian grass steppe (found at CL) that have naturally low fuel loads and low probability of fire (Paritsis et al. 2013). Given the historically low frequency of fires in the Patagonian grass steppe due to fuel limitation, it is unlikely that the native plant community there is resilient to high-severity fire. Further study is necessary to determine how the threshold for a positive feedback between pine invasion and fire differs between different ecosystems.

Overall our study shows the strong potential for invasive pines to alter fuel loads, fire behavior, and post-fire plant communities, particularly when invasion densities cross a threshold and where woody species represent a novel life form. Although it has been suggested that a positive feedback between pines and fire is inevitable, our data suggest

that there is a threshold density below which a positive feedback is unlikely. Above this threshold, fires will be more intense and facilitate a conversion to pine domination. This threshold may represent the tradeoff between the benefits of disturbance for establishment and the decline in propagule supply associated with disturbance induced mortality in invaded areas (Buckley et al. 2007). However, given the widespread nature of pine invasions and the tendency of these invasions to create dense stands in open habitat that exceed the threshold identified here, the interaction between pine invasions and fire will be significant in the future. The implications for management are clear, in areas vulnerable to pine invasions (especially grasslands and sparse shrubland/steppe), the removal of propagule pressure is likely necessary to prevent invading pine densities from crossing thresholds at which increased fuel loads lead to more fire-prone landscapes.

Acknowledgements

We thank Hannah Funke, Maria Theresa Jessen and Sam Wall for field assistance and Pablo Bravo, Jonathan Urrutia and Jorgelina Franzese for help with species identification. KTT, BDM, DBM, and CW were funded by NSF-WildFIRE PIRE, OISE 09667472.

References

Agee, J. K. 1998. Fire and pine ecosystems. Pages 193-249 *in* D. M. Richardson, editor. Ecology and Biogeography of *Pinus*. Cambridge University Press, Cambridge.

Albini, F. A., J. K. Brown, E. D. Reinhardt, and R. D. Ottmar. 1995. Calibration of a large fuel burnout model. International Journal of Wildland Fire **5**:173-192.

Albini, F. A., and E. D. Reinhardt. 1997. Improved calibration of a large fuel burnout model. International Journal of Wildland Fire **7**:21-28.

Baker, W. L. 2009. Fire Ecology in Rocky Mountain Landscapes. Island Press, Washington D.C.

Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gomez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980-2009). Global Change Biology **19**:173-183.

Brooks, M. L. 1999. Alien annual grasses and fire in the Mojave Desert. Madrono **46**:13-19.

Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. Bioscience **54**:677-688.

Brown, J. 1975. Fire cycles and community dynamics in lodgepole pine forests. Pages 429-456 *in* D. Baumgartner, editor. Management of lodgepole pine ecosystems.

Brown, J. K., M. M. Marsden, K. C. Ryan, and E. D. Reinhardt. 1985. Predicting duff and woody fuel consumed by prescribed fire in the northern Rocky Mountains. Research Paper INT-337, USDA Forest Service.

Buckley, Y. M., B. M. Bolker, and M. Rees. 2007. Disturbance, invasion and re-invasion: managing the weed-shaped hole in disturbed ecosystems. Ecology Letters **10**:809-817.

Campbell, G. S., J. D. Jungbauer, K. L. Bristow, and R. D. Hungerford. 1995. Soil temperature and water content beneath a surface fire. Soil Science **159**:363-374.

Campbell, G. S., J. D. Jungbauer, S. Shiozawa, and R. D. Hungerford. 1993. A one-parameter equation for water sorption isotherms of soils. Soil Science **156**:302-305.

Coates, K. D., W. H. Emmingham, and S. R. Radosevich. 1991. Conifer-seedling success and microclimate at different levels of herb and shrub cover in a *Rhododendron-Vaccinium-Menziesia* community of south central British Columbia. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **21**:858-866.

Cuevas, Y. A., and S. M. Zalba. 2010. Recovery of native grasslands after removing invasive pines. Restoration Ecology **18**:711-719.

Cóbar-Carranza, A. J., R. A. Garcia, A. Pauchard, and E. Peña. 2014. Effect of *Pinus contorta* invasion on forest fuel properties and its potential implications on the fire regime of *Araucaria araucana* and *Nothofagus antarctica* forests. Biological Invasions **16**:2273-2291.

Cóbar-Carranza, A. J., R. A. García, A. Pauchard, and E. Peña. 2015. Effects of high temperatures in the germination and seed survival of the invasive species *Pinus contorta* and two native species of South Chile. Bosque **36**:53-60.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics **23**:63-87.

Despain, D. G. 2001. Dispersal ecology of lodgepole pine (*Pinus contorta* Dougl.) in its native environment as related to Swedish forestry. Forest Ecology and Management **141**:59-68.

Dibble, A. C., and C. A. Rees. 2005. Does the lack of reference ecosystems limit our science? A case study in nonnative invasive plants as forest fuels. Journal of Forestry **103**:329-338.

Dibble, A. C., R. H. White, and P. K. Lebow. 2007. Combustion characteristics of north-eastern USA vegetation tested in the cone calorimeter: invasive versus non-invasive plants. International Journal of Wildland Fire **16**:426-443.

Flory, S. L., K. Clay, S. M. Emery, J. R. Robb, and B. Winters. 2015. Fire and non-native grass invasion interact to suppress tree regeneration in temperate deciduous forests. Journal of Applied Ecology **52**:992-1000.

Fournier, D. A., H. J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M. N. Maunder, A. Nielsen, and J. Sibert. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods & Software **27**:233-249.

Gaertner, M., R. Biggs, M. Te Beest, C. Hui, J. Molofsky, and D. M. Richardson. 2014. Invasive plants as drivers of regime shifts: identifying high-priority invaders that alter feedback relationships. Diversity and Distributions **20**:733-744.

Hicke, J. A., M. C. Johnson, L. H. D. Jane, and H. K. Preisler. 2012. Effects of bark beetle-caused tree mortality on wildfire. Forest Ecology and Management **271**:81-90.

Holmes, P. M., D. M. Richardson, B. W. Van Wilgen, and C. Gelderblom. 2000. Recovery of South African fynbos vegetation following alien woody plant clearing and fire: implications for restoration. Austral Ecology **25**:631-639.

Hungerford, R. D., M. G. Harrington, W. H. Frandsen, K. C. Ryan, and G. J. Niehoff. 1991. Influence of fire on factors that affect site productivity. Pages 32-50. In: Harvey, Alan E.; Neuenschwander, Leon F. (compilers). Proceedings-management and productivity of western-montane forest soils. General Technical Report INT-GTR-280. Ogden, UT: USDA Forest Service, Intermountain Research Station.

Jaffré, T., F. Rigault, and G. Dagostini. 1998. Impact des feux de brousse sur les maquis ligno-herbacés des roches ultramafiques de Nouvelle-Calédonie. Adansonia **20**:173-189.

Jenkins, J. C., D. C. Chojnacky, L. S. Heath, and R. A. Birdsey. 2004. Comprehensive Database of Diameter-based Biomass Regressions for North American Tree Species Page 45. USDA Forest Service Northeastern Research Station, Newtown Square, PA.

Keane, R. E., and L. J. Dickinson. 2007. The photoload sampling technique: estimating surface fuel loadings from downward-looking photographs of synthetic fuelbeds. General Technical Report RMRS-GTR-190. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station. 44 p.

Keeley, J. E., J. G. Pausas, P. W. Rundel, W. J. Bond, and R. A. Bradstock. 2011. Fire as an evolutionary pressure shaping plant traits. Trends in Plant Science **16**:406-411.

Langdon, B., A. Pauchard, and M. Aguayo. 2010. *Pinus contorta* invasion in the Chilean Patagonia: local patterns in a global context. Biological Invasions **12**:3961-3971.

Ledgard, N. 2001. The spread of lodgepole pine (*Pinus contorta*, Dougl.) in New Zealand. Forest Ecology and Management **141**:43-57.

Ledgard, N. J. 2006. Determining the effect of increasing vegetation competition through fertiliser use on the establishment of wildings in unimproved high country grassland. New Zealand Journal of Forestry **51**:29-34.

Ledgard, N. J., and T. S. H. Paul. 2008. Vegetation successions over 30 years of high country grassland invasion by *Pinus contorta* New Zealand Plant Protection **61**:98-104.

Levine, J.M., Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society B **270**: 775-781.

Lonsdale, W. M., and I. L. Miller. 1993. Fire as a management tool for a tropical woody weed: *Mimosa pigra* in Northern Australia. Journal of Environmental Management **39**:77-87.

Mandle, L., J. L. Bufford, I. B. Schmidt, and C. C. Daehler. 2011. Woody exotic plant invasions and fire: reciprocal impacts and consequences for native ecosystems. Biological Invasions **13**:1815-1827.

Mermoz, M., T. Kitzberger, and T. T. Veblen. 2005. Landscape influences on occurrence and spread of wildfires in Patagonian forests and shrublands. Ecology **86**:2705-2715.

Nuñez, M. A., and E. Raffaele. 2007. Afforestation causes changes in post-fire regeneration in native shrubland communities of northwestern Patagonia, Argentina. Journal of Vegetation Science **18**:827-834.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2013. vegan: Community Ecology Package. R package version 2.0-10. http://CRAN.R-project.org/package=vegan

Page-Dumroese, D. S., R. K. Dumroese, C. M. Carpenter, and D. L. Wenny. 2002. Relationship of seed microsite to germination and survival of lodgepole pine on high-elevation clearcuts in northeastern Utah. USDA Forest Service Rocky Mountain Research Station, Ogden, UT. Note RMRS-RN-14. 4 p.

Paritsis, J., A. Holz, T. T. Veblen, and T. Kitzberger. 2013. Habitat distribution modeling reveals vegetation flammability and land use as drivers of wildfire in SW Patagonia. Ecosphere **4**:art53.

Pauchard, A., R. A. Garcia, E. Peña, C. Gonzalez, L. A. Cavieres, and R. O. Bustamante. 2008. Positive feedbacks between plant invasions and fire regimes: *Teline*

monspessulana (L.) K. Koch (Fabaceae) in central Chile. Biological Invasions **10**:547-553.

Pausas, J. G., and J. E. Keeley. 2014. Abrupt climate-independent fire regime changes. Ecosystems **17**:1109-1120.

Perry, G. L. W., J. M. Wilmshurst, and M. S. McGlone. 2014. Ecology and long-term history of fire in New Zealand. New Zealand Journal of Ecology **38**:157-176.

Peña, E., M. Hidalgo, B. Langdon, and A. Pauchard. 2008. Patterns of spread of *Pinus contorta* Dougl. ex Loud. invasion in a Natural Reserve in southern South America. Forest Ecology and Management **256**:1049-1054.

Pierce, A. D., and A. H. Taylor. 2011. Fire severity and seed source influence lodgepole pine (*Pinus contorta* var. *murrayana*) regeneration in the southern cascades, Lassen volcanic National Park, California. Landscape Ecology **26**:225-237.

Reinhardt, E. D. 2003. Using FOFEM 5.0 to estimate tree mortality, fuel consumption, smoke production and soil heating from wildland fire. Page P5.2 *in* Proceedings of the Second International Wildland Fire Ecology and Fire Management Congress and Fifth Symposium on Fire and Forest Meteorology. American Meteorological Society, Orlando, Florida, USA.

Reinhardt, E. D., R. E. Keane, J. K. Brown, and D. L. Turner. 1991. Duff consumption from prescribed fire in the U.S. and Canada: a broadly based empirical approach.*in* Proceedings of the 11th Conference on Fire and Forest Meteorology. Society of American Foresters, Missoula, MT.

Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology **77**:1655-1661.

Rejmanek, M., and D. M. Richardson. 2013. Trees and shrubs as invasive alien species-2013 update of the global database. Diversity and Distributions **19**:1093-1094.

Richardson, D. M. 1988. Age structure and regeneration after fire in a self-sown *Pinus halepensis* forest on the Cape Peninsula, South Africa. South African Journal of Botany **54**:140-144.

Richardson, D. M., and S. I. Higgins. 1998. Pines as invaders in the southern hemisphere. Pages 450-473 *in* D. M. Richardson, editor. Ecology and Biogeography of *Pinus*. Cambridge University Press, Cambridge.

Rossiter, N. A., S. A. Setterfield, M. M. Douglas, and L. B. Hutley. 2003. Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. Diversity and Distributions **9**:169-176.

Sarasola, M. M., V. E. Rusch, T. M. Schlichter, and C. M. Ghersa. 2006. Tree conifers invasion in steppe areas and *Austrocedus chilensis* forests in NW Patagonia. Ecologia Austral **16**:143-156.

Scott, D. F., and D. B. Van Wyk. 1990. The effects of wildfire on soil wettability and hydrological behavior of an afforested catchment. Journal of Hydrology **121**:239-256.

Setterfield, S. A., N. A. Rossiter-Rachor, L. B. Hutley, M. M. Douglas, and R. J. Williams. 2010. Turning up the heat: the impacts of *Andropogon gayanus* (gamba grass) invasion on fire behaviour in northern Australian savannas. Diversity and Distributions **16**:854-861.

Simberloff, D., M. A. Nuñez, N. J. Ledgard, A. Pauchard, D. M. Richardson, M. Sarasola, B. W. Van Wilgen, S. M. Zalba, R. D. Zenni, R. Bustamante, E. Peña, and S. R. Ziller. 2010. Spread and impact of introduced conifers in South America: Lessons from other southern hemisphere regions. Austral Ecology **35**:489-504.

Skaug, H., D. Fournier, A. Nielsen, A. Magnusson, and B. Bolker. 2013. Generalized Linear Mixed Models using AD Model Builder.

Stevens, J. T., and B. Beckage. 2009. Fire feedbacks facilitate invasion of pine savannas by Brazilian pepper (*Schinus terebinthifolius*). New Phytologist **184**:365-375.

Taylor, K. T., B. D. Maxwell, A. Pauchard, M. A. Nuñez, D. A. Peltzer, A. Terwei, and L. J. Rew. 2016a. Drivers of plant invasion vary globally: evidence from pine invasions within six ecoregions. Global Ecology and Biogeography **25**:96-106.

Taylor, K. T., B. D. Maxwell, A. Pauchard, M. A. Nuñez, and L. J. Rew. 2016b. Native versus non-native invasions: similarities and differences in the biodiversity impacts of *Pinus contorta* in introduced and native ranges. Diversity and Distributions.

Turner, M. G., W. H. Romme, R. H. Gardner, and W. W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs **67**:411-433.

Turner, M. G., D. B. Tinker, W. H. Romme, D. M. Kashian, and C. M. Litton. 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary

production in postfire lodgepole pine forests, Yellowstone National Park (USA). Ecosystems **7**:751-775.

Urrutia, J., A. Pauchard, and R. A. Garcia. 2013. Differences in plant composition in an *Araucaria araucana* (Molina) K.Koch and *Nothofagus antarctica* (G. Forst.) Oerst. forest in a *Pinus contorta* Douglas ex Loudon invasion gradient. Gayana Botanica **70**:92-100.

van Wilgen, B. W., and D. M. Richardson. 1985. The effects of alien shrub invasions on vegetation structure and fire behavior in South African fynbos shrublands: A simulation study. Journal of Applied Ecology **22**:955-966.

Veblen, T. T., T. Kitzberger, E. Raffaele, and D. C. Lorenz. 2003. Fire History and Vegetation Changes in Northern Patagonia, Argentina. Pages 265-295 *in* T. T. Veblen, W. L. Baker, G. Montenegro, and T. W. Swetnam, editors. Fire and Climatic Changes in Temperate Ecosystems of the Western Americas. Springer-Verlag, New York.

Veblen, T. T., T. Kitzberger, E. Raffaele, M. Mermoz, M. E. Conzalez, J. S. Sibold, and A. Holz. 2008. The historical range of variability of fires in the Andean-Patagonian *Nothofagus* forest region. International Journal of Wildland Fire **17**:724-741.

Ver Hoef, J. M., and P. L. Boveng. 2007. Quasi-poisson vs. negative binomial regression: how should we model overdispersed count data? Ecology **88**:2766-2772.

Vila, M., F. Lloret, E. Ogheri, and J. Terradas. 2001. Positive fire-grass feedback in Mediterranean Basin woodlands. Forest Ecology and Management **147**:3-14.

Wagner, S. A., and J. M. Fraterrigo. 2015. Positive feedbacks between fire and non-native grass invasion in temperate deciduous forests. Forest Ecology and Management **354**:170-176.

Widenmaier, K. J., and W. L. Strong. 2010. Tree and forest encroachment into fescue grasslands on the Cypress Hills plateau, southeast Alberta, Canada. Forest Ecology and Management **259**:1870-1879.

Zalba, S. M., Y. A. Cuevas, and R. M. Boo. 2008. Invasion of *Pinus halepensis* Mill. following a wildfire in an Argentine grassland nature reserve. Journal of Environmental Management **88**:539-546.

CHAPTER FIVE

SIMULATION MODEL SUGGESTS THAT FIRE PROMOTES LODGEPOLE PINE (*PINUS CONTORTA*) INVASION IN PATAGONIA

Contribution of Authors and Co-Authors

Manuscript in Chapter 5

Author: Kimberley T. Taylor

Contributions: Developed simulation model, executed experimental runs and statistical analysis, and wrote initial manuscript.

Co-Author: Bruce D. Maxwell

Contributions: Assisted in model development, statistical analysis and manuscript preparation.

Co-Author: Paul Caplat

Contributions: Assisted in model development and statistical analysis.

Manuscript Information Page

Kimberley T. Taylor, Bruce D. Maxwell, Paul Caplat
Journal Name: Biological Invasions
Status of Manuscript:
__x_ Prepared for submission to a peer-reviewed journal
____ Officially submitted to a peer-review journal
____ Accepted by a peer-reviewed journal
____ Published in a peer-reviewed journal

Springer

Abstract

To best understand plant invasions and predict unexpected outcomes it is necessary to integrate information on disturbance, the local environment, and demography. Fire is widely expected to promote pine (genus *Pinus*) invasions; however, interactions between fire, pine and the invaded community make the dynamics unclear. A positive feedback between lodgepole pine (*Pinus contorta*) invasions and fire has been identified but only above an invasion threshold. Above this threshold, fire resulted in increased pine dominance at the plot level, however below this threshold establishment rates did not change. Therefore, tradeoffs likely exist between fire-induced mortality of the *P. contorta* seed source and increased establishment post-fire that determine invasion outcomes across a larger landscape. We used a spatially explicit invasion simulation model modified to include fire to explore the implications of these complex interactions between pine invasions and fire. We asked if fire promoted *P. contorta* invasion across a Patagonian steppe site and if this depended on the age of the invasion when it burned? Additionally, the invasion density threshold above which post-fire *P. contorta* establishment increased likely varies by site depending on native plant adaptations to fire, so we examined how changes in this threshold altered invasion outcomes. We found that, although fire was not necessary to initiate invasion, fire in communities where pine invasions were at least 10 years old resulted in increased spatial extent and maximum invasion density compared to unburned simulations. Fire through younger invasions did not alter the progression of the invasion compared to unburned simulations. Invasion threshold had little effect on invasion outcomes, suggesting that our results may be robust

across sites. Pine invasions should be managed before they reach an advanced stage where positive feedbacks between fire and pine invasion could lead to dramatic increases in invasion rate.

Introduction

Plant invasions that have the capacity to alter fire regimes and create positive feedbacks with fire have the potential to cause significant impacts on native ecosystems (Brooks et al. 2004; Gaertner et al. 2014; Mack & D'Antonio 1998). Although many studies have examined how invasive plants alter fire regimes (e.g. Balch et al. 2013; Pauchard et al. 2008; Rossiter et al. 2003; van Wilgen & Richardson 1985), few have integrated information on invasion-fire feedbacks to study the effects of these complex interactions on invasion extent. We developed a spatially explicit invasion simulation model to determine the potential role of *Pinus contorta*-fire feedbacks in promoting invasions in the Southern Hemisphere. This type of integrated simulation model is necessary to determine how fire across a landscape will alter invader population dynamics and determine the consequent impacts on native communities (Gaertner et al. 2014). These dynamics will guide and influence post-fire management options.

Disturbance is widely believed to increase invasion success for many plant species by creating an invasion window with increased resource availability (Davis et al. 2000; Johnstone 1986; Sher & Hyatt 1999). For pine species (genus *Pinus*) introduced to the Southern Hemisphere, invasion is often correlated with human-caused or natural disturbances (Richardson & Bond 1991; Richardson et al. 1994). In particular, fire has been found to promote the invasion of *Pinus radiata*, *P. pinaster*, and *P. halepensis* into

South African fynbos (Richardson & Cowling 1992) and *P. halepensis* into the Argentine Pampas grasslands (Zalba et al. 2008). Additionally, areas dominated by tall shrubs that are generally resistant to invasion by *Pinus contorta* (Taylor et al. 2016a) were significantly more vulnerable after fire (Chapter 4). Other studies suggest that when disturbance is more likely in invaded than uninvaded areas it may actually decrease the likelihood of further invasion, due to tradeoffs between increased invader habitat quality in disturbed areas and disturbance-induced invader mortality (Buckley et al. 2007). Therefore, it is necessary to consider both the negative and positive effects of disturbance on invasion when predicting landscape-level changes in invasion as a result of disturbance. Examining these interactions may be best achieved through simulation modeling (Higgins et al. 1996). Several invasion simulation models have incorporated disturbance into their simulations and found that the effects of disturbance on invasion depends on the vegetation type and the disturbance regime (e.g. Higgins & Richardson 1998; Pausas et al. 2006; Shackelford et al. 2013; Stevens & Beckage 2009). Such modeling efforts have also shown that including feedbacks between fire and vegetation in models can lead to abrupt non-linear state changes (Stevens & Beckage 2009).

Invasive pine species introduced to the Southern Hemisphere are thought to create a positive feedback with fire whereby they alter some aspect of the fire regime which then promotes their own success over native plants (Veblen et al. 2011). Recent work has shown that one of the commonly invading pine species, *Pinus contorta*, alters fuel loads and structure compared to uninvaded communities and that this likely increases fire spread and severity (Chapter 4; Cobar-Carranza et al. 2014). The effect of disturbance on

invasion success varies when the likelihood of disturbance differs between uninvaded and invaded areas (Buckley et al. 2007), as is the case for *P. contorta* invasions into previously fuel-limited steppe systems (Paritsis et al. 2013; Veblen et al. 2011). *Pinus contorta* experiences high levels of fire-induced mortality (Baker 2009), and it recovers rapidly following fire in its native range in western North America (e.g. Kemp et al. 2015; Pierce & Taylor 2011; Turner et al. 1997). However, we have found that in the introduced range, fire only promotes *P. contorta* establishment when the invasion density prior to the fire was high (Chapter 4). In other words, a positive feedback between pine invasions and fire is likely to form above an invasion density threshold (Chapter 4).

Given the potential for *P. contorta* to alter fire behavior in invaded systems and to respond differently to fire depending on pre-fire invasion density, it is unknown how fire will affect invasion success across a site. For example, although fire through a dense invasion will increase the quality of the seedbed and the rate of pine establishment, it may also destroy a large part of the invasion seed source. Given the threshold effect we found, we may expect that fires through a young (low density) invasion would reduce post-fire invasion rates, whereas fire through an older (high density) invasion would increase the rates. Additionally, the invasion threshold at which a positive feedback forms with fire likely depends on the native vegetation. To explore the interactions between *P. contorta* invasions and fire we created a spatially explicit invasion-fire simulation model. This study aims to answer two questions through simulations with the invasion-fire model. First, will fire through an invaded system promote further invasion and does this depend on the age of the invasion when it burns? Second, will changes in the invasion density

threshold that results in increased post-fire *P. contorta* establishment alter invasion density and extent?

We hypothesized that fire early in an invasion would reduce *P. contorta* occupied cells (invasion extent) and mean densities by killing invading trees but not promoting high post-fire establishment rates (due to low pre-fire invasion densities). We expected that fire through older invasions (>10 years) would result in higher invasion densities, but reduced spatial extent in the short term.

Methods

Simulation Model

We created a spatially explicit cellular automata simulation model in the modeling environment Netlogo (Wilensky 1999) based on the general tree invasion model created by Caplat et al. (2014; Fig. 5.1). We adapted the tree dynamics of the Caplat et al. model so that the demographic and dispersal characteristics matched observations for *P. contorta* (Table 5.1). We also added fire to the model as described below (Table 5.2). The model simulates a well-studied site in Coyhaique Alto, Chile (CA) (Langdon et al. 2010; Taylor et al. 2016a) that has dimensions of 1800 m by 1430 m, divided into 10 m x 10 m cells. Simulations ran for 35 years.

Tree Dynamics. The model is composed of a grid where each cell is a cellular-automaton and population dynamics occur within the cell. Each cell was assigned a vegetation type (grass, *Nothofagus antarctica*, or *P. contorta* plantation) based on a map previously created at CA (Langdon et al. 2010; Taylor et al. 2016a). The plantation

started with 15 three-year-old *P. contorta* per cell. Cells outside of the plantation contained no *P. contorta* at time zero. At each time step (annual) we calculated the number of trees in each individual age class, from the seedbank through 9 years old, within each cell (10 m x 10 m; see Table 5.1 for all demographic parameters and their sources). Once trees reached the age of 10 years, they were added to the adult stage class and the total number of adults was tracked. Demographic parameters driving population dynamics were derived from emergence experiments (Langdon 2011), 5 years of monitoring all *P. contorta* individuals in 3 hectares at the Coyhaique Alto site (Pauchard, unpublished), and a large observational data set from the site (Taylor et al. 2016a). Emergence was lowered by 90% in cells in which *N. antarctica* was present, based on the extremely low levels of invasion observed in this vegetation type despite its proximity to the plantation (Taylor et al. 2016a). Emergence and survival were also subject to density dependence based on our data and supported by the lack of *P. contorta* regeneration seen beneath *P. contorta* canopies elsewhere in the introduced range (Howell & McAlpine 2016).

Seed production was calculated separately for adult trees (age 10 and older) and for trees between the ages of 5 and 9 (hereafter subadults) based on field observations (Table 5.1). Seed production was determined separately for each cell by drawing a random number of cones per tree from the measured distribution at the Coyhaique Alto site (Taylor et al. 2016a) and multiplying by 20 seeds per cone (Taylor unpublished data). For subadults, it was first determined if they were reproductive in a given year or not,

based on the proportion of subadults that contained cones in each sampling year at CA; then, the number of cones per tree was drawn from the sampled distribution for subadults.

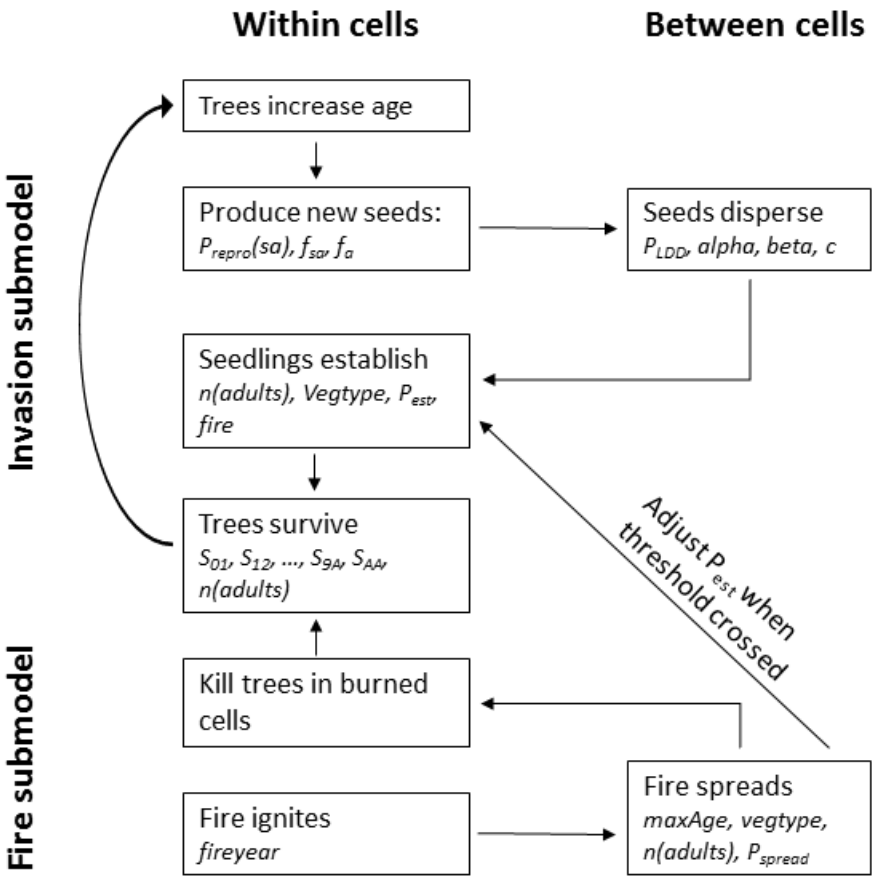

Figure 5.1. Diagram of the model flow. Abbreviations explained in Tables 5.1 and 5.2, except n(adults) which signifies the number of adults in a cell. This variable affects establishment and survival at some stages through density dependence.

Seeds were dispersed from a cell based on two exponential functions, one for normal dispersal and one for long distance dispersal. Each seed had a probability P_{LDD} of being dispersed by the long distance dispersal function. The majority of seeds were dispersed within 100 meters of the parent tree (Ledgard 2001). We included a separate

function for long distance dispersal in the model because long distance dispersal of up to 40 kilometers has been found for *P. contorta* (Ledgard 2001), a simple exponential model does not capture this long distance dispersal (Nathan & Muller-Landau 2000), and long distance dispersal is important in explaining plant invasions and range expansions (Higgins & Richardson 1999; Shigesada et al. 1995). CA experiences consistent strong winds and frequent wind events, suggesting that long distance dispersal is important at this site. Our dispersal kernel allowed occasional long distance dispersal farther than 1 km, although the majority of our long distance dispersal occurred between 200 and 600 m from the parent tree. The appropriate parameters for the dispersal functions were determined with a sensitivity analysis that compared the resulting invasion metrics (mean invasion density, maximum invasion density, and mean density at different distances from the plantation edge) to known values sampled at CA. Although we captured mean densities and densities at each distance fairly well, we were less successful in capturing the rare long distance events that led to establishment of lone trees farther than 500 m from the plantation (Table 5.3).

Table 5.1. Model demographic parameters and their sources.

Parameter	Value	Description & Source
Plantation density	15	Pauchard communication with forestry company that owns plantation
Dispersal	Alpha = 3.5; beta = 0.0035; C = 50; pLDD = 0.1	Alpha, beta, C are dispersal parameters and pLDD is probability of LDD. Sensitivity analysis described in methods
pEst	0.01	Probability of establishment Langdon 2011 experiments at Coyhaique
pEst in NOAN	0.1*pEst	pEst in *N. antarctica* plots Taylor et al. 2016a
S_{12}	0.9	Survival year 1 to 2 Pauchard unpublished data
S_{23}, S_{34}, S_{45}, S_{56}	0.97	Survival year 2 to 3 up to survival year 5 to 6 Pauchard unpublished data
S_{67}, S_{78}, S_{89}, S_{9A}, S_{AA}	0.99	Survival year 6 to 7 up to adult survival Pauchard unpublished data
Seedbank survival	0.2	Ledgard 2004
Seed predation	0.03	Taylor unpublished data
Adult cones produced	Mean: 38; sd: 20	Adult cones produced mean and standard deviation Taylor et al. 2016a
P_{repro}	0.28	Probability a subadult has cones in given year Taylor et al. 2016a
Subadult cones	Mean: 9.5; sd: 8	Subadult cones produced mean and standard deviation Taylor et al. 2016a
$f_{A,}$ f_{SA}	Cones * 20	Adult and subadult fecundity Taylor unpublished data

Fire Dynamics. A maximum of one fire per simulation occurred and was started in the same cell for each simulation. Given our simulation time of 35 years it is unlikely that more than one fire would burn our study site. Fire spread probabilistically to surrounding cells (Fig. 5.1) and continued to spread until no new cells were ignited (Perry et al. 2012; Perry et al. 2015). Therefore, the size of the fires was not fixed but emerged as a function of fire-vegetation-invasion feedbacks. Probability of spread between cells

depended on the vegetation type in each cell and was based on the literature for native vegetation (*Nothofagus antarctica* and steppe; Paritsis et al. 2013) and prior measurements of fuel loads and bareground with different levels of *P. contorta* invasion at CA for invaded cells (Table 5.2; Chapter 4). We did not include the effects of topography or wind on fire spread. Given the flat nature of our study site, we do not expect that excluding topography greatly influenced fire spread, however the lack of wind effects in the model could result in smaller fires than might naturally occur.

All *P. contorta* individuals were killed in burned cells (Baker 2009). After fire, the probability of *P. contorta* establishment increased in *N. antarctica* cells to match the level in the steppe for five years (Burns 1993). *Pinus contorta* generally establishes well post-fire in its native range (e.g. Turner et al. 1997; Kemp et al. 2015), even where it is not serontinous (e.g. Pierce & Taylor 2011). However, a steppe site in Northern Patagonia showed high post-fire densities only in plots with older, dense pre-fire invasions (Chapter 4). Based on these observations that (1) native vegetation seemed to recover and become dominant where pre-fire densities of *P. contorta* were low, and (2) invasion was enhanced when pre-fire pine densities were high, we increased post-fire *P. contorta* establishment in model cells that had a pre-fire invasion density of subadult and adult *P contorta* greater than a threshold value (Chapter 4). We found that 10 trees per 100 m^2 was a threshold density at a site in Northern Patagonia (Chapter 4) but we vary the value in the model simulations as described below. The elevated establishment rate in the model, based on pre- and post-fire densities in a steppe site in Northern Patagonia (Chapter 4), persisted for three years post-fire. We also reduced the seedbank by 50% in

model cells with maximum *P. contorta* age of >= 15 years based on modeled soil temperatures during fire in different age invasions (Chapter 4) and the known temperature tolerances of *P. contorta* seeds (Knapp & Anderson 1980).

Table 5.2. Fire-related model parameters and their sources.

Parameter	Value	Description & Source
Invasion density threshold	5, 10, 15	Pre-fire density above which *P. contorta* establishment is increased post-fire for 3 years. Chapter 4
Post-fire establishment in plots above invasion density threshold	0.043 for 3 years post-fire	Chapter 4
Post-fire establishment in *N. antarctica* plots	pEst (0.01) for first 5 yrs post-fire	Same as steppe plots because assume that fire reduces shade and increases resources so better for *P. contorta* establishment
Seedbank (sb) response to fire	Sb=sb*0.5 if maxage>15 Sb=sb otherwise	Chapter 4 Knapp & Anderson 1980
Probability fire spread in *P. contorta*	If density > 40 or oldest tree > 10 years spread prob. = 0.8 Otherwise = spread in that vegetation type (steppe or *N. antarctica*)	Chapter 4
Probability fire spread in *N. antarctica*	0.61	Paritsis et al. 2013
Probability fire spread in *N. antarctica* with steppe neighbors	0.71	Higher probably of burning due to drying effect of edge with steppe
Probability fire spread in *N. antarctica* with *P. contorta* neighbors older than 10 years	0.71	Higher probably of burning when next to mature lodgepole because their crowns will likely be burning
Probability fire spread in steppe	0.3	Paritsis et al 2013 Chapter 4

Model Scenarios and Statistical Analysis

To test the effects of fire at different stages of invasion on invasion density and spread, we ran simulations with a single fire ignition for each simulation at five-year intervals (no fire, fire in year 5, year 10, year 15, and year 20). We crossed this fire year treatment with an invasion threshold treatment. We estimated the invasion threshold that increased rates of post-fire *P. contorta* establishment was 10 trees per 100 m^2 at a shrub steppe site in Argentinian Patagonia (Chapter 4). We assessed the effect of changing the *P. contorta* density threshold on invasion density and extent by including simulations with the invasion threshold set at 5, 10, or 15 trees per 100 m^2. We included an invasion threshold treatment because we expect that this threshold may vary by site. Adjusting fire year and invasion threshold left us with a total of 15 treatment combinations (5 fire year levels x 3 threshold levels). We ran simulations for 35 years with 100 replicates for each treatment combination (1,500 model runs). We recorded outputs at the end of 35 simulation years for each scenario. Model output included number of burned cells, number of pine-occupied cells, mean pine density in pine-occupied cells, maximum pine density, and maximum distance from the plantation to an invaded cell.

To better explain patterns that emerged from the initial model runs, we also ran the model with each fire year and threshold treatment combination for 35 years and obtained output for each year so that we could determine changes in pine density and number of cells occupied by pine over time. This process was replicated 12 times for each treatment combination.

Model output was analyzed in R (R Core Team 2015) with generalized linear models with fire year and pre-fire invasion density threshold as the explanatory variables and the output as the response. Where necessary (e.g., for number of pine-occupied cells, maximum pine density), a Poisson error distribution fit with quasi-likelihood was used for the models. To examine trends over time we used generalized additive mixed models to model mean and maximum pine density, pine-occupied cells and maximum distance from a plantation as a function of the threshold value and the interaction between year and fire year, with model simulation (run) as a random effect. When necessary (e.g., for number of pine-occupied cells, maximum pine density) we used a Poisson error distribution.

Table 5.3. Observed and simulated (30 runs, no fire) pine invasion metrics for the Coyhaique Alto site. For the simulation the mean and the standard deviation (SD) from the 30 runs for each invasion metric is shown.

	Observed	Observed	Simulation	
	2012	2014	Mean	SD
Plantation age	24	26	26	-
Mean density of pine-occupied cells	10.15	11	12.86	0.10
Mean adult pine density in cells with adults	-	5	4.88	0.08
Farthest invaded cell (m from plantation)	901	901	459.02	18.83
Mean density in *Nothofagus* cells occupied by at least one *P. contorta*	1.6	2	2.24	0.22
Maximum *P. contorta* density	83	67	36.43	1.68
Mean pine density occupied plots 0-100 m	28.05	19.88	22.29	0.15
Mean pine density occupied plots 100-200 m	16.57	25.24	10.79	0.13
Mean pine density occupied plots 200-300 m	4.09	5.9	7.13	0.52
Mean pine density occupied plots 300-400 m	3.58	4	4.02	0.45
Mean pine density occupied plots 400-500 m	1.75	2.77	1.31	0.24

Results

Burned Area

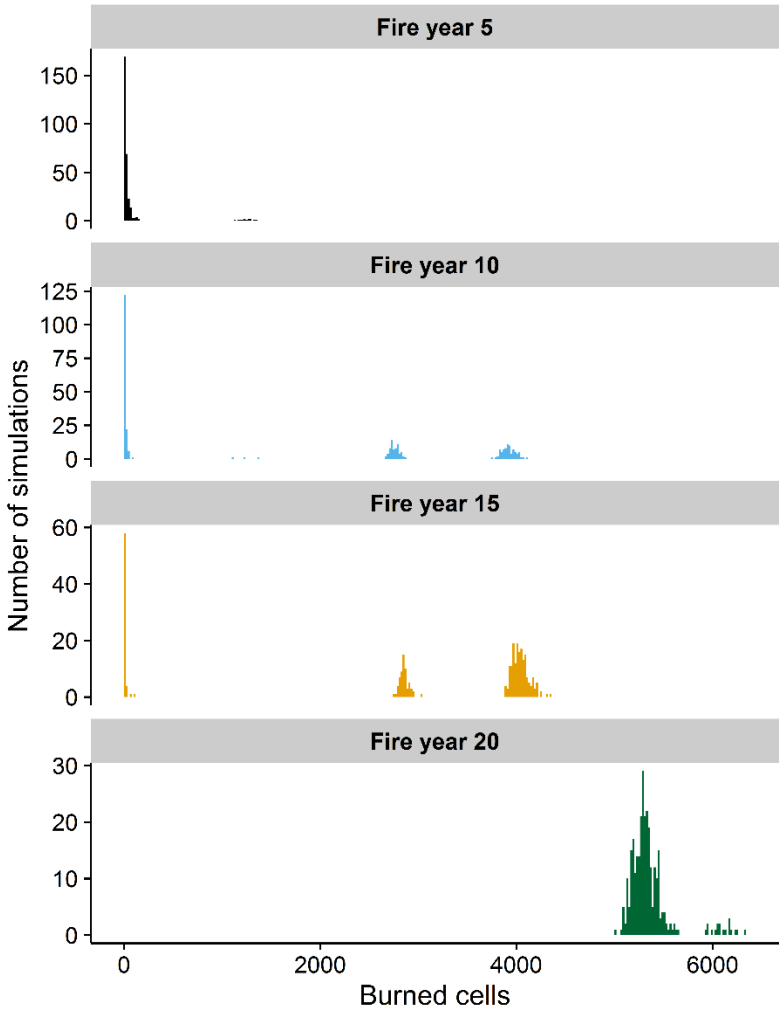

Figure 5.2. Frequency of fire size (number of burned cells) by fire year during *P. contorta* simulated invasion.

Fires that burned in simulation year 5 remained small (<2000 cells; Fig. 5.2) due to the low fuel loads associated with low density pine invasions. Fires in year 10 or 15 had a trimodal distribution with some fires remaining extremely small, while others entered the pine plantation and/or flammable *Nothofagus antarctica* stands and grew

large (>2000 cells; Fig. 5.2). All fires in year 20 became much larger (>4000 cells) than the fires in year 5 (Fig. 5.2) due to the presence of large, connected areas of fuel resulting from the high-density of *P. contorta*.

Effect of Fire Year and Invasion Density Threshold on Invasion

Overall, the fire year caused significant differences in *P. contorta* invasion response metrics (Fig. 5.3). In general, fires that occurred late in invasion had the most impact on invasion metrics, causing increases in pine occupancy, maximum pine density, and distance from plantation. Contrary to our expectations, invasion parameters did not decline compared to unburned simulations when fire burned early in the invasion (fire year 5; Fig. 5.3); fuels were insufficient to carry the fire (Fig. 5.2) and small fires had little effect on *P. contorta* mortality. Differences in the pre-fire invasion density threshold that resulted in increased *P. contorta* establishment post-fire were less important than fire year in explaining invasion density and extent.

Specifically, fire year, threshold, and their interaction were significant predictors of pine-occupied cells ($\chi^2 = 1656.14$, df = 4, $P<0.001$; $\chi^2 = 39.8$, df = 2, $P<0.001$; and $\chi^2 = 54.49$, df = 8, $P<0.001$ respectively), mean pine density of pine-occupied cells ($F_{4,1485} = 1307.3$, $P<0.001$; $F_{2,1485} = 320.6$, $P<0.001$; and $F_{8,1485} = 276.9$, $P<0.001$ respectively), and maximum distance of a pine-occupied cell from the plantation ($F_{4,1485} = 362.2$, $P<0.001$; $F_{2,1485} = 16.4$, $P<0.001$; and $F_{8,1485} = 7.1$, $P<0.001$ respectively) after 35 simulation years (Fig. 5.3). While the number of pine-occupied cells and maximum distance from plantation both increased with increasing fire year, mean density declined. Different pre-

fire invasion density thresholds only resulted in different post-fire invasion rates when the fire burned at later invasion stages (Fig. 5.3). Maximum pine density increased with increasing fire year (χ^2 = 24125.8, df = 4, P<0.001; Fig. 5.3), but was not related to invasion density threshold or the interaction between threshold and fire year (χ^2 = 2.7, df = 2, P = 0.25; and χ^2 = 5.5, df = 8, P = 0.70, respectively). The large variability in invasion responses for simulations with fires in year 10 (Fig. 5.3) can be explained by the size of the fire, with more pine-occupied cells and greater maximum distance from the plantation in the simulations with larger fires (Fig. D1 in Appendix D).

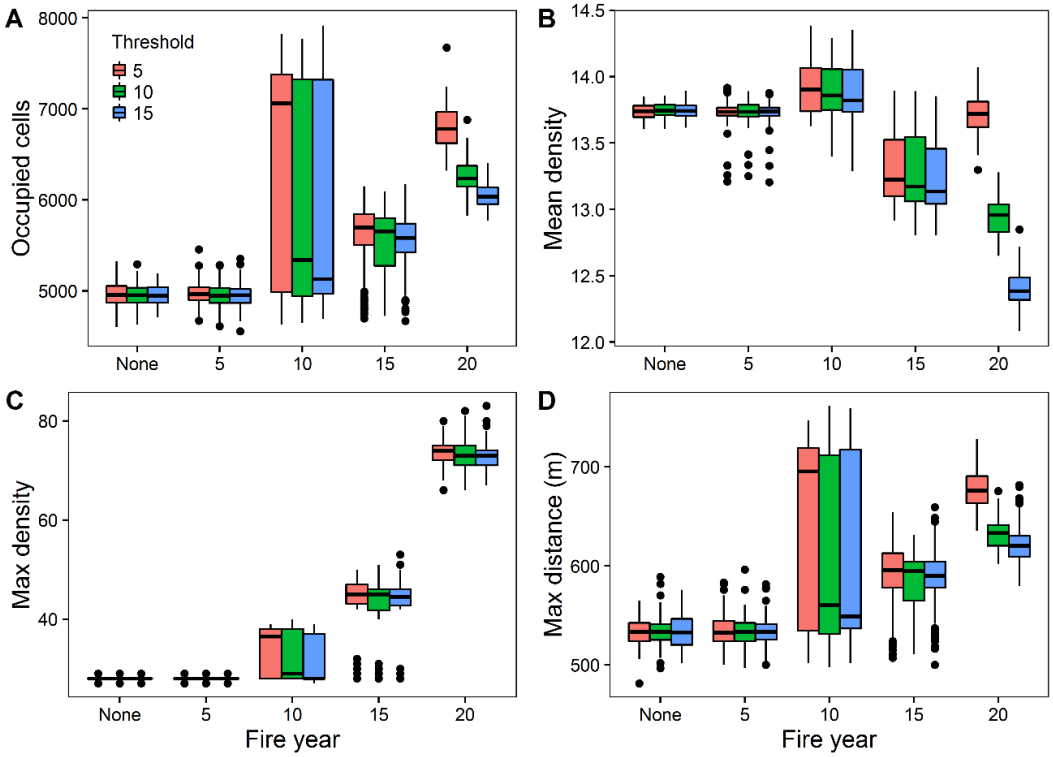

Figure 5.3. Simulation results for (A) number of *P. contorta* occupied cells; (B) mean pine density in occupied cells; (C) maximum pine density; and (D) maximum distance of a pine-invaded cell from the plantation plotted for cells that did not burn (None) and burned in years, 5, 10, 15, and 20. Number of pine-occupied cells and their densities exclude cells in the plantation. Colors show three different threshold densities for *P. contorta* (number of trees per cell) prior to fire. Exceeding these threshold densities was required to increase in *P. contorta* establishment post-fire.

Trends Over Time

The trends over time for all responses (pine-occupied cells, mean pine density, maximum pine density, and maximum distance to plantation) differed between the unburned simulations and those burned in years 10, 15, and 20 ($P<0.001$ for all comparisons); however, trends over time did not differ between unburned and burned in year 5 ($P>0.05$ for all responses; Fig. 5.4). Mean pine density was the only response variable where the invasion density threshold was significant: lower mean densities occurred in simulations with a threshold of 15 than in those with a threshold of 5 ($P<0.001$).

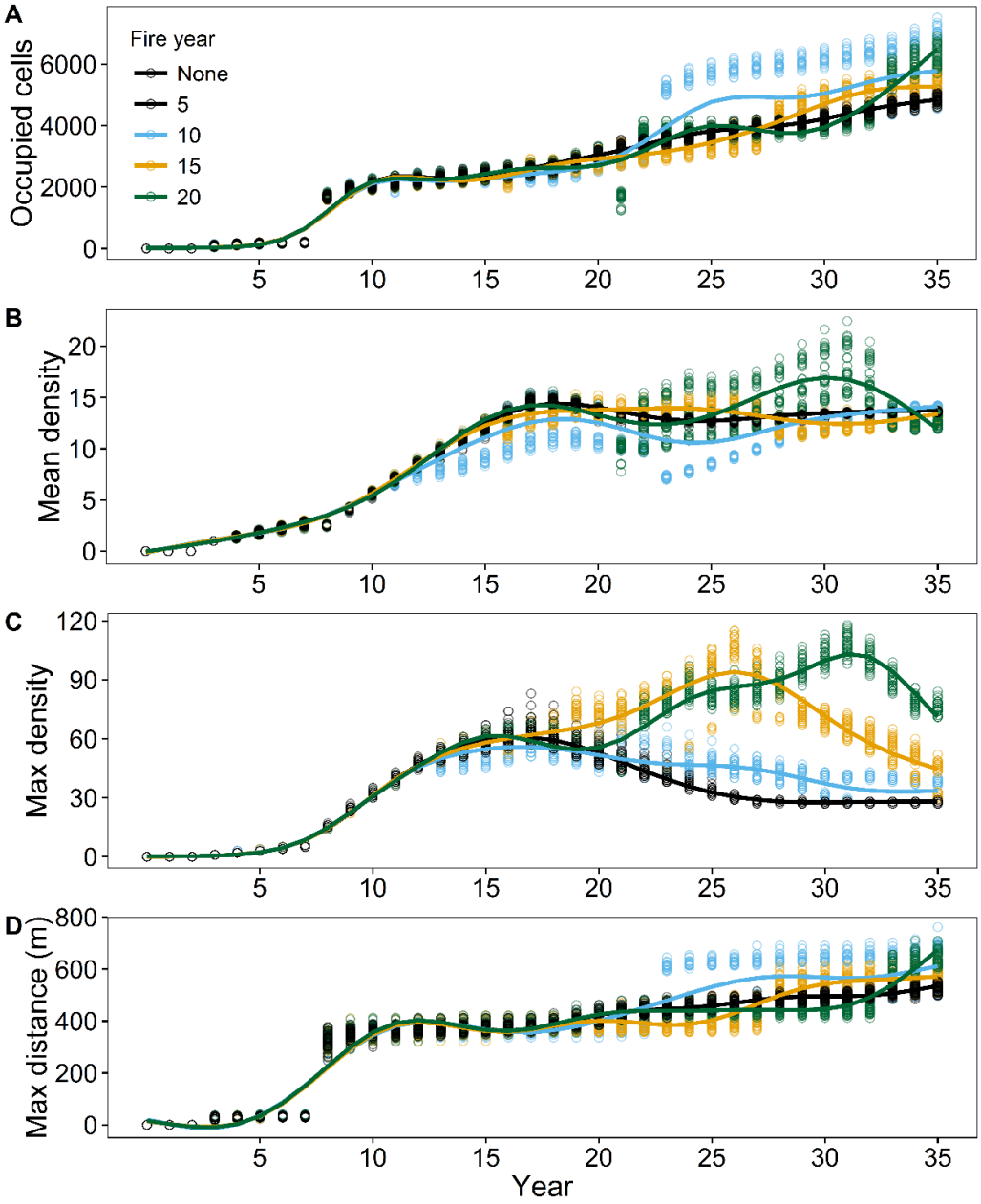

Figure 5.4. Time series show changes in plot parameters of the course of the model simulation: (A) Change in *P. contorta* occupied cells; (B) mean density of pine-occupied cells: (C) maximum pine density; and (D) maximum distance of an invaded cell from the plantation over simulation time. Smooth lines are predicted trends from the GAMM model. There was no statistical difference in the relationship between year and occupied cells for the unburned and fire year 5 simulations so only one line is shown (black). Colored lines and points represent simulations burned in year 10 (blue), 15 (yellow), and 20 (green). Note that the line for fire year 10 does not appear to match the data because some points from fire year 10 simulations are hidden behind other points and represent the simulations where fires remained small.

In all treatment combinations, the number of pine-occupied cells jumped significantly in year 8 when the plantation trees matured and increased seed production (Fig. 5.4). The unburned and fire year 5 simulations indicated that pine-occupied cells and maximum distance to plantation increased steadily after year 8. With fires in years 10, 15 and 20, pine-occupied cells briefly declined the year following fire (Fig. 5.4). In simulations with fire in years 10 and 15, some runs showed that the fire grew large whereas in others fire size remained small. In runs where the number of burned cells was large, a large jump in pine-occupied cells and maximum distance to plantation occurred as soon as the post-fire cohort became mature and started dispersing seeds (Fig. 5.4). All fires burned in year 20 became large, due to more continuous pine fuels, and the number of pine- occupied cells and the maximum distance to plantation increased when the post-fire cohort matured (Fig. 5.4). In all cases, in the years the number of pine-occupied cells and maximum distance to plantation increased, mean density declined due to lower densities in the front of the invasion wave. Maximum densities peaked at simulation year 17 for the unburned and the fire year 5 simulations. For the other simulations (fire years 10, 15 and 20) the maximum density peaked 11 years after fire (Fig. 5.4) before declining due to the density-dependent feedback on establishment included in the model.

Discussion

To best understand the ecology of plant invasions and predict unexpected outcomes, it is necessary to integrate information on disturbance, the local environment, invasive plant traits, and demography (Buckley et al. 2007; Higgins & Richardson 1998; Stevens & Beckage 2009). The model developed in this study is unique in that it

combined a mechanistic explanation for feedbacks (altered fuel loads and fire spread) with a population model (Gaertner et al. 2014) to examine the complexity and potential for non-intuitive outcomes resulting from the interaction between fire and pine invasions. Although fire was not necessary to initiate a *P. contorta* invasion, simulated fire through invasions that were at least 10 years old increased the spatial extent of pine and its maximum invasion density.

The age of the invasion when the fire occurred proved to be an important parameter, because it affected both the size of the fire and the ability of *P. contorta* to recruit successfully post-fire. The model suggests that the probability of an ignition becoming a large fire increases greatly in older invasions compared with uninvaded steppe sites. Empirical studies show that steppe vegetation is generally fuel limited (Paritsis et al. 2013; Chapter 4), and pine invasions increase the fuel loads and result in more continuous fire spread (Chapter 4). Once fuel levels are sufficient for fire to spread, the pine invasion is generally above the density threshold necessary to cause an increase in *P. contorta* establishment post-fire. This interaction sets up a positive feedback: older, dense invasions promote larger fires which in turn promote denser post-fire invasions that eventually spread more rapidly than invasions in unburned simulations. A similar positive feedback between flammable native shrubs and fire occurs in Patagonia (Mermoz et al. 2005), and increasing fire could promote further shifts from fire-sensitive *Nothofagus pumilio* forests to fire-prone shrublands (Kitzberger et al. 2012; Paritsis et al. 2015). Flammable pine plantations, which are often located on the forest-steppe ecotone, and pine invasions, exacerbate this positive fire feedback and further contribute to losses of

fire sensitive *Nothofagus* species. The situation is particularly acute when plantations are placed adjacent to the fire-sensitive *Nothofagus pumilio* forest, as occurs frequently in the Chilean Aysén Region.

When disturbance is more likely in invaded areas than in uninvaded areas it was predicted that disturbance would decrease invasion rates (Buckley et al. 2007). In contrast, even though fires spread more readily through invaded than uninvaded areas in our simulations, fire increased invasion rates. We attribute this finding to several factors. First, the inherently patchy nature of fires ensures that some mature seed trees survive fires and promote recolonization of the burned area (Pierce & Taylor 2011). Second, *P. contorta* seeds can withstand high temperatures in the soil (Cóbar-Carranza et al. 2015; Knapp & Anderson 1980), and these temperatures generally exceed modeled soil temperatures in fire simulations that are based on fuel loads recorded at four sites with *P. contorta* invasions (Chapter 4). For that reason, rapid regeneration of pine could come from an in-situ post-fire seedbank. Third, *P. contorta* reproduces at a young age, particularly in its introduced range (Taylor et al. 2016a). We found that invasion was only slowed for 5 years post-fire until a new cohort became reproductive. The post-fire cohort was denser than invasions in unburned simulations, allowing the invasion to proceed more quickly than in the unburned simulations. In our model experiment, the benefits of disturbance for establishment rates outweighed the negative effects of disturbance on tree survival.

It has long been known that fire and other disturbances promote pine invasions (Richardson & Bond 1991; Richardson & Higgins 1998); however, it has also been

recognized that the effects of disturbance are context specific. In the case of invasive species, disturbance must be understood in light of the native vegetation and disturbance regime as well as the plant traits of the invader (Higgins & Richardson 1998). We suggest that *P. contorta* invasion will be promoted by fire across much of the world, based on several factors: first, the pre-fire invasion pine density (threshold) necessary to promote establishment of pine after a fire only altered some response variables when fire burned in year 20. Thus, even if critical levels of pine density varies by site, the response of pine invasion after fire will not show significant variation.

Second, our intermediate threshold level (1000 trees/ha) was estimated from a site with fire-adapted species that readily resprout after fire (Nuñez & Raffaele 2007). We would expect the threshold to be even lower in sites with less fire-adapted vegetation (e.g., New Zealand, Perry et al. 2014) because reduced recovery of native vegetation after fire would decrease competition with pine seedlings. Additionally, sites with less fire-adapted vegetation are also particularly vulnerable to human-induced changes in fire regimes (Perry et al. 2014; Whitlock et al. 2015).

Third, *P. contorta* growth is slower at CA than at other sites in Argentina and New Zealand where *P. contorta* is also currently invading (Taylor et al. 2016a). Thus fuel accumulation with invasion is more rapid in these other sites suggesting that a positive feedback could form sooner.

Fourth, *P. contorta* individuals also have higher fecundity at a younger age at other sites in Argentina and New Zealand than at CA (Taylor et al. 2016a). Therefore, the post-fire cohort of pine will become reproductive sooner and produce more seeds,

promoting an even larger increase in post-fire invasion spread rates. However, our study site in CA was relatively homogenous in terms of suitable habitat for *P. contorta* but in sites with more heterogeneous habitat, spread rates will depend on other factors, including density dependence (Pachepsky & Levine 2011) and background habitat suitability variation.

The trends seen in pine-occupied cells and their density over time (Fig. 5.4) explained several patterns seen in the snapshot results from year 35 (Fig. 5.3). Mean density declined when the number of pine- occupied cells increased due to an increase in low-density cells at the invasion front. Density dependence caused the overall mean density to remain fairly constant between fire year treatments, after an initial brief increase in mean pine density post-fire in the later year burns. However, the maximum density was significantly higher in simulations with large fires. High maximum pine densities will likely result in strong declines in native plant density and richness, which are both negatively correlated with *P. contorta* cover (Taylor et al. 2016b). Therefore, synergies between disturbance and invasion may accelerate impacts due to *P. contorta* invasion on native ecosystems.

Our modeling experiments indicate that high maximum densities of *P. contorta* after fire abruptly increased the number of pine-occupied cells and the maximum distance of invasion from plantations. This stepwise invasion process with rapid and nonlinear increases in spread rates contrasts with unburned and small fire (fire year 5 and some fire year 10) simulations where the increase in occupied cells was linear after the initial jump in year 8 (Fig. 5.4). Other studies have also found that feedbacks between tree invasions

and fire led to nonlinear behavior (Stevens & Beckage 2009) and thus rapid increases in tree invasions may be expected in other systems that also have feedbacks between invasion and fire.

Our results highlight the necessity of managing pine invasions before they reach an advanced stage where positive feedbacks between fire and pine invasion could lead to dramatic increases in invasion rate. The increasing density and extent of post-fire pine will exacerbate non-fire driven invasion impacts, such as declines in native biodiversity (Ledgard & Paul 2008; Pawson et al. 2010; Taylor et al. 2016b), changes in soil microbial communities and nutrient cycling (Dehlin et al. 2008; Dickie et al. 2011, 2014), and altered hydrological regimes (Farley et al. 2005; Fernandez et al. 2009). Pine plantations in Patagonia became widespread beginning in the 1970s, while pine plantations were already widespread by that point in South Africa, Australia, and New Zealand (Simberloff et al. 2010). Therefore, many pine invasions across the Southern Hemisphere are likely at the stage where fire will promote invasion. Fires in the study region, and other parts of the Southern Hemisphere with introduced pines (South Africa, southeast Australia, and New Zealand), are predicted to increase in the future given climate trends and changes in land use (Holz & Veblen 2011; Moritz et al. 2012; Veblen et al. 2011; Veblen et al. 2008). Large fires in pine plantations in the study region (near Coyhaique, Chile in 2016) and in other regions invaded by *P. contorta* (Craigieburn, New Zealand 2015) occurred during recent warmer-than-average summers, which underpins the need to seriously consider the potential impact of wildfires on pine plantations and invasions. While fire is not necessary to promote pine invasions, it could certainly

increase the invasion rate and further complicate management efforts going into the future.

References

Baker, W. L. 2009. Fire Ecology in Rocky Mountain Landscapes. Island Press, Washington D.C.

Balch, J. K., B. A. Bradley, C. M. D'Antonio, and J. Gomez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980-2009). Global Change Biology **19**:173-183.

Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. Bioscience **54**:677-688.

Buckley, Y. M., B. M. Bolker, and M. Rees. 2007. Disturbance, invasion and re-invasion: managing the weed-shaped hole in disturbed ecosystems. Ecology Letters **10**:809-817.

Burns, B. R. 1993. Fire-induced dynamics of *Araucaria araucana - Nothofagus antartica* forest in the Southern Andes. Journal of Biogeography **20**:669-685.

Caplat, P., C. Hui, B. D. Maxwell, and D. A. Peltzer. 2014. Cross-scale management strategies for optimal control of trees invading from source plantations. Biological Invasions **16**:677-690.

Cóbar-Carranza, A. J., R. A. García, A. Pauchard, and E. Peña. 2015. Effects of high temperatures in the germination and seed survival of the invasive species *Pinus contorta* and two native species of South Chile. Bosque **36**:53-60.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology **88**:528-534.

Dehlin, H., D. A. Peltzer, V. J. Allison, G. W. Yeates, M. C. Nilsson, and D. A. Wardle. 2008. Tree seedling performance and below-ground properties in stands of invasive and native tree species. New Zealand Journal of Ecology **32**: 67-79.

Dickie, I. A., M. G. St John, G. W. Yeates, C. W. Morse, K. I. Bonner, K. Orwin, and D. A. Peltzer. 2014. Belowground legacies of *Pinus contorta* invasion and removal result in multiple mechanisms of invasional meltdown. AoB Plants **6**: plu056.

Dickie, I.A., G. W. Yeates, M. G. St John, B. A. Stevenson, J. T. Scott, M. C. Rillig, D. A. Peltzer, K. H. Orwin, M. U. F. Kirschbaum, J. E. Hunt, L. E. Burrows, M. M. Barbour, and J. Aislabie. 2011. Ecosystem service and biodiversity trade-offs in two woody successions. Journal of Applied Ecology **48**: 926-934.

Farley, K. A., E. G. Jobbagy, and R. B. Jackson. 2005. Effects of afforestation on water yield: a global synthesis with implications for policy. Global Change Biology **11**:1565-1576.

Fernandez, M. E., J. Gyenge, and T. Schlichter. 2009. Water flux and canopy conductance of natural versus planted forests in Patagonia, South America. Trees-Structure and Function **23**:415-427.

Gaertner, M., R. Biggs, M. Te Beest, C. Hui, J. Molofsky, and D. M. Richardson. 2014. Invasive plants as drivers of regime shifts: identifying high-priority invaders that alter feedback relationships. Diversity and Distributions **20**:733-744.

Higgins, S. I., and D. M. Richardson. 1998. Pine invasions in the southern hemisphere: modelling interactions between organism, environment and disturbance. Plant Ecology **135**:79-93.

Higgins, S. I., and D. M. Richardson. 1999. Predicting plant migration rates in a changing world: The role of long-distance dispersal. American Naturalist **153**:464-475.

Higgins, S. I., D. M. Richardson, and R. M. Cowling. 1996. Modeling invasive plant spread: The role of plant-environment interactions and model structure. Ecology **77**:2043-2054.

Holz, A., and T. T. Veblen. 2011. Variability in the Southern Annular Mode determines wildfire activity in Patagonia. Geophysical Research Letters **38**: L14710.

Howell, C. J., and K. G. McAlpine. 2016. Native plant species richness in non-native *Pinus contorta* forest. New Zealand Journal of Ecology **40**:131-136.

Johnstone, I. M. 1986. Plant invasion windows - a time-based classification of invasion potential. Biological Reviews of the Cambridge Philosophical Society **61**:369-394.

Kemp, K., P. Higuera, and P. Morgan. 2015. Fire legacies impact conifer regeneration across environmental gradients in the U.S. northern Rockies. Landscape Ecology:1-18.

Kitzberger, T., E. Araoz, J. H. Gowda, M. Mermoz, and J. M. Morales. 2012. Decreases in fire spread probability with forest age promotes alternative community states, reduced resilience to climate variability and large fire regime shifts. Ecosystems **15**:97-112.

Knapp, A. K., and J. E. Anderson. 1980. Effect of heat on germination of seeds from serotinous lodgepole pine cones. American Midland Naturalist **104**:370-372.

Langdon, B. 2011. Invasión de *Pinus contorta* Doug. ex Loud. en la Patagonia Chilena: patrones y mecanismos tras el proceso Page 103. Facultad de Ciencias Forestales. Universidad de Concepción, Concepción, Chile.

Langdon, B., A. Pauchard, and M. Aguayo. 2010. *Pinus contorta* invasion in the Chilean Patagonia: local patterns in a global context. Biological Invasions **12**:3961-3971.

Ledgard, N. 2001. The spread of lodgepole pine (*Pinus contorta*, Dougl.) in New Zealand. Forest Ecology and Management **141**:43-57.

Ledgard, N. J. 2004. Wilding conifers - New Zealand history and research background in R. L. Hill, S. M. Zydenbos, and C. M. Bezar, editors. Managing wilding conifers in New Zealand - present and future. New Zealand Plant Proetction Society Inc., Christchurch.

Ledgard, N. J., and T. S. H. Paul. 2008. Vegetation successions over 30 years of high country grassland invasion by *Pinus contorta* New Zealand Plant Protection **61**:98-104.

Mack, M. C., and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. Trends in Ecology & Evolution **13**:195-198.

Mermoz, M., T. Kitzberger, and T. T. Veblen. 2005. Landscape influences on occurrence and spread of wildfires in Patagonian forests and shrublands. Ecology **86**:2705-2715.

Moritz, M. A., M. A. Parisien, E. Batllori, M. A. Krawchuk, J. Van Dorn, D. J. Ganz, and K. Hayhoe. 2012. Climate change and disruptions to global fire activity. Ecosphere **3**:1-22.

Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology & Evolution **15**:278-285.

Nuñez, M. A., and E. Raffaele. 2007. Afforestation causes changes in post-fire regeneration in native shrubland communities of northwestern Patagonia, Argentina. Journal of Vegetation Science **18**:827-834.

Pachepsky, E., and J. M. Levine. 2011. Density dependence slows invader spread in fragmented landscapes. American Naturalist **177**:18-28.

Paritsis, J., A. Holz, T. T. Veblen, and T. Kitzberger. 2013. Habitat distribution modeling reveals vegetation flammability and land use as drivers of wildfire in SW Patagonia. Ecosphere **4**:art53.

Paritsis, J., T. T. Veblen, and A. Holz. 2015. Positive fire feedbacks contribute to shifts from *Nothofagus pumilio* forests to fire-prone shrublands in Patagonia. Journal of Vegetation Science **26**:89-101.

Pauchard, A., R. A. Garcia, E. Peña, C. Gonzalez, L. A. Cavieres, and R. O. Bustamante. 2008. Positive feedbacks between plant invasions and fire regimes: *Teline monspessulana* (L.) K. Koch (Fabaceae) in central Chile. Biological Invasions **10**:547-553.

Pausas, J. G., F. Lloret, and M. Vila. 2006. Simulating the effects of different disturbance regimes on *Cortaderia selloana* invasion. Biological Conservation **128**:128-135.

Pawson, S. M., J. K. McCarthy, N. J. Ledgard, and R. K. Didham. 2010. Density-dependent impacts of exotic conifer invasion on grassland invertebrate assemblages. Journal of Applied Ecology. **47**: 1053-1062.

Perry, G. L. W., J. M. Wilmshurst, and M. S. McGlone. 2014. Ecology and long-term history of fire in New Zealand. New Zealand Journal of Ecology **38**:157-176.

Perry, G. L. W., J. M. Wilmshurst, M. S. McGlone, D. B. McWethy, and C. Whitlock. 2012. Explaining fire-driven landscape transformation during the Initial Burning Period of New Zealand's prehistory. Global Change Biology **18**:1609-1621.

Perry, G. L. W., J. M. Wilmshurst, J. Ogden, and N. J. Enright. 2015. Exotic mammals and invasive plants alter fire-related thresholds in southern temperate forested landscapes. Ecosystems **18**:1290-1305.

Pierce, A. D., and A. H. Taylor. 2011. Fire severity and seed source influence lodgepole pine (*Pinus contorta* var. *murrayana*) regeneration in the southern cascades, Lassen volcanic National Park, California. Landscape Ecology **26**:225-237.

R Core Team (2015). R: A language and environment for statistical computing version 3.2.2. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Richardson, D. M., and W. J. Bond. 1991. Determinants of plant distribution - Evidence from pine invasions. American Naturalist **137**:639-668.

Richardson, D. M., and R. M. Cowling. 1992. Why is mountain fynbos invasible and which species invade? Pages 161-181 in B. W. van Wilgen, D. M. Richardson, F.

J. Kruger, and H. J. van Hensbergen, editors. Fire in South African Mountain Fynbos. Springer, Berlin.

Richardson, D. M., and S. I. Higgins. 1998. Pines as invaders in the southern hemisphere. Pages 450-473 in D. M. Richardson, editor. Ecology and Biogeography of *Pinus*. Cambridge University Press, Cambridge.

Richardson, D. M., P. A. Williams, and R. J. Hobbs. 1994. Pine invasion in the Southern Hemisphere: determinants of spread and invadability. Journal of Biogeography **21**:511-527.

Rossiter, N. A., S. A. Setterfield, M. M. Douglas, and L. B. Hutley. 2003. Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. Diversity and Distributions **9**:169-176.

Shackelford, N., M. Renton, M. P. Perring, and R. J. Hobbs. 2013. Modeling disturbance-based native invasive species control and its implications for management. Ecological Applications **23**:1331-1344.

Sher, A. A., and L. A. Hyatt. 1999. The disturbed resource-flux invasion matrix: a new framework for patterns of plant invasion Biological Invasions **1**:107-114.

Shigesada, N., K. Kawasaki, and Y. Takeda. 1995. Modeling stratified diffusion in biological invasions. American Naturalist **146**:229-251.

Simberloff, D., M. A. Nuñez, N. J. Ledgard, A. Pauchard, D. M. Richardson, M. Sarasola, B. W. Van Wilgen, S. M. Zalba, R. D. Zenni, R. Bustamante, E. Peña, and S. R. Ziller. 2010. Spread and impact of introduced conifers in South America: Lessons from other southern hemisphere regions. Austral Ecology **35**:489-504.

Stevens, J. T., and B. Beckage. 2009. Fire feedbacks facilitate invasion of pine savannas by Brazilian pepper (*Schinus terebinthifolius*). New Phytologist **184**:365-375.

Taylor, K. T., B. D. Maxwell, A. Pauchard, M. A. Nuñez, D. A. Peltzer, A. Terwei, and L. J. Rew. 2016a. Drivers of plant invasion vary globally: evidence from pine invasions within six ecoregions. Global Ecology and Biogeography **25**:96-106.

Taylor, K. T., B. D. Maxwell, A. Pauchard, M. A. Nuñez, and L. J. Rew. 2016b. Native versus non-native invasions: similarities and differences in the biodiversity impacts of *Pinus contorta* in introduced and native ranges. Diversity and Distributions **Early view**.

Turner, M. G., W. H. Romme, R. H. Gardner, and W. W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs **67**:411-433.

van Wilgen, B. W., and D. M. Richardson. 1985. The effects of alien shrub invasions on vegetation structure and fire behavior in South African fynbos shrublands: A simulation study. Journal of Applied Ecology **22**:955-966.

Veblen, T. T., A. Holz, J. Paritsis, E. Raffaele, T. Kitzberger, and M. Blackhall. 2011. Adapting to global environmental change in Patagonia: What role for disturbance ecology? Austral Ecology **36**:891-903.

Veblen, T. T., T. Kitzberger, E. Raffaele, M. Mermoz, M. E. Conzalez, J. S. Sibold, and A. Holz. 2008. The historical range of variability of fires in the Andean-Patagonian *Nothofagus* forest region. International Journal of Wildland Fire **17**:724-741.

Whitlock, C., D. B. McWethy, A. J. Tepley, T. T. Veblen, A. Holz, M. S. McGlone, G. L. W. Perry, J. M. Wilmshurst, and S. W. Wood. 2015. Past and present vulnerability of closed-canopy temperate forests to altered fire regimes: a comparison of the Pacific Northwest, New Zealand, and Patagonia. Bioscience **65**:151-163.

Wilensky, U. 1999. NetLogo. http://ccl.northwestern.edu/netlogo/. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL.

Zalba, S. M., Y. A. Cuevas, and R. M. Boo. 2008. Invasion of *Pinus halepensis* Mill. following a wildfire in an Argentine grassland nature reserve. Journal of Environmental Management **88**:539-546.

CHAPTER 6

CONCLUSION

In this conclusion I will first summarize the contribution that this work has made towards the study of context dependence and feedbacks and regime shifts in biological invasions. I will then suggest several avenues for continued study on the topic of pine invasions. Finally, I will discuss the management implications derived from the results of this dissertation.

Context Dependence

A major conclusion from this dissertation is that invasion age and local biotic context are important in explaining differences between invasion patterns and impacts across regions. Our studies focused on first understanding the context dependence of the invasion – where will *P. contorta* invade or not invade and are there invasion patterns that can we generalize? We then examined the context dependence of impacts. For example, while *P. contorta* will invade into both steppe and *Araucaria* forest, are the invasion impacts consistent across ecosystem types and biogeographic regions?

Our results suggest that steppe and grassland vegetation is most at risk of 1) being heavily invaded, 2) experiencing declines in native plant richness and cover, and 3) having increased fuel loads that could alter fire behavior and effects and post-fire recovery, even in fire-adapted sites. Therefore our results support the idea that novel life forms can most easily invade and have impacts in areas where that life form did not dominate previously (i.e. tree in a grass/shrubland; Levine et al. 2003). The consistency

of invasion and impacts across steppe- and grass-dominated sites on different continents suggests that pines invading into steppe ecosystems may constitute an "invasion syndrome" (Kueffer et al. 2013). In other words, we are likely to see significant levels of invasion and impacts in similar settings on other continents.

Even where trees are not a novel life form, we still observed significant pine invasion in some systems. *Nothofagus* forests experienced drastically different patterns of pine invasion than *Araucaria araucana* forests. Little to no invasion was observed in *Nothofagus* forests in South America and New Zealand, and impacts on plant communities in *Nothofagus* forests were limited due to *P. contorta*'s inability to invade this forest type. In contrast, invasion densities in the *Araucaria* forest were high. Although plantations in *Araucaria* forest were older than at many of the steppe sites, distance to initial plantation was still the most important factor explaining invasion density at this site. Thus, pine seed dispersal may be slower in *Araucaria* forest, potentially due to reduced wind flow through the canopy compared with the treeless sites, resulting in very high pine densities close to plantations but overall a rapid decline in density with increasing distance from the source. This situation contrasts markedly with other invasions of the same age in open habitats where high pine densities were found at great distances from the plantations. Additionally, although the *Araucaria* forest was readily invaded, the impacts on native understory communities were less apparent than in steppe environments. Therefore, a gradient of sites could be prioritized for management based on the potential for and consequences of pine invasion in different plant

communities. Although, the protected status of *Araucaria araucana* as an iconic and culturally important species in Chile may warrant more concern across its range.

Overall, the composition of the native vegetation community was enormously important in determining the patterns and extent of *P. contorta* invasion, as well as the strength of the impacts. Understanding the specific biological context is important in assessing the potential for invasions and invasion impacts. Although previous work has focused on the importance of propagule pressure in invasion success (Lockwood et al. 2005; Simberloff 2009), we found that propagule pressure does not always overwhelm other factors and that the biotic context can determine the extent of invasion even in areas with high propagule pressure.

In addition to context dependence based on native biotic communities, we also found context dependence based on the stage of invasion (Kueffer et al. 2013). Theoharides and Duke (2007) suggested that the failure of many studies to find a consistent suite of factors promoting invasion success was due to the fact that most studies compare invasions at different stages. Our results support this assertion because we found that early in pine invasion, propagule pressure dominated as a primary factor determining invasion density. In later stages of invasion, patterns of pine density were largely described by native vegetation patterns. Thus, our conclusions support the theoretical model proposed by Dietz and Edwards (2006) that drivers of invasion change over time and that habitat factors such as native vegetation become more important than propagule pressure at later invasion stages.

Detailed observational studies, such as ours, that elucidate specific patterns are necessary to further our understanding of invasion biology and develop targeted hypotheses. Without field observations, it is not possible to know which experiments will elucidate the mechanisms and processes governing invasion. For example, experiments now should focus on the differences in invasion level between areas dominated by *Auracaria araucana* and *Nothofagus* forests. One hypothesis for the difference between the two forest types is that competition between *Nothofagus* specific and *Pinus* specific ectomycorrhizae may limit *P. contorta* establishment in *Nothofagus* forests even when sufficient bareground and sunlight (open niche) is available. *A. araucana* does not form associations with ectomycorrhizae (Diehl & Fontenla 2010) leaving a vacant niche for *Pinus* specific ectomycorrhizae and consequently this forest type is susceptible to invasion. The large spatial and long time scales of tree invasions make observational studies imperative given the likelihood that small-scale, short-term experiments will miss important processes governing these invasions (Sagarin & Pauchard 2012). Observational approaches make ecological theories more valuable by validating them with real data (Sagarin & Pauchard 2012), as seen by comparison of our results to those predicted by various theoretical invasion frameworks.

Feedbacks & Regime Shifts

Our investigation has made a significant contribution to the study of regime shifts and invasive plant-fire feedbacks because few studies have examined the specific mechanisms that cause positive feedbacks between woody invasions and fire (Gaertner et al. 2014; Stevens & Beckage 2009). Furthermore, by identifying the invasion threshold

above which a positive feedback between *P. contorta* and fire is likely, we provide a quantitative examination of actual thresholds in the field, which is relatively rare. In our study, post-fire *P. contorta* density increased rapidly when pre-fire plots had pine densities above the invasion threshold and plant community composition shifted dramatically, rather than gradually, once the invasion threshold was crossed. Additionally, at certain sites fuel loads were low until a certain invasion age was reached and then they increased dramatically, suggesting a mechanism for the post-fire *P. contorta* density threshold. Once invasions cross a density or age threshold, high fuel loads increase fire severity, decreasing post-fire native plant recovery. The result is dense *P. contorta* invasion. Although changes in fuel loads and fire behavior due to plant invasions have been well studied (Brooks et al. 2004; Mandle et al. 2011), our project took the next step of examining the how feedbacks between fire and invasion alter invasion rates over time. To our knowledge this topic has only been addressed in one other study (Stevens & Beckage 2009). Our simulation model showed that the increase in *P. contorta* establishment after fire outweighed the fire-induced *P. contorta* mortality, and the high density in post-fire cohorts resulted in faster *P. contorta* spread across the landscape.

Future Questions

This dissertation raises further questions regarding the patterns of invasion. For example, we found significant correlations between climate and invasion density; however, this issue needs to be more closely examined to determine the relative role of climate in shaping spatial patterns of pine invasion. Additionally, it would be interesting

to compare the climate niche in the introduced range with that in the native range to determine if climate variability influences rates of pine invasion in the same way in different settings. This information may help predict other areas where invasions would be likely. It would also be interesting to compare the suite of past climate conditions that governed the expansion of *P. contorta* in the early Holocene with current climate conditions (Iglesias et al., 2015) with those that support *P. contorta* spread in its introduced range. In this context, it is important to separate those climate drivers responsible for invasion success (establishment and spread) from non-climatic factors to better predict how changing climate may alter pine invasion success in the future. To address these types of climate questions, we would need climate data as well as pine invasion densities and spread rates adjacent to a range of plantations, including those experiencing no pine invasion, to gain a broader understanding of the climate dimensions that govern invasion.

An important question for the future is how the genetic background of the source populations affects spread rates and adaptation to different abiotic conditions. In other types of pine invasions, certain genotypes have been found to be more invasive than others depending on the climate setting (Zenni et al. 2014). Similar genetic patterns may exist for *P. contorta* and understanding these could help explain variability in invasion success across sites. Additionally, linking certain genes to physiological traits that make the pines more invasive in certain settings would be a powerful way to connect processes leading to invasion across scales (genes to landscape).

Another issue that we did not thoroughly address is the importance of soil abiotic and biotic characteristics in mediating invasion success. Studies have described mycorrhizae or soil feedbacks in pine invasions (Gundale et al. 2014; Hayward et al. 2015; Nuñez et al. 2009), but the importance of mycorrhizae, soil pathogens, soil nutrients or physical properties relative to vegetation type, propagule pressure and climate in explaining pine invasion success is unknown. Furthermore, the interactions between *Nothofagus* and *Pinus* specific ectomycorrhizae (Dickie et al. 2010) and the consequent potential for driving pine invasions should be explored.

While we found strong resistance of certain native vegetation types to pine invasion, it would be interesting to use experimental approaches to determine what level of propagule pressure or disturbance is necessary to overcome biotic resistance. Such studies could influence management decision making by helping prioritize areas for monitoring that are not currently invaded but could become invaded at higher levels of propagule pressure.

Future studies on the impacts of pine invasions should focus on the mechanisms explaining the decline in species richness and cover that we observed with increasing pine cover and how these mechanisms shift in importance among ecosystem types or native species. For example, experiments to determine the relative importance of shade versus increased litter could be conducted. Furthermore, biogeochemical studies of changes in soil nutrient cycling beneath invading pine stands could determine if a shift in litter composition has cascading impacts on belowground communities in Patagonia, as found in New Zealand (Dehlin et al. 2008; Dickie et al. 2014; Dickie et al. 2011).

Furthermore, indirect impacts of an invader, such as changes in fire frequency, deserves more study. Future studies on the impacts of pines on fire regimes should examine trends of fire severity and spread in areas of pine invasion or plantations relative to uninvaded areas. Understanding the extent to which the natural disturbance regime has been altered is especially important because pine plantations are often located next to fire-sensitive *Nothofagus* forest in New Zealand and Patagonia. If the presence of pine results in more burning of native forests, this could have significant implication for conservation efforts to protect native biodiversity. Fire is already increasing in these regions as a result of climate changes and increased human ignitions (Holz & Veblen 2011; Veblen et al. 2011).

A final direction of study would be to build on the information that we gained on trends and patterns of invasion for *P. contorta* and how that compares with those of other introduced tree species. Understanding how *P. contorta* invasions are similar or different to other tree invasions could help to better comprehend the most important processes in tree invasions. An important applied question that remains unanswered is, why is *P. ponderosa* not invading as rapidly as *P. contorta* in the Southern Hemisphere and might it become invasive in the future? This is an extremely important question given the land area currently being planted into *P. ponderosa* plantations throughout Patagonia.

Management Implications

Identifying a threshold response in pine invasions has practical implications, because it suggests that pine invasions should be managed before they reach a tree density where significant impacts on fire behavior and a reduction of native plant species

diversity are likely to occur. We found that pine invasions with densities above the threshold (1,000 trees/ha) can have transformative impacts on several aspects of the invaded ecosystems (fire risk, biodiversity). Once a threshold is crossed it will likely be more difficult to restore native ecosystems due to the loss of species richness and native plant cover. In addition, the risk of a positive feedback with fire, in which pines promote larger and more severe fires and then dominate the post-fire community, becomes more likely. A similar situation has been observed with *Pinus halepensis* invasions in Argentina, where areas where young pine were manually cleared were able to return to a plant species composition that was similar to adjacent uninvaded areas (Cuevas & Zalba 2010. Areas where older pines were cleared maintained an altered species composition (Cuevas & Zalba 2010). Similar legacy effects after the removal of pines have also been observed in New Zealand where after older invasions were removed the plant community did not return to the pre-invasion state but instead was dominated by exotic herbaceous species (Dickie et al. 2014). Our results identify an invasion threshold that results in altered species composition, even without fire. In our study systems, pine management once this threshold has been crossed may not result in a return to pre-invasion native communities. Therefore, in terms of maintaining biodiversity and managing fire risk, it is important to maintain *P. contorta*, and probably other invasive pine species, at low densities. As scientists, it is our natural inclination to proceed with caution, highlight uncertainty, and weigh the benefits and costs of management. However, pine invasions can and likely will transform steppe and grassland ecosystems (Chapters 2-4) and we should try to manage them as soon as possible.

Pine invasions present one of the largest invasive plant management problems in the world, in terms of the transformative nature of these invasions particularly into non-forest habitats and the costs associated with management (Le Maitre et al. 2002; Ledgard 2001; Marais et al. 2004; van Wilgen & Richardson 2014). Observed pine invasions in New Zealand and South Africa suggest that managers in Patagonia should act now to prevent major invasion and species diversity loss (Richardson et al. 2008; Simberloff et al. 2010). Costs to remove invasive trees increases sharply with increasing invasion densities (Ledgard 2001; Marais et al. 2004). Other analyses have also suggested that the expense of early control efforts will greatly reduce future management costs and increase the likelihood of success over the long term (Stephens 2004). In New Zealand, the advanced stage of the pine invasions leaves few management options (Ledgard 2004) beyond the use of potent herbicide mixes (e.g. “Lucifer” and “Armageddon”) and physical removal (Fig. 6.1). The barren clearcuts that result from removal are rapidly recolonized by *P. contorta* (Ledgard 2001), which only exacerbates the problem. An obvious way to prevent this recolonization is to remove the source plantations for the most invasive species (i.e. *P. contorta*) now (Ledgard 2001; van Wilgen & Richardson 2012, 2014). Once the source populations have been removed, managing invading adult trees may have a significant impact. More urgent management effort may be particularly desirable in places such as Bariloche, Argentina that are experiencing growing outdoor recreation and exurban development in places with increased human-ignited fires (Veblen et al. 2011). If management is undertaken now to prevent invasions from reaching the threshold density, then perhaps invasion can be slowed. For the moment *Pinus ponderosa*

appears to be less invasive and could be a good substitute forest industry species following removal of the *P. contorta* plantations. *P. ponderosa* plantation edges would need to be monitored in case a budding invasion is currently in the lag phase. *Pinus ponderosa* plantations have also been found to promote soil conditions that are more similar to native Patagonian forests than *P. contorta* plantations (Fajardo & Gundale 2015) suggesting that there may be better restoration potential or opportunities for native plants to establish in the understory in *P. ponderosa* plantations.

Figure 6.1 Photo from Flock Hill Station and Craigieburn Forest Park New Zealand showing areas invaded by *P. contorta* and areas where significant management has occurred to remove the pines. In the foreground the flat areas are dominated by regrowth of *P. contorta* after attempted management. The gray area devoid of vegetation in the center of the photo was a *P. contorta* plantation that has been removed, but little to no vegetation recovery has occurred there.

Pines in the Southern Hemisphere have been called “conflict-generating species” in terms of management because they are both useful and invasive (van Wilgen & Richardson 2014). Differences in perception among stakeholders can be complicated but

are necessary to consider in management decision making (Garcia-Llorente et al. 2008; van Wilgen & Richardson 2014). In New Zealand land owners are usually reluctant to spend money on invasive conifer control, except in the case of loss of forage land or neighbor complaints, and occasionally landowners will wait to control the trees on purpose to try to make money from the timber harvest (although this is not always profitable; Bowman 2004). A major issue in Patagonia is increasing the recognition that pine invasions need to be managed (Richardson et al. 2008).

Once it is recognized that some form of management needs to be undertaken, the major issue becomes determining how to manage and who should pay for management (Holl & Howarth 2000). Should the land owner, forestry company, national forest service, park service or local government pay for the removal of pines and is there a way for the removal to pay for itself? Often the negative effects of invasive pines are externalized and it is the adjacent landowners, and not the forestry companies, who pay the price for the impacts (loss of biodiversity, loss of forage, increased fire risk) and management of invasion (van Wilgen & Richardson 2014). In New Zealand both the landowner and the owner of the seed source which has created the problem are legally responsible to pay to remove invading conifers (Bowman 2004). In practice however, landowners are reluctant (or cannot afford) to pay for management of a problem they did not create, particularly when the seed source is on government-owned land (Bowman 2004). On the other hand, government funded programs to remove invasive tree species in both South Africa (van Wilgen et al. 2012) and New Zealand (Burrows, L. personal communication) have only addressed small areas despite significant spending (Froude

2011; Harding 2001). Local examples of successful management have occurred in New Zealand in areas where landowners, local and national government, and other groups have collaborated to create a management plan, seek funding from all possible sources, and promote volunteer work pulling conifers on the invasion front (Mid Dome Wilding Trees Management Group & Mid Dome Wilding Conifer Trust; Bowman 2004). While it seems logical that commercial use of the invasive trees could help to control invasions, there are currently no successful examples of this type of program (van Wilgen & Richardson 2014) and forestry companies doubt the profitability of this type of harvesting (Dyck 2004).

In addition to determining the best way to pay for management, it is also important to consider the best management strategy. Management should not be haphazard. Invasive pine management in New Zealand without a management plan resulted in a waste of well-intentioned efforts, poor use of limited resources, and disillusioned stakeholders (Ledgard 2004). Similarly, in Nahuel Huapi National Park in Argentina, pine management efforts are haphazard and do not identify the most vulnerable locations (Sample, M. personal communication). Targeted management of invading populations that are furthest from the source or in areas of high habitat quality will be the most effective (Caplat et al. 2014). It is important to consider the likelihood of spread and impacts when deciding if management of pines is necessary. A nation-wide plan to manage wilding conifers was recently published in New Zealand (New Zealand MPI 2014). A comprehensive monitoring and management strategy should also be developed in Patagonia. This type of plan could help identify management objectives and

strategies in ways to make it most effective, although it remains unclear how to fund this type of project. It is also unclear if there is consensus among stakeholders (local residents, forestry companies and government officials) as to whether or not invasive pines are problematic and if they are, what to do with them. Many social and management questions remain unanswered and were not addressed by this study, but are clearly important next steps.

Although New Zealand and Patagonia are different ecologically and culturally, lessons should still be drawn from New Zealand and elsewhere around the world where pines have become a growing large management problem (Richardson et al. 2008; Simberloff et al. 2010; van Wilgen & Richardson 2014). Two of the main lessons from New Zealand are: 1) where possible pine invasions should be managed at an early stage to ensure the highest potential for management success (as discussed above), and 2) management actions should be guided by what is desired on the landscape following pine removal, rather than just by the objective of killing pines. Planning for desired outcomes and trying to restore or promote succession of native plant communities may be more expensive in terms of time and money up front, but it is likely to save both time and money over the long run, rather than repeating the same management strategy every five years when *P. contorta* recolonizes managed areas (Fig. 6.1). We found that certain types of native vegetation (dense grass, tall shrubs, southern beech forests) are highly resistant to invasion and therefore it may make sense to invest in longer term solutions that promote the growth of these invasion resistant plant communities rather than just repeatedly spraying and cutting trees.

The question of what type of vegetation is desired where pines are currently dominant is especially difficult in the South Island of New Zealand and the Aysén Region of Chile where deforestation resulted from human-caused fires and created anthropogenic grasslands (McWethy et al. 2010; Quintanilla Pérez 2008). In these areas pines are often invading into grasslands, dominated by non-native species, that were established and maintained for grazing by the early European settlers or into native tussock grasslands that are culturally and economically important (Harding 2001). It is difficult in restoration projects to justify what time period is the target for restoration (i.e. back 50 years, 100 years, before human occupation, etc.) and instead it has been suggested that we should move on from the notion that we can return ecosystems to some prior static state (Hobbs et al. 2011). Human value judgements based on land management goals need to be made that will determine which types of vegetation are desired in these areas that are currently dominated by pines. Although these are tough decisions, it is preferable to recognize the subjective human component of restoration (Higgs 1997) and express desired outcomes, rather than focusing on killing pines and leaving the end goals undefined.

The management goal will determine the restoration strategy and potential for success. Where grazing is the main management goal, restoration may simply involve cutting trees and then sowing aggressive forage grasses and applying fertilizer, as this is an effective way to prevent *P. contorta* seedling establishment (Ledgard 2006). In situations where the land management goals are more conservation oriented, decisions need to be made about the desired vegetation type. In some cases, abandoned pine

plantations or invasions have been colonized by native forest species (Brockerhoff et al. 2003; Howell & McAlpine 2016). In other cases, underplanting of native tree seedlings resulted in successful establishment, particularly with further management treatments such as creating canopy gaps (Forbes et al. 2015a; Forbes et al. 2015b). Stem poisoning *P. radiata* and leaving the dead trees standing also resulted in significant native species colonization in the understory, whereas felling and harvesting *P. radiata* stands led to recolonization by *P. radiata* and other exotic species (Paul & Ledgard 2009). Pine plantations can create soil conditions more suitable for the return of native tree species than found in the historically burned areas now dominated by grass (Fajardo & Gundale 2015). Many native woody species in New Zealand have difficulty establishing in competition with pasture species, and *Nothofagus solandri* var. *cliffortioides* seedlings may have lower survival in areas with little shade (Ledgard & Davis 2004; Wiser et al. 1997). In areas where *P. contorta* was felled and native *N. solandri* var. *cliffortioides* seedlings were planted, they successfully established beneath the shade and protection of the fallen pines (Ledgard, N. personal communication). Therefore, if the management goal is to reestablish forests in areas recently dominated by grass or shrublands, pine invasions may actually provide a suitable transitional state in which to try to establish native trees. Over long time periods, these native trees may eventually overtop and outcompete the shade intolerant *P. contorta* (Howell & McAlpine 2016). However, the results will also depend on climate, with native species more likely to colonize pine understories where precipitation is higher (Paul & Ledgard 2009). While there is some opportunity for more widespread restoration based on native plant colonization of pine

understories, it is important to recognize that in areas with a long history of deforestation, native propagule supply is often limited and introducing seedlings may be expensive and time intensive (Coomes et al. 2003). Additionally, in many areas *P. contorta* is extremely dense and so thinning or complete removal may need to occur before native species can be established (Forbes et al. 2015a). Furthermore, soil legacies may promote competitive exotic pasture species over native woody species (Dickie et al. 2014) and introduced herbivores also prevent native tree recovery (Coomes et al. 2003). Therefore, more experimentation is necessary before this type of restoration is implemented at larger scales (Froude 2011).

In areas where the desired outcome is a return to native grassland or shrubland, restoration may be more difficult because these areas are readily reinvaded by *P. contorta*. There is some evidence that microsites adjacent to felled pines create conditions that promote growth of the native grass *Festuca novae-zelandiae* and the exotic grass *Anthoxanthum odoratum*, as well as native shrubs, relative to nearby uninvaded grasslands (Paul & Ledgard 2008). However, there is also evidence that this effect may be short lived (< 10 years) and ultimately result in lower diversity in the plots with felled pines than uninvaded plots (Paul & Ledgard 2009).

In some situations, such as Craigieburn on South Island, New Zealand, it may be necessary to ask if management is feasible and what benefits would be gained from extensive management operations in that region. Perhaps a “novel ecosystem” (Hobbs et al. 2009) has emerged that should be accepted and contained (Ledgard 2001). I know this is a controversial subject, but given the density and extent of *P. contorta* in that area,

despite hundreds of thousands of dollars spent on control annually (Froude 2011; Harding 2001), I think it is a necessary question. While some argue that the concept of novel ecosystems is just an excuse to stop trying to manage invasive species (Murcia et al. 2014), I think there is value in discussing alternative management goals and actions if current management practices are ineffective. In any type of management intervention, it is important to be explicit both about the goals and the possibility of achieving them (Hobbs et al. 2011). Tree invasions are inherently difficult to manage for social, economic and ecological reasons, and therefore, adaptive management that focuses on experimenting with alternative management options, monitoring success and engaging diverse stakeholders is the only possible strategy that will lead to successful outcomes.

Epilogue

My views on invasive species have evolved through the course of my PhD research. Although I came into this study with the idea that invasions may only be a problem where land is mismanaged and heavily impacted by human use, my first trip to New Zealand dispelled this idea. The pine invasions there were a stark contrast to our relatively uninvaded mountain systems in the Greater Yellowstone Ecosystem. After studying pine invasions across such a range of land-use types with different histories, I am more inclined to think that some invasive plants can have significant impacts. I appreciate the work that Simberloff and others have done to increase public and political awareness of invasive species and their potential impacts, but now that many people are generally aware of invasive species, I think there is an opportunity to promote a more nuanced view of exotic species and their management. Working in the Invasive Plant

Ecology and Management Lab has taught me to consider the impacts of weed management as much as the impacts of the weeds themselves and I think this is an issue that needs to become more prevalent in land management world. This idea of trying to understand when, where, and if management is necessary and what the impacts of it will be, is an important perspective that can be carried across subjects and my future work. For example, forest managers often manage after wildfires, but is this necessary? In many cases it probably is not and in some cases may do more harm than good.

Throughout my project I have interacted with a diversity of people with differing views on invasions and this experience has significantly broadened my perspective. Working with paleoecologists has made me step back and think about issues across a longer time scale than most ecologists. This is a valuable skill that is important in the context of all types of environmental change. In the case of invasions, it has made me occasionally question the difference between historic range expansions and current invasions. Yes, technically by definition current invasions stem from human introductions of species. But humans are part of ecological systems (and have been for thousands of years) so is it that different for humans to introduce species than for birds to spread seeds across oceans and continents? I know that humans are spreading more species more rapidly than has happened by non-human long distance dispersal in the past, but does this negate the fact that humans are ecological agents? On the other hand, working with people in the Southern Hemisphere who watch pines take over their native systems made me better understand the urgency and strong emotional response that plant invasions can cause. If an exotic tree was threatening the sagebrush steppe in the

Intermountain West I would be less inclined to see it as an opportunity to test ecological theories and more inclined to try to manage the invasion immediately.

Often when we try to answer the question why we care about biological invasions, we resort to putting the impacts or benefits in economic terms (e.g. monetizing ecosystem services, calculating costs of control, or economic gains from exotic plantations). It is not possible to monetize all the benefits of biodiversity and when we attempt to do this we validate the utilitarian ethic that sees nature only through the lens of how it might benefit humans. I agree with the ideas promoted by Aldo Leopold, Ricardo Rozzi, and others that in order to best deal with environmental problems we need to 1) recognize that humans are part of the system, and 2) accept that values that do not have an economic basis are equally valid as the ones that do. Personally, I inherently value biodiversity and would like to see species introductions limited on the basis that the more species that are introduced the more likely it is that one will become highly invasive and reduce native biodiversity. I would not want to see the same homogenized biota everywhere in the world and I think many people share this sentiment. While there are proven ecological and economic benefits to maintaining biodiversity, there are also cultural and ethical reasons that are equally valuable (Rozzi 2013).

Working on a large project that crossed disciplinary and cultural boundaries increased my ability to see issues from diverse perspectives, both scientifically and socially. This ability will help in all future scientific endeavors I undertake. I greatly appreciate the different skills and expertise of my committee members and other members of WildFIRE PIRE. Working on a large interdisciplinary project such as

WildFIRE PIRE has prompted me to think about questions from angles other than just those of an invasion biologist. I know that my graduate experience was greatly enhanced by the opportunity to interact with so many diverse experts. As a detail-oriented person I feel that in a different lab I could have focused too much on my individual questions. I am grateful for my experience which instead forced me to consider how my small pieces of the puzzle fit into a broader context.

References

Bowman, R.G. (2004) Responsibilities of local government in wilding conifer management *Managing wilding conifers in New Zealand: Present and future* (ed. by R.L. Hill, S.M. Zydenbos and C.M. Bezar), pp. 45-53. New Zealand Plant Protection Society, Christchurch.

Brockerhoff, E.G., Ecroyd, C.E., Leckie, A.C. & Kimberley, M.O. (2003) Diversity and succession of adventive and indigenous vascular understorey plants in *Pinus radiata* plantation forests in New Zealand. *Forest Ecology and Management*, **185**, 307-326.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M. & Pyke, D. (2004) Effects of invasive alien plants on fire regimes. *Bioscience*, **54**, 677-688.

Caplat, P., Hui, C., Maxwell, B.D. & Peltzer, D.A. (2014) Cross-scale management strategies for optimal control of trees invading from source plantations. *Biological Invasions*, **16**, 677-690.

Coomes, D.A., Allen, R.B., Forsyth, D.M. & Lee, W.G. (2003) Factors preventing the recovery of New Zealand forests following control of invasive deer. *Conservation Biology*, **17**, 450-459.

Cuevas, Y.A. & Zalba, S.M. (2010) Recovery of Native Grasslands after Removing Invasive Pines. *Restoration Ecology*, **18**, 711-719.

Dehlin, H., Peltzer, D.A., Allison, V.J., Yeates, G.W., Nilsson, M.-C. & Wardle, D.A. (2008) Tree seedling performance and below-ground properties in stands of invasive and native tree species. *New Zealand Journal of Ecology*, **32**, 67-79.

Dickie, I.A., Bolstridge, N., Cooper, J.A. & Peltzer, D.A. (2010) Co-invasion by *Pinus* and its mycorrhizal fungi. *New Phytologist*, **187**, 475-484.

Dickie, I.A., St John, M.G., Yeates, G.W., Morse, C.W., Bonner, K.I., Orwin, K. & Peltzer, D.A. (2014) Belowground legacies of *Pinus contorta* invasion and removal result in multiple mechanisms of invasional meltdown. *AoB Plants*, **6**, plu056.

Dickie, I.A., Yeates, G.W., St John, M.G., Stevenson, B.A., Scott, J.T., Rillig, M.C., Peltzer, D.A., Orwin, K.H., Kirschbaum, M.U.F., Hunt, J.E., Burrows, L.E., Barbour, M.M. & Aislabie, J. (2011) Ecosystem service and biodiversity trade-offs in two woody successions. *Journal of Applied Ecology*, **48**, 926-934.

Diehl, P. & Fontenla, S.B. (2010) Arbuscular mycorrhizal infection in two morphological root types of *Araucaria araucana* (Molina) K. Koch. *Revista Argentina De Microbiologia*, **42**, 133-137.

Dietz, H. & Edwards, P.J. (2006) Recognition that causal processes change during plant invasion helps explain conflicts in evidence. *Ecology*, **87**, 1359-1367.

Dyck, W.J. (2004) A forestry industry view of wilding conifers and options for their control *Managing wilding conifers in New Zealand: Present and future* (ed. by R.L. Hill, S.M. Zydenbos and C.M. Bezar), pp. 41-44. New Zealand Plant Protection Society, Christchurch.

Fajardo, A. & Gundale, M.J. (2015) Combined effects of anthropogenic fires and land-use change on soil properties and processes in Patagonia, Chile. *Forest Ecology and Management*, **357**, 60-67.

Forbes, A.S., Norton, D.A. & Carswell, F.E. (2015a) Underplanting degraded exotic *Pinus* with indigenous conifers assists forest restoration. *Ecological Management & Restoration*, **16**, 41-49.

Forbes, A.S., Norton, D.A. & Carswell, F.E. (2015b) Artificial canopy gaps accelerate restoration within an exotic *Pinus radiata* plantation. *Restoration Ecology*, **Early View.**

Froude, V.A. (2011) Wilding conifers in New Zealand: Status report. Report prepared for the Ministry of Agriculture and Forestry. Pacific Eco-Logic, Bay of Islands.

Gaertner, M., Biggs, R., Te Beest, M., Hui, C., Molofsky, J. & Richardson, D.M. (2014) Invasive plants as drivers of regime shifts: identifying high-priority invaders that alter feedback relationships. *Diversity and Distributions*, **20**, 733-744.

Garcia-Llorente, M., Martin-Lopez, B., Gonzalez, J.A., Alcorlo, P. & Montes, C. (2008) Social perceptions of the impacts and benefits of invasive alien species: Implications for management. *Biological Conservation*, **141**, 2969-2983.

Gundale, M., Kardol, P., Nilsson, M.C., Nilsson, U., Lucas, R.W. & Wardle, D.A. (2014) Interactions with soil biota shift from negative to positive when a tree species is moved outside its native range. *New Phytologist*, **2**, 415-421.

Harding, M. (2001) South Island Wilding Conifer Strategy. Department of Conservation, Christchurch.

Hayward, J., Horton, T.R., Pauchard, A. & Nunez, M.A. (2015) A single ectomycorrhizal fungal species can enable a Pinus invasion. *Ecology*, **96**, 1438-1444.

Higgs, E.S. (1997) What is good ecological restoration? *Conservation Biology*, **11**, 338-348.

Hobbs, R.J., Higgs, E. & Harris, J.A. (2009) Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution*, **24**, 599-605.

Hobbs, R.J., Hallett, L.M., Ehrlich, P.R. & Mooney, H.A. (2011) Intervention Ecology: Applying Ecological Science in the Twenty-first Century. *Bioscience*, **61**, 442-450.

Holl, K.D. & Howarth, R.B. (2000) Paying for restoration. *Restoration Ecology*, **8**, 260-267.

Holz, A. & Veblen, T.T. (2011) Variability in the Southern Annular Mode determines wildfire activity in Patagonia. *Geophysical Research Letters*, **38**, L14710.

Howell, C.J. & McAlpine, K.G. (2016) Native plant species richness in non-native *Pinus contorta* forest. *New Zealand Journal of Ecology*, **40**, 131-136.

Iglesias, V., Krause, T.R. & Whitlock, C. (2015) Complex Response of White Pines to Past Environmental Variability Increases Understanding of Future Vulnerability. *Plos One*, **10**, e0124439.

Kueffer, C., Pysek, P. & Richardson, D.M. (2013) Integrative invasion science: model systems, multi-site studies, focused meta-analysis and invasion syndromes. *New Phytologist*, **200**, 615-633.

Le Maitre, D.C., van Wilgen, B.W., Gelderblom, C.M., Bailey, C., Chapman, R.A. & Nel, J.A. (2002) Invasive alien trees and water resources in South Africa: case studies of the costs and benefits of management. *Forest Ecology and Management*, **160**, 143-159.

Ledgard, N. (2001) The spread of lodgepole pine (*Pinus contorta*, Dougl.) in New Zealand. *Forest Ecology and Management*, **141**, 43-57.

Ledgard, N. & Davis, M. (2004) Restoration of mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest after fire. *New Zealand Journal of Ecology*, **28**, 125-135.

Ledgard, N.J. (2004) Wilding conifers - New Zealand history and research background. *Managing wilding conifers in New Zealand - present and future* (ed. by R.L. Hill, S.M. Zydenbos and C.M. Bezar). New Zealand Plant Proetction Society Inc., Christchurch.

Ledgard, N.J. (2006) Determining the effect of increasing vegetation competition through fertiliser use on the establishment of wildings in unimproved high country grassland. *New Zealand Journal of Forestry*, **51**, 29-34.

Levine, J.M., Vila, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society B*, **270**, 775-781.

Lockwood, J.L., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution*, **20**, 223-228.

Mandle, L., Bufford, J.L., Schmidt, I.B. & Daehler, C.C. (2011) Woody exotic plant invasions and fire: reciprocal impacts and consequences for native ecosystems. *Biological Invasions*, **13**, 1815-1827.

Marais, C., van Wilgen, B.W. & Stevens, D. (2004) The clearing of invasive alien plants in South Africa: a preliminary assessment of costs and progress. *South African Journal of Science*, **100**, 97-103.

McWethy, D.B., Whitlock, C., Wilmshurst, J.M., McGlone, M.S., Fromont, M., Li, X., Dieffenbacher-Krall, A., Hobbs, W.O., Fritz, S.C. & Cook, E.R. (2010) Rapid landscape transformation in South Island, New Zealand, following initial Polynesian settlement. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 21343-21348.

Murcia, C., Aronson, J., Kattan, G.H., Moreno-Mateos, D., Dixon, K. & Simberloff, D. (2014) A critique of the 'novel ecosystem' concept. *Trends in Ecology & Evolution*, **29**, 548-553.

New Zealand Ministry for Primary Industries. 2014. New Zealand Wilding Conifer Management Strategy 2015-2030. The right tree in the right place. http://www.wildingconifers.org.nz/images/wilding/articles/2014_new_zealand_wilding_conifer_management_strategy_2.pdf.

Nuñez, M.A., Horton, T.R. & Simberloff, D. (2009) Lack of belowground mutualisms hinders Pinaceae invasions. *Ecology*, **90**, 2352-2359.

Paul, T.H.S. & Ledgard, N.J. (2008) Effect of felled wilding pines on plant growth in high country grasslands. *New Zealand Plant Protection*, **61** 105-110.

Paul, T.H.S. & Ledgard, N.J. (2009) Vegetation successions associated with wilding conifer removal. *New Zealand Plant Protection*, **62** 374-379.

Quintanilla Pérez, V. (2008) Perturbaciones a la vegetación nativa por grandes fuegos de 50 años atrás, en bosques Nordpatagónicos. Caso de estudio en Chile Meridional. *Anales de Geografía*, **28**, 85-104.

Richardson, D.M., van Wilgen, B.W. & Nuñez, M.A. (2008) Alien conifer invasions in South America: short fuse burning? *Biological Invasions*, **10**, 573-577.

Rozzi, R. (2013) Biocultural Ethics: From Biocultural Homogenization Toward Biocultural Conservation *Linking Ecology and Ethics for a Changing World* (ed. by R.P. Rozzi, S.T.A.Palmer, C.Armesto, J. J.Callicott, J.B.), pp. 9-32. Springer Netherlands, Dordrecht.

Sagarin, R. & Pauchard, A. (2012) *Observation and Ecology: Broadening the Scope of Science to Understand a Complex World*. Island Press, Washington.

Simberloff, D. (2009) The Role of Propagule Pressure in Biological Invasions. *Annual Review of Ecology Evolution and Systematics*, pp. 81-102. Annual Reviews, Palo Alto.

Simberloff, D., Nuñez, M.A., Ledgard, N.J., Pauchard, A., Richardson, D.M., Sarasola, M., Van Wilgen, B.W., Zalba, S.M., Zenni, R.D., Bustamante, R., Peña, E. & Ziller, S.R. (2010) Spread and impact of introduced conifers in South America: Lessons from other southern hemisphere regions. *Austral Ecology*, **35**, 489-504.

Stephens, R.T.T. (2004) Wilding conifer control: how important is it relative to other conservation actions? . *Managing wildling conifers in New Zealand: present and future* (ed. by R.L. Hill, S.M. Zydenbos and C.M. Bezar), pp. 27-39. New Zealand Plant Protection Society, Christchurch.

Stevens, J.T. & Beckage, B. (2009) Fire feedbacks facilitate invasion of pine savannas by Brazilian pepper (*Schinus terebinthifolius*). *New Phytologist*, **184**, 365-375.

Theoharides, K.A. & Dukes, J.S. (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist*, **176**, 256-273.

van Wilgen, B.W. & Richardson, D.M. (2012) Three centuries of managing introduced conifers in South Africa: Benefits, impacts, changing perceptions and conflict resolution. *Journal of Environmental Management*, **106**, 56-68.

van Wilgen, B.W. & Richardson, D.M. (2014) Challenges and trade-offs in the management of invasive alien trees. *Biological Invasions*, **16**, 721-734.

van Wilgen, B.W., Forsyth, G.G., Le Maitre, D.C., Wannenburgh, A., Kotze, J.D.F., van den Berg, E. & Henderson, L. (2012) An assessment of the effectiveness of a large, national-scale invasive alien plant control strategy in South Africa. *Biological Conservation*, **148**, 28-38.

Veblen, T.T., Holz, A., Paritsis, J., Raffaele, E., Kitzberger, T. & Blackhall, M. (2011) Adapting to global environmental change in Patagonia: What role for disturbance ecology? *Austral Ecology*, 891-903.

Wiser, S.K., Allen, R.B. & Platt, K.H. (1997) Mountain beech forest succession after a fire at Mount Thomas Forest, Canterbury, New Zealand. *New Zealand Journal of Botany*, **35**, 505-515.

Zenni, R.D., Bailey, J.K. & Simberloff, D. (2014) Rapid evolution and range expansion of an invasive plant are driven by provenance-environment interactions. *Ecology Letters*, **17**, 727-735.

REFERENCES CITED

Agee, J. K. 1998. Fire and pine ecosystems. Pages 193-249 *in* D. M. Richardson, editor. Ecology and Biogeography of *Pinus*. Cambridge University Press, Cambridge.

Albini, F.A. & Reinhardt, E.D. (1997) Improved calibration of a large fuel burnout model. *International Journal of Wildland Fire*, **7**, 21-28.

Albini, F.A., Brown, J.K., Reinhardt, E.D. & Ottmar, R.D. (1995) Calibration of a large fuel burnout model. *International Journal of Wildland Fire*, **5**, 173-192.

Allen, R.B. & Lee, W.G. (1989) Seedling establishment microsites of exotic conifers in *Chionochloa rigida* tussock grassland, Otago, New Zealand. *New Zealand Journal of Botany*, **27**, 491-498.

Baker, H. (1965) Characteristics and modes of origin of weeds. *The genetics of colonizing species* (ed. by H. Baker and G. Stebbins), pp. 147-172. Academic Press, New York.

Baker, W.L. (2009) *Fire Ecology in Rocky Mountain Landscapes*. Island Press, Washington D.C.

Balch, J.K., Bradley, B.A., D'Antonio, C.M. & Gomez-Dans, J. (2013) Introduced annual grass increases regional fire activity across the arid western USA (1980-2009). *Global Change Biology*, **19**, 173-183.

Bardgett, R.D. & Wardle, D.A. (2010) *Aboveground - Belowground Linkages*. Oxford University Press, Oxford.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) lme4: Linear mixed-effects models using Eigen and S4. http://CRAN.R-project.org/package=lme4.

Blackburn, T.M., Essl, F., Evans, T., Hulme, P.E., Jeschke, J.M., Kuehn, I., Kumschick, S., Markova, Z., Mrugala, A., Nentwig, W., Pergl, J., Pysek, P., Rabitsch, W., Ricciardi, A., Richardson, D.M., Sendek, A., Vila, M., Wilson, J.R.U., Winter, M., Genovesi, P. & Bacher, S. (2014) A Unified Classification of Alien Species Based on the Magnitude of their Environmental Impacts. *Plos Biology*, **12**, e1001850.

Blossey, B. & Notzold, R. (1995) Evolution of increased competitive ability in invasive nonindigenous plants - A hypothesis. *Journal of Ecology*, **83**, 887-889.

Boulant, N., Garnier, A., Curt, T. & Lepart, J. (2009) Disentangling the effects of land use, shrub cover and climate on the invasion speed of native and introduced pines in grasslands. *Diversity and Distributions*, **15**, 1047-1059.

Bowman, R.G. (2004) Responsibilities of local government in wilding conifer management *Managing wilding conifers in New Zealand: Present and future* (ed. by R.L. Hill, S.M. Zydenbos and C.M. Bezar), pp. 45-53. New Zealand Plant Protection Society, Christchurch.

Brewer, J.S. (1998) Patterns of plant species richness in a wet slash-pine (*Pinus elliottii*) savanna. *Journal of the Torrey Botanical Society*, **125**, 216-224.

Brockerhoff, E.G., Ecroyd, C.E., Leckie, A.C. & Kimberley, M.O. (2003) Diversity and succession of adventive and indigenous vascular understorey plants in *Pinus radiata* plantation forests in New Zealand. *Forest Ecology and Management*, **185**, 307-326.

Brooks, M.L. (1999) Alien annual grasses and fire in the Mojave Desert. *Madrono*, **46**,13-19.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M. & Pyke, D. (2004) Effects of invasive alien plants on fire regimes. *Bioscience*, **54**, 677-688.

Brown, J. 1975. Fire cycles and community dynamics in lodgepole pine forests. Pages 429-456 *in* D. Baumgartner, editor. Management of lodgepole pine ecosystems.

Brown, J. K., M. M. Marsden, K. C. Ryan, and E. D. Reinhardt. 1985. Predicting duff and woody fuel consumed by prescribed fire in the northern Rocky Mountains. Research Paper INT-337, USDA Forest Service.

Brummer, T.J., Maxwell, B.D., Higgs, M.D. & Rew, L.J. (2013) Implementing and interpreting local-scale invasive species distribution models. *Diversity and Distributions*, **19**, 919-932.

Buckley, Y.M., Brockerhoff, E., Langer, L., Ledgard, N., North, H. & Rees, M. (2005) Slowing down a pine invasion despite uncertainty in demography and dispersal. *Journal of Applied Ecology*, **42**, 1020-1030.

Buckley, Y.M., Bolker, B.M. & Rees, M. (2007) Disturbance, invasion and re-invasion: managing the weed-shaped hole in disturbed ecosystems. *Ecology Letters*, **10**, 809-817.

Burns, B.R. (1993) Fire-induced dynamics of *Araucaria araucana - Nothofagus antartica* forest in the Southern Andes. *Journal of Biogeography*, **20**, 669-685.

Buswell, J.M., Moles, A.T. & Hartley, S. (2011) Is rapid evolution common in introduced plant species? *Journal of Ecology*, **99**, 214-224.

Callaway, R.M. & Aschehoug, E.T. (2000) Invasive plants versus their new and old neighbors: A mechanism for exotic invasion. *Science*, **290**, 521-523.

Callaway, R.M. & Ridenour, W.M. (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment*, **2**, 436-443.

Callaway, R.M., Schaffner, U., Thelen, G.C., Khamraev, A., Juginisov, T. & Maron, J.L. (2012) Impact of *Acroptilon repens* on co-occurring native plants is greater in the invader's non-native range. *Biological Invasions*, **14**, 1143-1155.

Callaway, R.M., Waller, L.P., Diaconu, A., Pal, R., Collins, A.R., Mueller-Schaerer, H. & Maron, J.L. (2011) Escape from competition: Neighbors reduce *Centaurea stoebe* performance at home but not away. *Ecology*, **92**, 2208-2213.

Callaway, R.M., Cipollini, D., Barto, K., Thelen, G.C., Hallett, S.G., Prati, D., Stinson, K. & Klironomos, J. (2008) Novel weapons: Invasive plant suppresses fungal mutualists in America but not in its native Europe. *Ecology*, **89**, 1043-1055.

Camarillo, S.A., Stovall, J.P. & Sunda, C.J. (2015) The impact of Chinese tallow (*Triadica sebifera*) on stand dynamics in bottomland hardwood forests. *Forest Ecology and Management*, **344**, 10-19.

Campbell, G.S., Jungbauer, J.D., Shiozawa, S. & Hungerford, R.D. (1993) A one-parameter equation for water sorption isotherms of soils. *Soil Science*, **156**, 302-305.

Campbell, G.S., Jungbauer, J.D., Bristow, K.L. & Hungerford, R.D. (1995) Soil temperature and water content beneath a surface fire. *Soil Science*, **159**, 363-374.

Caplat, P., Hui, C., Maxwell, B.D. & Peltzer, D.A. (2014) Cross-scale management strategies for optimal control of trees invading from source plantations. *Biological Invasions*, **16**, 677-690.

Catford, J.A., Jansson, R. & Nilsson, C. (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, **15**, 22-40.

Coates, K.D., Emmingham, W.H. & Radosevich, S.R. (1991) Conifer-seedling success and microclimate at different levels of herb and shrub cover in a *Rhododendron-Vaccinium-Menziesia* community of south central British Columbia. *Canadian Journal of Forest Research*, **21**, 858-866.

Cóbar-Carranza, A.J., García, R.A., Pauchard, A. & Peña, E. (2014) Effect of *Pinus contorta* invasion on forest fuel properties and its potential implications on the fire regime of *Araucaria araucana* and *Nothofagus antarctica* forests. *Biological Invasions*, **16**, 2273-2291.

Cóbar-Carranza, A.J., García, R.A., Pauchard, A. & Peña, E. (2015) Effects of high temperatures in the germination and seed survival of the invasive species *Pinus contorta* and two native species of South Chile. *Bosque*, **36**, 53-60.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A. & MacIsaac, H.J. (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters*, **7**, 721-733.

Constán-Nava, S., Soliveres, S., Torices, R., Serra, L. & Bonet, A. (2015) Direct and indirect effects of invasion by the alien tree *Ailanthus altissima* on riparian plant communities and ecosystem multifunctionality. *Biological Invasions*, **17**, 1095-1108.

Coomes, D.A., Allen, R.B., Forsyth, D.M. & Lee, W.G. (2003) Factors preventing the recovery of New Zealand forests following control of invasive deer. *Conservation Biology*, **17**, 450-459.

Coutts, S.R., Caplat, P., Cousins, K., Ledgard, N. & Buckley, Y.M. (2012) Reproductive ecology of *Pinus nigra* in an invasive population: individual- and population-level variation in seed production and timing of seed release. *Annals of Forest Science*, **69**, 467-476.

Cuevas, Y.A. & Zalba, S.M. (2010) Recovery of Native Grasslands after Removing Invasive Pines. *Restoration Ecology*, **18**, 711-719.

D'Antonio, C.M. & Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, **23**, 63-87.

Davis, M.A., Grime, J.P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**, 528-534.

de Oliveira, S.M., Boll, P.K., Baptista, V.D. & Leal-Zanchet, A.M. (2014) Effects of pine invasion on land planarian communities in an area covered by Araucaria moist forest. *Zoological Studies*, **53**, 19.

Dehlin, H., Peltzer, D.A., Allison, V.J., Yeates, G.W., Nilsson, M.-C. & Wardle, D.A. (2008) Tree seedling performance and below-ground properties in stands of invasive and native tree species. *New Zealand Journal of Ecology*, **32**, 67-79.

Despain, D.G. (2001) Dispersal ecology of lodgepole pine (*Pinus contorta* Dougl.) in its native environment as related to Swedish forestry. *Forest Ecology and Management*, **141**, 59-68.

Dibble, A.C. & Rees, C.A. (2005) Does the lack of reference ecosystems limit our science? A case study in nonnative invasive plants as forest fuels. *Journal of Forestry*, **103**, 329-338.

Dibble, A.C., White, R. H. & Lebow, P.K. (2007) Combustion characteristics of north-eastern USA vegetation tested in the cone calorimeter: invasive versus non-invasive plants. *International Journal of Wildland Fire*, **16**, 426-443.

Dickie, I.A., Bolstridge, N., Cooper, J.A. & Peltzer, D.A. (2010) Co-invasion by *Pinus* and its mycorrhizal fungi. *New Phytologist*, **187**, 475-484.

Dickie, I.A., St John, M.G., Yeates, G.W., Morse, C.W., Bonner, K.I., Orwin, K. & Peltzer, D.A. (2014) Belowground legacies of *Pinus contorta* invasion and removal result in multiple mechanisms of invasional meltdown. *AoB Plants*, **6**, plu056.

Dickie, I.A., Yeates, G.W., St John, M.G., Stevenson, B.A., Scott, J.T., Rillig, M.C., Peltzer, D.A., Orwin, K.H., Kirschbaum, M.U.F., Hunt, J.E., Burrows, L.E., Barbour, M.M. & Aislabie, J. (2011) Ecosystem service and biodiversity trade-offs in two woody successions. *Journal of Applied Ecology*, **48**, 926-934.

Diehl, P. & Fontenla, S.B. (2010) Arbuscular mycorrhizal infection in two morphological root types of *Araucaria araucana* (Molina) K. Koch. *Revista Argentina De Microbiologia*, **42**, 133-137.

Dietz, H. & Edwards, P.J. (2006) Recognition that causal processes change during plant invasion helps explain conflicts in evidence. *Ecology*, **87**, 1359-1367.

Diez, J.M., Dickie, I., Edwards, G., Hulme, P.E., Sullivan, J.J. & Duncan, R.P. (2010) Negative soil feedbacks accumulate over time for non-native plant species. *Ecology Letters*, **13**, 803-809.

Donaldson, J.E., Hui, C., Richardson, D.M., Robertson, M.P., Webber, B.L. & Wilson, J.R.U. (2014) Invasion trajectory of alien trees: the role of introduction pathway and planting history. *Global Change Biology*, **20**, 1527-1537.

Drake, J.M., H.A., Di Castri, F., Groves, R., Kruger, F.J., Rejmanek, M. & Williamson, M. (1989) *Biological Invasions: a Global Perspective*. Wiley, Chichester.

Dyck, W.J. (2004) A forestry industry view of wilding conifers and options for their control *Managing wilding conifers in New Zealand: Present and future* (ed. by R.L. Hill, S.M. Zydenbos and C.M. Bezar), pp. 41-44. New Zealand Plant Protection Society, Christchurch.

Ehrenfeld, J.G. (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, **6**, 503-523.

Essl, F., Moser, D., Dullinger, S., Mang, T. & Hulme, P.E. (2010) Selection for commercial forestry determines global patterns of alien conifer invasions. *Diversity and Distributions*, **16**, 911-921.

Fajardo, A. & Gundale, M.J. (2015) Combined effects of anthropogenic fires and land-use change on soil properties and processes in Patagonia, Chile. *Forest Ecology and Management*, **357**, 60-67.

Farley, K.A., Jobbagy, E.G. & Jackson, R.B. (2005) Effects of afforestation on water yield: a global synthesis with implications for policy. *Global Change Biology*, **11**, 1565-1576.

Felker-Quinn, E., Schweitzer, J.A. & Bailey, J.K. (2013) Meta-analysis reveals evolution in invasive plant species but little support for Evolution of Increased Competitive Ability (EICA). *Ecology and Evolution*, **3**, 739-751.

Fernandez, M.E., Gyenge, J. & Schlichter, T. (2009) Water flux and canopy conductance of natural versus planted forests in Patagonia, South America. *Trees-Structure and Function*, **23**, 415-427.

Firn, J., Moore, J.L., MacDougall, A.S., Borer, E.T., Seabloom, E.W., HilleRisLambers, J., Harpole, W.S., Cleland, E.E., Brown, C.S., Knops, J.M.H., Prober, S.M., Pyke, D.A., Farrell, K.A., Bakker, J.D., O'Halloran, L.R., Adler, P.B., Collins, S.L., D'Antonio, C.M., Crawley, M.J., Wolkovich, E.M., La Pierre, K.J., Melbourne, B.A., Hautier, Y., Morgan, J.W., Leakey, A.D.B., Kay, A., McCulley, R., Davies, K.F., Stevens, C.J., Chu, C.-J., Holl, K.D., Klein, J.A., Fay, P.A., Hagenah, N., Kirkman, K.P. & Buckley, Y.M. (2011) Abundance of introduced species at home predicts abundance away in herbaceous communities. *Ecology Letters*, **14**, 274-281.

Fleishman, E., Noss, R.F. & Noon, B.R. (2006) Utility and limitations of species richness metrics for conservation planning. *Ecological Indicators*, **6**, 543-553.

Flory, S.L., Clay, K., Emery, S.M., Robb, J.R. & Winters, B. (2015) Fire and non-native grass invasion interact to suppress tree regeneration in temperate deciduous forests. *Journal of Applied Ecology*, **52**, 992-1000.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling, C.S. (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology Evolution and Systematics*, **35**, 557-581.

Forbes, A.S., Norton, D.A. & Carswell, F.E. (2015a) Underplanting degraded exotic Pinus with indigenous conifers assists forest restoration. *Ecological Management & Restoration*, **16**, 41-49.

Forbes, A.S., Norton, D.A. & Carswell, F.E. (2015b) Artificial canopy gaps accelerate restoration within an exotic *Pinus radiata* plantation. *Restoration Ecology*, **Early View**.

Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N., Nielsen, A. & Sibert, J. (2012) AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods & Software*, **27**, 233-249.

Froude, V.A. (2011) Wilding conifers in New Zealand: Status report. Report prepared for the Ministry of Agriculture and Forestry. Pacific Eco-Logic, Bay of Islands.

Gaertner, M., Den Breeyen, A., Hui, C. & Richardson, D.M. (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. *Progress in Physical Geography*, **33**, 319-338.

Gaertner, M., Biggs, R., Te Beest, M., Hui, C., Molofsky, J. & Richardson, D.M. (2014) Invasive plants as drivers of regime shifts: identifying high-priority invaders that alter feedback relationships. *Diversity and Distributions*, **20**, 733-744.

Garcia-Llorente, M., Martin-Lopez, B., Gonzalez, J.A., Alcorlo, P. & Montes, C. (2008) Social perceptions of the impacts and benefits of invasive alien species: Implications for management. *Biological Conservation*, **141**, 2969-2983.

Griffiths, R., Madritch, M. & Swanson, A. (2005) Conifer invasion of forest meadows transforms soil characteristics in the Pacific Northwest. *Forest Ecology and Management*, **208**, 347-358.

Gundale, M., Kardol, P., Nilsson, M.C., Nilsson, U., Lucas, R.W. & Wardle, D.A. (2014a) Interactions with soil biota shift from negative to positive when a tree species is moved outside its native range. *New Phytologist*, **2**, 415-421.

Gundale, M.J., Pauchard, A., Langdon, B., Peltzer, D.A., Maxwell, B.D. & Nuñez, M.A. (2014b) Can model species be used to advance the field of invasion ecology? *Biological Invasions*, **16**, 591-607.

Halpern, C.B., Antos, J.A., Rice, J.M., Haugo, R.D. & Lang, N.L. (2010) Tree invasion of a montane meadow complex: temporal trends, spatial patterns, and biotic interactions *Journal of Vegetation Science*, **21**, 717-732.

Harding, M. (2001) South Island Wilding Conifer Strategy. In. Department of Conservation, Christchurch.

Hayward, J., Horton, T.R., Pauchard, A. & Nunez, M.A. (2015) A single ectomycorrhizal fungal species can enable a Pinus invasion. *Ecology*, **96**, 1438-1444.

Haugo, R.D. & Halpern, C.B. (2007) Vegetation responses to conifer encroachment in a western Cascade meadow: a chronosequence approach. *Canadian Journal of Botany*, **85**, 285-298.

Hejda, M., Pyšek, P. & Jarosik, V. (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology*, **97**, 393-403.

Hicke, J.A., Johnson, M.C., Jane, L.H.D. & Preisler, H.K. (2012) Effects of bark beetle-caused tree mortality on wildfire. *Forest Ecology and Management*, **271**, 81-90.

Hierro, J.L., Maron, J.L. & Callaway, R.M. (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology*, **93**, 5-15.

Higgins, S.I. & Richardson, D.M. (1998) Pine invasions in the southern hemisphere: modelling interactions between organism, environment and disturbance. *Plant Ecology*, **135**, 79-93.

Higgins, S.I. & Richardson, D.M. (1999) Predicting plant migration rates in a changing world: The role of long-distance dispersal. *American Naturalist*, **153**, 464-475.

Higgins, S.I., Richardson, D.M. & Cowling, R.M. (1996) Modeling invasive plant spread: The role of plant-environment interactions and model structure. *Ecology*, **77**, 2043-2054.

Higgs, E.S. (1997) What is good ecological restoration? *Conservation Biology*, **11**, 338-348.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965-1978.

Hobbs, R.J., Higgs, E. & Harris, J.A. (2009) Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution*, **24**, 599-605.

Hobbs, R.J., Hallett, L.M., Ehrlich, P.R. & Mooney, H.A. (2011) Intervention Ecology: Applying Ecological Science in the Twenty-first Century. *Bioscience*, **61**, 442-450.

Holl, K.D. & Howarth, R.B. (2000) Paying for restoration. *Restoration Ecology*, **8**, 260-267.

Holmes, P.M., Richardson, D.M., Van Wilgen, B.W. & Gelderblom, C. (2000) Recovery of South African fynbos vegetation following alien woody plant clearing and fire: implications for restoration. *Austral Ecology*, **25**, 631-639.

Holz, A. & Veblen, T.T. (2011) Variability in the Southern Annular Mode determines wildfire activity in Patagonia. *Geophysical Research Letters*, **38**, L14710.

Howell, C.J. & McAlpine, K.G. (2016) Native plant species richness in non-native *Pinus contorta* forest. *New Zealand Journal of Ecology*, **40**, 131-136.

Hulme, P.E., Pysek, P., Jarosik, V., Pergl, J., Schaffner, U. & Vila, M. (2013) Bias and error in understanding plant invasion impacts. *Trends in Ecology & Evolution*, **28**, 212-218.

Hungerford, R. D., M. G. Harrington, W. H. Frandsen, K. C. Ryan, and G. J. Niehoff. 1991. Influence of fire on factors that affect site productivity. Pages 32-50. In: Harvey, Alan E.; Neuenschwander, Leon F. (compilers). Proceedings-management and productivity of western-montane forest soils. General Technical Report INT-GTR-280. Ogden, UT: USDA Forest Service, Intermountain Research Station.

Iglesias, V., Krause, T.R. & Whitlock, C. (2015) Complex Response of White Pines to Past Environmental Variability Increases Understanding of Future Vulnerability. *Plos One*, **10**, e0124439.

Inderjit, Evans, H., Crocoll, C., Bajpai, D., Kaur, R., Feng, Y.-L., Silva, C., Treviño Carreón, J., Valiente-Banuet, A., Gershenzon, J. & Callaway, R.M. (2011) Volatile chemicals from leaf litter are associated with invasiveness of a Neotropical weed in Asia. *Ecology*, **92**, 316-324.

Jaffré, T., Rigault, F. & Dagostini, G. (1998) Impact des feux de brousse sur les maquis ligno-herbacés des roches ultramafiques de Nouvelle-Calédonie *Adansonia*, **20**, 173-89.

Jakubos, B. & Romme, W.H. (1993) Invasion of sub-alpine meadows by lodgepole pine in Yellowstone National Park, Wyoming, USA. *Arctic and Alpine Research*, **25**, 382-390.

Jenkins, J.C., Chojnacky, D.C., Heath, L.S. & Birdsey, R.A. (2004) Comprehensive Database of Diameter-based Biomass Regressions for North American Tree Species, p. 45. USDA Forest Service Northeastern Research Station, Newtown Square, PA.

Johnstone, I.M. (1986) Plant invasion windows - a time-based classification of invasion potential. *Biological Reviews of the Cambridge Philosophical Society*, **61**, 369-394.

Joshi, J. & Vrieling, K. (2005) The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. *Ecology Letters*, **8**, 704-714.

Kaur, R., Gonzales, W.L., Daniel Llambi, L., Soriano, P.J., Callaway, R.M., Rout, M.E., Gallaher, T.J. & Inderjit (2012) Community impacts of *Prosopis juliflora* invasion: Biogeographic and congeneric comparisons. *Plos One*, **7**, e44966.

Keane, R. E., and L. J. Dickinson. 2007. The photoload sampling technique: estimating surface fuel loadings from downward-looking photographs of synthetic fuelbeds. General Technical Report RMRS-GTR-190. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station. 44 p.

Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, **17**, 164-170.

Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J. & Bradstock, R.A. (2011) Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, **16**, 406-411.

Kemp, K., Higuera, P. & Morgan, P. (2015) Fire legacies impact conifer regeneration across environmental gradients in the U.S. northern Rockies. *Landscape Ecology*, 1-18.

Kitzberger, T., Araoz, E., Gowda, J.H., Mermoz, M. & Morales, J.M. (2012) Decreases in fire spread probability with forest age promotes alternative community states, reduced resilience to climate variability and large fire regime shifts. *Ecosystems*, **15**, 97-112.

Klironomos, J.N. (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature*, **417**, 67-70.

Knapp, A.K. & Anderson, J.E. (1980) Effect of heat on germination of seeds from serotinous lodgepole pine cones. *American Midland Naturalist*, **104**, 370-372.

Kueffer, C., Pysek, P. & Richardson, D.M. (2013) Integrative invasion science: model systems, multi-site studies, focused meta-analysis and invasion syndromes. *New Phytologist*, **200**, 615-633.

Kumschick, S., Bacher, S., Dawson, W., Heikkilä, J., Sendek, A., Pluess, T., Robinson, T.B. & Kühn, I. (2012) A conceptual framework for prioritization of invasive alien species for management according to their impact. *Neobiota*, **15**, 69-100.

Kumschick, S., Gaertner, M., Vila, M., Essl, F., Jeschke, J.M., Pysek, P., Ricciardi, A., Bacher, S., Blackburn, T.M., Dick, J.T.A., Evans, T., Hulme, P.E., Kuehn, I., Mrugala, A., Pergl, J., Rabitsch, W., Richardson, D.M., Sendek, A. & Winter, M. (2015) Ecological impacts of alien species: quantification, scope, caveats, and recommendations. *Bioscience*, **65**, 55-63.

Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B. (2014) lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 2.0-11. http://CRAN.R-project.org/package=lmerTest.

Langdon, B. (2011) *Invasión de Pinus contorta Doug. ex Loud. en la Patagonia Chilena: patrones y mecanismos tras el proceso* Universidad de Concepción, Concepción, Chile.

Langdon, B., Pauchard, A. & Aguayo, M. (2010) *Pinus contorta* invasion in the Chilean Patagonia: local patterns in a global context. *Biological Invasions*, **12**, 3961-3971.

Lazzaro, L., Giuliani, C., Benesperi, R., Calamassi, R. & Foggi, B. (2015) Plant species loss and community nestedness after leguminous tree *Acacia pycnantha* invasion in a Mediterranean ecosystem. *Folia Geobotanica*, **50**, 229-238.

Le Maitre, D.C., van Wilgen, B.W., Gelderblom, C.M., Bailey, C., Chapman, R.A. & Nel, J.A. (2002) Invasive alien trees and water resources in South Africa: case studies of the costs and benefits of management. *Forest Ecology and Management*, **160**, 143-159.

Ledgard, N. (2001) The spread of lodgepole pine (*Pinus contorta*, Dougl.) in New Zealand. *Forest Ecology and Management*, **141**, 43-57.

Ledgard, N. & Davis, M. (2004) Restoration of mountain beech (Nothofagus solandri var. cliffortioides) forest after fire. *New Zealand Journal of Ecology*, **28**, 125-135.

Ledgard, N.J. (2004) Wilding conifers - New Zealand history and research background. *Managing wilding conifers in New Zealand - present and future* (ed. by R.L. Hill, S.M. Zydenbos and C.M. Bezar). New Zealand Plant Proetction Society Inc., Christchurch.

Ledgard, N.J. (2006) Determining the effect of increasing vegetation competition through fertiliser use on the establishment of wildings in unimproved high country grassland. *New Zealand Journal of Forestry*, **51**, 29-34.

Ledgard, N.J. & Paul, T.S.H. (2008) Vegetation successions over 30 years of high country grassland invasion by *Pinus contorta New Zealand Plant Protection*, **61**, 98-104.

Leishman, M. R., Cooke, J., & Richardson, D. M. (2014). Evidence for shifts to faster growth strategies in the new ranges of invasive alien plants. *Journal of Ecology*, ***102***, 1451-1461.

Lesica, P. (2012) *Manual of Montana Vascular Plants*. Brit Press, Fort Worth.

Levine, J.M., Vila, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society B*, **270**, 775-781.

Lindenmayer, D.B., Hobbs, R.J., Likens, G.E., Krebs, C.J. & Banks, S.C. (2011) Newly discovered landscape traps produce regime shifts in wet forests. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 15887-15891.

Lockwood, J.L., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution*, **20**, 223-228.

Lonsdale, W.M. & Miller, I.L. (1993) Fire as a management tool for a tropical woody weed: *Mimosa pigra* in Northern Australia. *Journal of Environmental Management*, **39**, 77-87.

Lotan, J.E. & Critchfield, W.B. (1990) *Pinus contorta* Dougl. ex. Loud. lodgepole pine. *Silvics of North America. Volume 1. Conifers. Agric. Handb. 654* (ed. by R.M. Burns and B.H. Honkala), pp. 302-315. U.S. Department of Agriculture, Forest Service, Washington, DC.

Mack, M.C. & D'Antonio, C.M. (1998) Impacts of biological invasions on disturbance regimes. *Trends in Ecology & Evolution*, **13**, 195-198.

Mandle, L., Bufford, J.L., Schmidt, I.B. & Daehler, C.C. (2011) Woody exotic plant invasions and fire: reciprocal impacts and consequences for native ecosystems. *Biological Invasions*, **13**, 1815-1827.

Marais, C., van Wilgen, B.W. & Stevens, D. (2004) The clearing of invasive alien plants in South Africa: a preliminary assessment of costs and progress. *South African Journal of Science*, **100**, 97-103.

Maron, J.L. & Marler, M. (2008) Effects of native species diversity and resource additions on invader impact. *American Naturalist*, **172**, S18-S33.

McWethy, D.B., Whitlock, C., Wilmshurst, J.M., McGlone, M.S., Fromont, M., Li, X., Dieffenbacher-Krall, A., Hobbs, W.O., Fritz, S.C. & Cook, E.R. (2010) Rapid landscape transformation in South Island, New Zealand, following initial Polynesian settlement. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 21343-21348.

Melbourne, B.A., Cornell, H.V., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A.L., Hall, R.J., Harrison, S., Hastings, A., Holland, M., Holyoak, M., Lambrinos, J., Moore, K. & Yokomizo, H. (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecology Letters*, **10**, 77-94.

Mermoz, M., Kitzberger, T. & Veblen, T.T. (2005) Landscape influences on occurrence and spread of wildfires in Patagonian forests and shrublands. *Ecology*, **86**, 2705-2715.

Moodley, D., Geerts, S., Rebelo, T., Richardson, D.M. & Wilson, J.R.U. (2014) Site-specific conditions influence plant naturalization: The case of alien Proteaceae in South Africa. *Acta Oecologica-International Journal of Ecology*, **59**, 62-71.

Murcia, C., Aronson, J., Kattan, G.H., Moreno-Mateos, D., Dixon, K. & Simberloff, D. (2014) A critique of the 'novel ecosystem' concept. *Trends in Ecology & Evolution*, **29**, 548-553.

Nathan, R. & Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, **15**, 278-285.

Ni, G.-Y., Schaffner, U., Peng, S.-L. & Callaway, R.M. (2010) *Acroptilon repens*, an Asian invader, has stronger competitive effects on species from America than species from its native range. *Biological Invasions*, **12**, 3653-3663.

Nilsson, C., Engelmark, O., Cory, J., Forsslund, A. & Carlborg, E. (2008) Differences in litter cover and understorey flora between stands of introduced lodgepole pine and native scots pine in Sweden. *Forest Ecology and Management*, **255**, 1900-1905.

Nuñez, M.A. & Medley, K.A. (2011) Pine invasions: climate predicts invasion success; something else predicts failure. *Diversity and Distributions*, **17**, 703-713.

Nuñez, M.A. & Raffaele, E. (2007) Afforestation causes changes in post-fire regeneration in native shrubland communities of northwestern Patagonia, Argentina. *Journal of Vegetation Science*, **18**, 827-834.

Nuñez, M.A., Simberloff, D. & Relva, M.A. (2008) Seed predation as a barrier to alien conifer invasions. *Biological Invasions*, **10**, 1389-1398.

Nuñez, M.A., Horton, T.R. & Simberloff, D. (2009) Lack of belowground mutualisms hinders Pinaceae invasions. *Ecology*, **90**, 2352-2359.

Nuñez, M.A., Hayward, J., Horton, T.R., Amico, G.C., Dimarco, R.D., Barrios-Garcia, M.N. & Simberloff, D. (2013) Exotic mammals disperse exotic fungi that promote invasion by exotic trees. *Plos One*, **8**, e66832.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2013) vegan: Community Ecology Package. R package version 2.0-10. http://CRAN.R-project.org/package=vegan

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the worlds: A new map of life on Earth. *Bioscience*, **51**, 933-938.

Pachepsky, E. & Levine, J.M. (2011) Density dependence slows invader spread in fragmented landscapes. *American Naturalist*, **177**, 18-28.

Page-Dumroese, D. S., R. K. Dumroese, C. M. Carpenter, and D. L. Wenny. 2002. Relationship of seed microsite to germination and survival of lodgepole pine on high-elevation clearcuts in northeastern Utah. USDA Forest Service Rocky Mountain Research Station, Ogden, UT. Note RMRS-RN-14. 4 p.

Paritsis, J. & Aizen, M.A. (2008) Effects of exotic conifer plantations on the biodiversity of understory plants, epigeal beetles and birds in *Nothofagus dombeyi* forests. *Forest Ecology and Management*, **255**, 1575-1583.

Paritsis, J., Veblen, T.T. & Holz, A. (2015) Positive fire feedbacks contribute to shifts from *Nothofagus pumilio* forests to fire-prone shrublands in Patagonia. *Journal of Vegetation Science*, **26**, 89-101.

Paritsis, J., Holz, A., Veblen, T.T. & Kitzberger, T. (2013) Habitat distribution modeling reveals vegetation flammability and land use as drivers of wildfire in SW Patagonia. *Ecosphere*, **4**, art53.

Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E. & Goldwasser, L. (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, **1**, 3-19.

Parker, J.D., Burkepile, D.E. & Hay, M.E. (2006) Opposing effects of native and exotic herbivores on plant invasions. *Science*, **311**, 1459-1461.

Parker, J.D., Torchin, M.E., Hufbauer, R.A., Lemoine, N.P., Alba, C., Blumenthal, D.M., Bossdorf, O., Byers, J.E., Dunn, A.M., Heckman, R.W., Hejda, M., Jarosik, V., Kanarek, A.R., Martin, L.B., Perkins, S.E., Pysek, P., Schierenbeck, K., Schloeder, C., van Klinken, R., Vaughn, K.J., Williams, W. & Wolfe, L.M. (2013) Do invasive species perform better in their new ranges? *Ecology*, **94**, 985-994.

Patten, D.T. (1969) Succession from sagebrush to mixed conifer forest in Northern Rocky Mountains. *American Midland Naturalist*, **82**, 229-240.

Pauchard, A., Cavieres, L.A. & Bustamante, R.O. (2004) Comparing alien plant invasions among regions with similar climates: where to from here? *Diversity and Distributions*, **10**, 371-375.

Pauchard, A., Garcia, R.A., Peña, E., Gonzalez, C., Cavieres, L.A. & Bustamante, R.O. (2008) Positive feedbacks between plant invasions and fire regimes: *Teline monspessulana* (L.) K. Koch (Fabaceae) in central Chile. *Biological Invasions*, **10**, 547-553.

Paul, T.H.S. & Ledgard, N.J. (2008) Effect of felled wilding pines on plant growth in high country grasslands. *New Zealand Plant Protection*, **61**, 105-110.

Paul, T.H.S. & Ledgard, N.J. (2009) Vegetation successions associated with wilding conifer removal. *New Zealand Plant Protection*, **62**, 374-379.

Pausas, J.G. & Keeley, J.E. (2014) Abrupt climate-independent fire regime changes. *Ecosystems*, **17**, 1109-1120.

Pausas, J.G., Lloret, F. & Vila, M. (2006) Simulating the effects of different disturbance regimes on *Cortaderia selloana* invasion. *Biological Conservation*, **128**, 128-135.

Pawson, S.M., McCarthy, J.K., Ledgard, N.J. & Didham, R.K. (2010) Density-dependent impacts of exotic conifer invasion on grassland invertebrate assemblages. *Journal of Applied Ecology*, **47**, 1053-1062.

Perry, G.L.W., Wilmshurst, J.M. & McGlone, M.S. (2014) Ecology and long-term history of fire in New Zealand. *New Zealand Journal of Ecology*, **38**, 157-176.

Perry, G.L.W., Wilmshurst, J.M., Ogden, J. & Enright, N.J. (2015) Exotic mammals and invasive plants alter fire-related thresholds in southern temperate forested landscapes. *Ecosystems*, **18**, 1290-1305.

Perry, G.L.W., Wilmshurst, J.M., McGlone, M.S., McWethy, D.B. & Whitlock, C. (2012) Explaining fire-driven landscape transformation during the Initial Burning Period of New Zealand's prehistory. *Global Change Biology*, **18**, 1609-1621.

Peña, E., Hidalgo, M., Langdon, B. & Pauchard, A. (2008) Patterns of spread of *Pinus contorta* Dougl. ex Loud. invasion in a Natural Reserve in southern South America. *Forest Ecology and Management*, **256**, 1049-1054.

Pierce, A.D. & Taylor, A.H. (2011) Fire severity and seed source influence lodgepole pine (*Pinus contorta* var. *murrayana*) regeneration in the southern cascades, Lassen volcanic National Park, California. *Landscape Ecology*, **26**, 225-237.

Powell, K.I., Chase, J.M. & Knight, T.M. (2011) A synthesis of plant invasion effects on biodiversity across spatial scales. *American Journal of Botany*, **98**, 539-548.

Pysek, P., Jarosik, V., Hulme, P.E., Pergl, J., Hejda, M., Schaffner, U. & Vila, M. (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology*, **18**, 1725-1737.

Quintanilla Pérez, V. (2008) Perturbaciones a la vegetación nativa por grandes fuegos de 50 años atrás, en bosques Nordpatagónicos. Caso de estudio en Chile Meridional. *Anales de Geografía*, **28**, 85-104.

R Core Team (2015). R: A language and environment for statistical computing version 3.2.2. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Raffaele, E. & Schlichter, T. (2000) Efectos de las plantaciones de pino ponderosa sobre la heterogeneidad de micrositios en estepas del noroeste patagónico. *Ecología Austral*, **10**, 151-158.

Ratajczak, Z., Nippert, J.B. & Collins, S.L. (2012) Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology*, **93**, 697-703.

Ray-Mukherjee, J., Nimon, K., Mukherjee, S., Morris, D.W., Slotow, R. & Hamer, M. (2014) Using commonality analysis in multiple regressions: a tool to decompose regression effects in the face of multicollinearity. *Methods in Ecology and Evolution*, **5**, 320-328.

Reinhardt, E. D. 2003. Using FOFEM 5.0 to estimate tree mortality, fuel consumption, smoke production and soil heating from wildland fire. P*roceedings of the Second International Wildland Fire Ecology and Fire Management Congress and Fifth Symposium on Fire and Forest Meteorology*. American Meteorological Society, Orlando, Florida, USA.

Rehfeldt, G.E., Ying, C.C., Spittlehouse, D.L. & Hamilton, D.A. (1999) Genetic responses to climate in *Pinus contorta*: Niche breadth, climate change, and reforestation. *Ecological Monographs*, **69**, 375-407.

Reinhardt, E.D., Keane, R.E., Brown, J.K. & Turner, D.L. (1991) Duff consumption from prescribed fire in the U.S. and Canada: a broadly based empirical approach. *11th Conference on Fire and Forest Meteorology* (ed by D.F. Potts). Missoula, MT.

Rejmánek, M. & Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology*, **77**, 1655-1661.

Rejmánek, M. & Richardson, D.M. (2013) Trees and shrubs as invasive alien species - 2013 update of the global database. *Diversity and Distributions*, **19**, 1093-1094.

Rew, L.J., Lehnhoff, E.A. & Maxwell, B.D. (2007) Non-indigenous species management using a population prioritization framework. *Canadian Journal of Plant Science*, **87**, 1029-1036.

Richardson, D.M. (1988) Age structure and regeneration after fire in a self-sown *Pinus halepensis* forest on the Cape Peninsula, South Africa. *South African Journal of Botany*, **54**, 140-144.

Richardson, D.M. (ed.). (1998) *Ecology and Biogeography of Pinus*. Cambridge University Press, Cambridge.

Richardson, D.M. & Bond, W.J. (1991) Determinants of plant distribution - Evidence from pine invasions. *American Naturalist*, **137**, 639-668.

Richardson, D.M. & Cowling, R.M. (1992) Why is mountain fynbos invasible and which species invade? *Fire in South African Mountain Fynbos* (ed. by B.W. Van Wilgen, D.M. Richardson, F.J. Kruger and H.J. Van Hensbergen), pp. 161-181. Springer, Berlin.

Richardson, D.M. & Higgins, S.I. (1998) Pines as invaders in the southern hemisphere. *Ecology and Biogeography of Pinus* (ed. by D.M. Richardson), pp. 450-473. Cambridge University Press, Cambridge.

Richardson, D.M. & Pyšek, P. (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography*, **30**, 409-431.

Richardson, D.M., van Wilgen, B.W. & Nuñez, M.A. (2008) Alien conifer invasions in South America: short fuse burning? *Biological Invasions*, **10**, 573-577.

Richardson, D.M., Williams, P.A. & Hobbs, R.J. (1994) Pine invasion in the Southern Hemisphere: determinants of spread and invadability. *Journal of Biogeography*, **21**, 511-527.

Richardson, D.M., Hui, C., Nuñez, M.A. & Pauchard, A. (2014) Tree invasions: patterns, processes, challenges and opportunities. *Biological Invasions*, **16**, 473-481.

Rossiter, N.A., Setterfield, S.A., Douglas, M.M. & Hutley, L.B. (2003) Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. *Diversity and Distributions*, **9**, 169-176.

Rouget, M. & Richardson, D.M. (2003) Inferring process from pattern in plant invasions: A semimechanistic model incorporating propagule pressure and environmental factors. *American Naturalist*, **162**, 713-724.

Rozzi, R. (2013) Biocultural Ethics: From Biocultural Homogenization Toward Biocultural Conservation *Linking Ecology and Ethics for a Changing World* (ed. by R.P. Rozzi, S.T.A.Palmer, C.Armesto, J. J.Callicott, J.B.), pp. 9-32. Springer Netherlands, Dordrecht.

Rundel, P.W., Dickie, I.A. & Richardson, D.M. (2014) Tree invasions into treeless areas: mechanisms and ecosystem processes. *Biological Invasions*, **16**, 663-675.

Sagarin, R. & Pauchard, A. (2012) *Observation and Ecology: Broadening the Scope of Science to Understand a Complex World*. Island Press, Washington.

Sarasola, M.M., Rusch, V.E., Schlichter, T.M. & Ghersa, C.M. (2006) Tree conifers invasion in steppe areas and *Austrocedus chilensis* forests in NW Patagonia. *Ecologia Austral*, **16**, 143-156.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B. (2001) Catastrophic shifts in ecosystems. *Nature*, **413**, 591-596.

Schoennagel, T., Turner, M.G. & Romme, W.H. (2003) The influence of fire interval and serotiny on postfire lodgepole pine density in Yellowstone National Park. *Ecology*, **84**, 2967-2978.

Scott, D.F. & Van Wyk, D.B. (1990) The effects of wildfire on soil wettability and hydrological behavior of an afforested catchment. *Journal of Hydrology*, **121**, 239-256.

Setterfield, S.A., Rossiter-Rachor, N.A., Hutley, L.B., Douglas, M.M. & Williams, R.J. (2010) Turning up the heat: the impacts of *Andropogon gayanus* (gamba grass) invasion on fire behaviour in northern Australian savannas. *Diversity and Distributions*, **16**, 854-861.

Shackelford, N., Renton, M., Perring, M.P. & Hobbs, R.J. (2013) Modeling disturbance-based native invasive species control and its implications for management. *Ecological Applications*, **23**, 1331-1344.

Shackleton, R.T., Le Maitre, D.C., Van Wilgen, B.W. & Richardson, D.M. (2015) The impact of invasive alien *Prosopis species* (mesquite) on native plants in different environments in South Africa. *South African Journal of Botany*, **97**, 25-31.

Shah, M.A., Callaway, R.M., Shah, T., Houseman, G.R., Pal, R.W., Xiao, S., Luo, W., Rosche, C., Reshi, Z.A., Khasa, D.P. & Chen, S. (2014) *Conyza canadensis* suppresses plant diversity in its nonnative ranges but not at home: a transcontinental comparison *New Phytologist*, **202**, 1286–1296.

Sher, A.A. & Hyatt, L.A. (1999) The disturbed resource-flux invasion matrix: a new framework for patterns of plant invasion *Biological Invasions*, **1**, 107-114.

Shigesada, N., Kawasaki, K. & Takeda, Y. (1995) Modeling stratified diffusion in biological invasions. *American Naturalist*, **146**, 229-251.

Siemann, E. & Rogers, W.E. (2001) Genetic differences in growth of an invasive tree species. *Ecology Letters*, **4**, 514-518.

Simberloff, D. (2009) The Role of Propagule Pressure in Biological Invasions. *Annual Review of Ecology Evolution and Systematics*, pp. 81-102. Annual Reviews, Palo Alto.

Simberloff, D. (2011a) Charles Elton: Neither Founder Nor Siren, But Prophet *Fifty Years of Invasion Ecology* (ed. by D.M. Richardson). Wiley-Blackwell, Chichester.

Simberloff, D. (2011b) How common are invasion-induced ecosystem impacts? *Biological Invasions*, **13**, 1255-1268.

Simberloff, D. & Von Holle, B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, **1**, 21-32.

Simberloff, D., Relva, M.A. & Nuñez, M. (2002) Gringos en el Bosque: Introduced tree invasion in a *Nothofagus*/*Austrocedrus* forest. *Biological Invasions*, **4**, 35-53.

Simberloff, D., Souza, L., Nuñez, M.A., Barrios-Garcia, M.N. & Bunn, W. (2012) The natives are restless, but not often and mostly when disturbed. *Ecology*, **93**, 598-607.

Simberloff, D., Nuñez, M.A., Ledgard, N.J., Pauchard, A., Richardson, D.M., Sarasola, M., Van Wilgen, B.W., Zalba, S.M., Zenni, R.D., Bustamante, R., Peña, E. & Ziller, S.R. (2010) Spread and impact of introduced conifers in South America: Lessons from other southern hemisphere regions. *Austral Ecology*, **35**, 489-504.

Skaug, H., Fournier, D., Nielsen, A., Magnusson, A. & Bolker, B. (2013) Generalized Linear Mixed Models using AD Model Builder. R package version 0.7.7.

Skurski, T.C., Rew, L.J. & Maxwell, B.D. (2014) Mechanisms underlying nonindigenous plant impacts: A review of recent experimental research. *Invasive Plant Science and Management*, **7**, 432-444.

Steers, R.J., Fritzke, S.L., Rogers, J.J., Cartan, J. & Hacker, K. (2013) Invasive pine tree effects on northern coastal scrub structure and composition. *Invasive Plant Science and Management*, **6**, 231-242.

Stephens, R.T.T. (2004) Wilding conifer control: how important is it relative to other conservation actions? . *Managing wildling conifers in New Zealand: present and future* (ed. by R.L. Hill, S.M. Zydenbos and C.M. Bezar), pp. 27-39. New Zealand Plant Protection Society, Christchurch.

Stevens, J.T. & Beckage, B. (2009) Fire feedbacks facilitate invasion of pine savannas by Brazilian pepper (*Schinus terebinthifolius*). *New Phytologist*, **184**, 365-375.

Stock, W.D., Wienand, K.T. & Baker, A.C. (1995) Impacts of invading N-2-fixing acacia species on patterns of nutrient cycling in 2 cape ecosystems: Evidence from soil incubation studies and n-15 natural-abundance values. *Oecologia*, **101**, 375-382.

Sutherland, S. (2004) What makes a weed a weed: life history traits of native and exotic plants in the USA. *Oecologia*, **141**, 24-39.

Taylor, K.T., Maxwell, B.D., Pauchard, A., Nuñez, M.A., Peltzer, D.A., Terwei, A. & Rew, L.J. (2016a) Drivers of plant invasion vary globally: evidence from pine invasions within six ecoregions. *Global Ecology and Biogeography*, **25**, 96-106.

Taylor, K.T., Maxwell, B.D., Pauchard, A., Nuñez, M.A. & Rew, L.J. (2016b) Native versus non-native invasions: similarities and differences in the biodiversity impacts of *Pinus contorta* in introduced and native ranges. *Diversity and Distributions*.

Theoharides, K.A. & Dukes, J.S. (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist*, **176**, 256-273.

Thorpe, A.S. & Callaway, R.M. (2011) Biogeographic differences in the effects of *Centaurea stoebe* on the soil nitrogen cycle: novel weapons and soil microbes. *Biological Invasions*, **13**, 1435-1445.

Thorpe, A.S., Thelen, G.C., Diaconu, A. & Callaway, R.M. (2009) Root exudate is allelopathic in invaded community but not in native community: field evidence for the novel weapons hypothesis *Journal of Ecology*, **97**, 641-645.

Turner, M.G., Romme, W.H., Gardner, R.H. & Hargrove, W.W. (1997) Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecological Monographs*, **67**, 411-433.

Turner, M.G., Tinker, D.B., Romme, W.H., Kashian, D.M. & Litton, C.M. (2004) Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). *Ecosystems*, **7**, 751-775.

Urrutia, J., Pauchard, A. & Garcia, R.A. (2013) Differences in plant composition in an *Araucaria araucana* (Molina) K.Koch and *Nothofagus antarctica* (G. Forst.) Oerst. forest in a *Pinus contorta* Douglas ex Loudon invasion gradient. *Gayana Botanica*, **70**, 92-100.

van Kleunen, M., Weber, E. & Fischer, M. (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, **13**, 235-245.

van Wilgen, B.W. & Richardson, D.M. (1985) The effects of alien shrub invasions on vegetation structure and fire behavior in South African fynbos shrublands: A simulation study. *Journal of Applied Ecology*, **22**, 955-966.

van Wilgen, B.W. & Richardson, D.M. (2012) Three centuries of managing introduced conifers in South Africa: Benefits, impacts, changing perceptions and conflict resolution. *Journal of Environmental Management*, **106**, 56-68.

van Wilgen, B.W. & Richardson, D.M. (2014) Challenges and trade-offs in the management of invasive alien trees. *Biological Invasions*, **16**, 721-734.

van Wilgen, B.W., Forsyth, G.G., Le Maitre, D.C., Wannenburgh, A., Kotze, J.D.F., van den Berg, E. & Henderson, L. (2012) An assessment of the effectiveness of a large, national-scale invasive alien plant control strategy in South Africa. *Biological Conservation*, **148**, 28-38.

Veblen, T.T., Kitzberger, T., Raffaele, E. & Lorenz, D.C. (2003) Fire History and Vegetation Changes in Northern Patagonia, Argentina. *Fire and Climatic Changes in Temperate Ecosystems of the Western Americas* (ed. by T.T. Veblen, W.L. Baker, G. Montenegro and T.W. Swetnam), pp. 265-295. Springer-Verlag, New York.

Veblen, T.T., Holz, A., Paritsis, J., Raffaele, E., Kitzberger, T. & Blackhall, M. (2011) Adapting to global environmental change in Patagonia: What role for disturbance ecology? *Austral Ecology*, **36**, 891-903.

Veblen, T.T., Kitzberger, T., Raffaele, E., Mermoz, M., Conzalez, M.E., Sibold, J.S. & Holz, A. (2008) The historical range of variability of fires in the Andean-Patagonian *Nothofagus* forest region. *International Journal of Wildland Fire*, **17**, 724-741.

Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*, Fourth Edition. edn. Springer, New York.

Ver Hoef, J.M. & Boveng, P.L. (2007) Quasi-poisson vs. negative binomial regression: how should we model overdispersed count data? *Ecology*, **88**, 2766-2772.

Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarosik, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y. & Pysek, P. (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, **14**, 702-708.

Vilà, M., Lloret, F., Ogheri, E. & Terradas, J. (2001) Positive fire-grass feedback in Mediterranean Basin woodlands. *Forest Ecology and Management*, **147**, 3-14.

Von Holle, B. & Simberloff, D. (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology*, **86**, 3212-3218.

Wagner, S.A. & Fraterrigo, J.M. (2015) Positive feedbacks between fire and non-native grass invasion in temperate deciduous forests. *Forest Ecology and Management*, **354**, 170-176.

Walker, B.H. & Meyers, J.A. (2004) Thresholds in ecological and social-ecological systems: a developing database. *Ecology & Society*, **9**, 3.

Wardle, D.A., Nicholson, K.S. & Rahman, A. (1995) Ecological effects of the invasive weed species *Senecio jacobaea* L (ragwort) in a New Zealand pasture. *Agriculture Ecosystems & Environment*, **56**, 19-28.

Whitlock, C., McWethy, D.B., Tepley, A.J., Veblen, T.T., Holz, A., McGlone, M.S., Perry, G.L.W., Wilmshurst, J.M. & Wood, S.W. (2015) Past and present vulnerability of closed-canopy temperate forests to altered fire regimes: a comparison of the Pacific Northwest, New Zealand, and Patagonia. *Bioscience*, **65**, 151-163.

Widenmaier, K.J. & Strong, W.L. (2010) Tree and forest encroachment into fescue grasslands on the Cypress Hills plateau, southeast Alberta, Canada. *Forest Ecology and Management*, **259**, 1870-1879.

Wilensky, U. (1999) NetLogo. http://ccl.northwestern.edu/netlogo/. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL.

Williamson, M. & Fitter, A. (1996) The varying success of invaders. *Ecology*, **77**, 1661-1666.

Willis, A.J. & Blossey, B. (1999) Benign environments do not explain the increased vigour of non-indigenous plants: a cross-continental transplant experiment. *Biocontrol Science and Technology*, **9**, 567-577.

Willis, A.J., Thomas, M.B. & Lawton, J.H. (1999) Is the increased vigour of invasive weeds explained by a trade-off between growth and herbivore resistance? *Oecologia*, **120**, 632-640.

Wilson, J.R.U., Caplat, P., Dickie, I.A., Hui, C., Maxwell, B.D., Nuñez, M.A., Pauchard, A., Rejmánek, M., Richardson, D.M., Robertson, M. P., Spear, D., Webber, B.L.,

van Wilgen, B.W. & Zenni, R.D. (2014) A standardized set of metrics to assess and monitor tree invasions. *Biological Invasions*, **16,** 535-551.

Wiser, S.K., Allen, R.B. & Platt, K.H. (1997) Mountain beech forest succession after a fire at Mount Thomas Forest, Canterbury, New Zealand. *New Zealand Journal of Botany*, **35**, 505-515.

Wood, J.R., Dickie, I.A., Moeller, H.V., Peltzer, D.A., Bonner, K.I., Rattray, G. & Wilmshurst, J.M. (2015) Novel interactions between non-native mammals and fungi facilitate establishment of invasive pines. *Journal of Ecology*, **103**, 121-129.

Xiao, S., Ni, G.Y. & Callaway, R.M. (2013) Models of experimentally derived competitive effects predict biogeographical differences in the abundance of invasive and native plant species. *Plos One*, **8**, e78625.

Zalba, S.M., Cuevas, Y.A. & Boo, R.M. (2008) Invasion of *Pinus halepensis* Mill. following a wildfire in an Argentine grassland nature reserve. *Journal of Environmental Management*, **88**, 539-546.

Zenni, R.D. & Nuñez, M.A. (2013) The elephant in the room: the role of failed invasions in understanding invasion biology. *Oikos*, **122**, 801-815.

Zenni, R.D., Bailey, J.K. & Simberloff, D. (2014) Rapid evolution and range expansion of an invasive plant are driven by provenance-environment interactions. *Ecology Letters*, **17**, 727-735.

Zuloaga, F.O., Morrone, O. & Belgrano, M.J. (2008) *Catálogo de las Plantas Vasculares del Conosur (Argentina, Sur de Brasil, Chile, Paraguay y Uruguay)*. Missouri Botanical Garden Press, St. Louis.

APPENDICES

APPENDIX A

SUPPORTING INFORMATION FOR CHAPTER 2

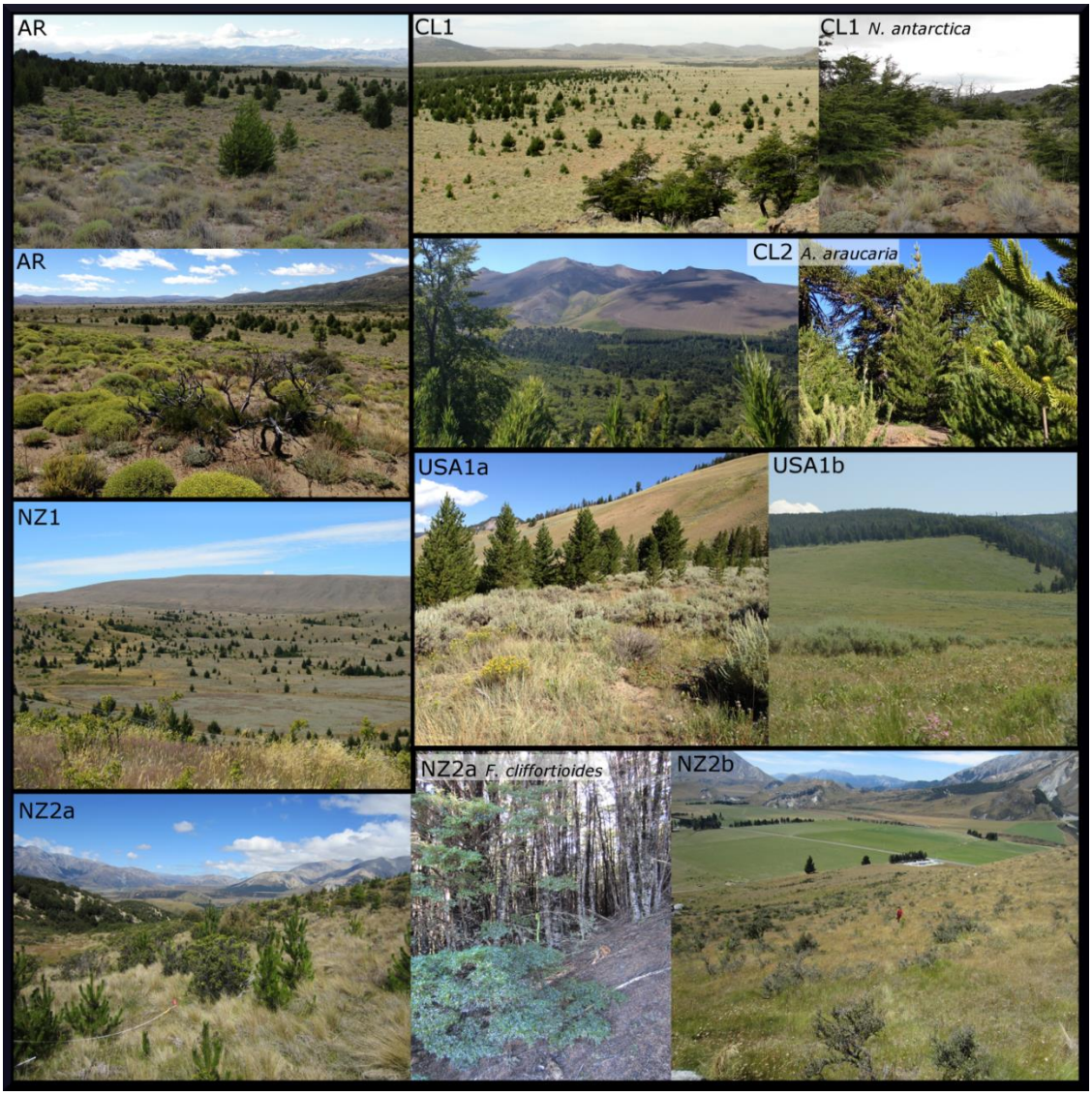

Figure A1. Photographs of each site to demonstrate the dominant vegetation and habitat types at each site. See table S1 for detailed site information.

Table A1. Descriptions of all study regions (AR1, CL1, CL2, NZ1, NZ2, USA1) and sites within regions. Abbreviations include temperature (temp.), precipitation (precip.), elevation (elev.), minimum (min.) and maximum (max.). Introduced range regions included AR1 in Argentina; CL1 and CL2 in Chile; and NZ1 and NZ2 in New Zealand. The native range region USA1 was in Montana and Wyoming, United States of America.

Site	Longitude	Latitude	Ecoregion	Density plots	Source type	Source Age (years)	Elev. range (M.S.L)	Annual mean temp. (°C)	Max. temp. (°C)	Min. temp. (°C)	Annual precip. (mm)	Precip. warmest quarter (mm)
AR1a	-71.2	-41.1	Patagonian shrub steppe	786	Plantation	34	845-892	8.2	21.9	-1.6	846	81
AR1b	-71.2	-41.1		153	Planted shelter	25	853-883	8.2	21.9	-1.6	846	81
CL1	-71.7	-45.5	Patagonian grass steppe	434	Plantation	23	703-823	5.8	16.3	-3	715	108
CL2	-71.5	-38.4	Valdivian temperate forests	54	Forestry trial plots	43	1349-1482	6.7	22.1	-2	1586	123
NZ1	170.2	-44.1	Canterbury-Otago tussock grasslands	402	Plantation	45	544-655	9.3	21.5	-1.5	658	153
NZ2a	171.7	-43.2	South Island montane grasslands	247	Plantation	53	785-1040	7.3	17.8	-2.2	2241	490
NZ2b	171.7	-43.2		84	Planted shelter	46	754-870	8.3	18.6	-1.3	1652	356
USA1a	-111.1	45.1	South Central Rockies forest - shrub steppe	1024	Native Forest	>100	2030-2411	1.4	23.7	-16	643	162
USA1b	-111.0	44.7		827	Native Forest	25	2045-2208	1.6	25	-17	587	145

Table A2. The vegetation types that transects passed through in each site. Vegetation type was scored for each plot based on the vegetation type with the most aerial cover. AR1a, AR1b, CL1, NZ1, and NZ2a were all mainly open habitats dominated by grass or short shrubs but did have patches of tall shrubs and/or southern beech in which we conducted plots. "Southern beech" includes both *Nothofagus* spp. (South America) and *Fuscospora cliffortioides* (New Zealand).

Site	*Araucaria araucana*	Grass	Southern beech	*Pinus ponderosa*	Short shrubs	Tall shrubs
AR1a		x	x		x	x
AR1b		x			x	x
CL1		x	x	x		
CL2	x	x	x			x
NZ1		x				x
NZ2a		x	x		x	x
NZ2b		x				
USA1a		x			x	
USA1b		x			x	

Table A3. 95% confidence intervals for the coefficients from the full model of each ecoregion as estimated by a post hoc Markov chain run for 10,000 simulations. Burned was the reference level for fire in AR1. AR1a, NZ2a, and USA1a were the reference levels for site. Grass was the reference level for vegetation type. "--" signifies the category did not exist at that site. "Beech" includes both *Nothofagus* spp. and *Fuscospora cliffortioides*. "SCC" is the squared correlation coefficient between the fitted and observed values.

Region (SCC)	AR1 (0.31)		CL1 (0.39)		CL2 (0.99)		NZ1 (0.76)		NZ2 (0.39)		USA1 (0.59)	
Quartile	2.5%	97.5%	2.5%	97.5%	2.5%	97.5%	2.5%	97.5%	2.5%	97.5%	2.5%	97.5%
Intercept	-0.77	-0.15	-1.67	14.86	15.62	184.55	-23.93	6.35	13.97	24.48	19.41	50.08
Site	-4.28	-2.06	--	--	--	--	--	--	-7.27	-4.72	-4.93	-1.35
Distance source	-0.0026	-0.0009	-0.0091	-0.0063	-0.016	-0.0022	-0.0017	-0.0003	-0.0037	-0.0018	-0.0414	-0.0169
Fire	0.91	2.11	--	--	--	--	--	--	--	--	--	--
Short shrub	-0.57	0.61	--	--	--	--	-2.42	1.61	-0.21	0.66	-1.26	1.75
Tall shrub	-3.30	0.58	--	--	-2.21	2.33	--	--	-1.13	-0.11	--	--
Beech	-15.81	-3.72	-5.84	-3.20	-8.56	-0.96	--	--	-10.11	-3.86	--	--
Araucaria araucana	--	--	--	--	-1.04	3.92	--	--	--	--	--	--
Pinus ponderosa	--	--	-4.77	3.02	--	--	--	--	--	--	--	--
Elevation	0.02	0.09	-0.02	0.01	-0.13	-0.01	-0.01	0.04	-0.02	-0.01	-0.02	-0.01
Slope	-0.09	0.03	-0.08	0.02	-0.49	0.16	0.007	0.24	-0.04	0.03	-0.12	0.05
CosAspect	-0.16	0.22	-0.07	0.40	-0.28	2.17	-0.49	0.15	-0.05	0.03	-0.25	0.41
SinAspect	-0.15	0.20	-0.17	0.31	0.50	2.09	-0.04	0.52	0.04	0.38	-0.28	0.42
Distance * Beech	0.0004	0.0140	0.0028	0.0093	--	--	--	--	--	--	--	--
Distance * Short shrub	-0.0011	0.0003	--	--	--	--	--	--	--	--	0.0051	0.0314
Distance * Tall shrub	-0.0039	0.0006	--	--	--	--	--	--	--	--	--	--
Distance * *P. ponderosa*	--	--	-0.0058	0.0110	--	--	--	--	--	--	--	--

Table A4. The improvement in the AICc of each model over the null model (random cluster effect, and where necessary, site) within each ecoregion. P stands for the model containing the propagule pressure (distance from source) covariate, B for the model containing the biotic covariate (vegetation type), A for the model containing abiotic covariates (elevation, slope, aspect (sine and cosine), and fire), and PAB for the model containing all covariates. logLik is the log likelihood of the model. df is model degrees of freedom. AICc is the Akaike information criterion corrected for small sample sizes. Im. AICc refers to the difference between the AICc of the selected model and the AICc of the null model (the more negative, the more improvement over the null model).

Region		Null	P	A	B	PAB
AR1	logLik	-1997.4	-1988.9	-1988.1	-1945.3	-1916.2
AR1	AICc	4002.7	3987.9	3994.4	3904.0	3865.0
AR1	df	4	5	9	7	16
AR1	Im. AICc	0	-14.8	-8.3	-98.7	-137.7
CL1	logLik	-696.7	-671.3	-695.1	-675.7	-633.6
CL1	AICc	1399.5	1350.7	1404.4	1361.6	1292.0
CL1	df	3	4	7	5	12
CL1	Im. AICc	0	-48.8	4.9	-37.9	-107.5
CL2	logLik	-129.6	-122.7	-123.3	-127.3	-111.3
CL2	AICc	265.7	254.2	263.1	268.4	250.9
CL2	df	3	4	7	6	11
CL2	Im. AICc	0	-11.5	-2.6	2.7	-14.8
NZ1	logLik	-952.1	-944.7	-943.7	-952.1	-939.5
NZ1	AICc	1910.2	1897.4	1901.8	1912.3	1897.4
NZ1	df	3	4	7	4	9
NZ1	Im. AICc	0	-12.8	-8.4	2.1	-12.8
NZ2	logLik	-924.3	-924.2	-913.9	-897.1	-876.9
NZ2	AICc	1856.8	1858.6	1844.2	1808.5	1778.8
NZ2	df	4	5	8	7	12
NZ2	Im. AICc	0	1.8	-12.6	-48.3	-78.0
USA1	logLik	-739.6	-731.4	-734.3	-738.5	-714.7
USA1	AICc	1487.3	1472.8	1484.6	1487.1	1449.4
USA1	df	4	5	8	5	10
USA1	Im. AICc	0	-14.5	-2.7	-0.2	-37.9

Table A5. Coefficient estimates and standard errors (SE) from the mixed negative binomial global model with all plots. Grass was the reference level for vegetation type. USA1a was the reference level for site. Cluster was the random effect. The approximate *P* values are from Wald Z-tests. See Table 2.1, Fig. A1, and Tables A1 and A2 for site descriptions.

Variable	Estimate	SE	z	P
Intercept	-2.78	0.40	-7.01	<0.0001
Distance to source	-4.50	1.58	-2.85	0.0044
Forest	-2.36	0.59	-3.98	<0.0001
Short shrub	0.49	0.21	2.33	0.0196
Tall shrub	-2.09	0.44	-4.79	<0.0001
AR1a	4.51	0.55	8.20	<0.0001
AR1b	3.88	0.95	4.07	<0.0001
CL1	5.94	0.64	9.34	<0.0001
CL2	7.34	0.94	7.83	<0.0001
NZ1	5.44	0.58	9.33	<0.0001
NZ2a	4.46	0.91	4.89	<0.0001
NZ2b	5.67	1.19	4.76	<0.0001
USA1b	2.97	0.67	4.46	<0.0001
Distance to source * Forest	-0.08	0.99	-0.08	0.9368
Distance to source * Short shrub	-0.64	0.25	-2.53	0.0113
Distance to source * Tall shrub	0.34	0.45	0.75	0.453
Distance to source * AR1a	3.24	1.63	1.98	0.0475
Distance to source * AR1b	-4.27	3.16	-1.35	0.1762
Distance to source * CL1	-2.56	1.91	-1.34	0.1799
Distance to source * CL2	-3.66	2.51	-1.46	0.1445
Distance to source * NZ1	3.28	1.60	2.05	0.0407
Distance to source * NZ2a	5.07	1.73	2.92	0.0035
Distance to source * NZ2b	-8.09	4.18	-1.94	0.0528
Distance to source * USA1b	-62.65	10.48	-5.98	<0.0001

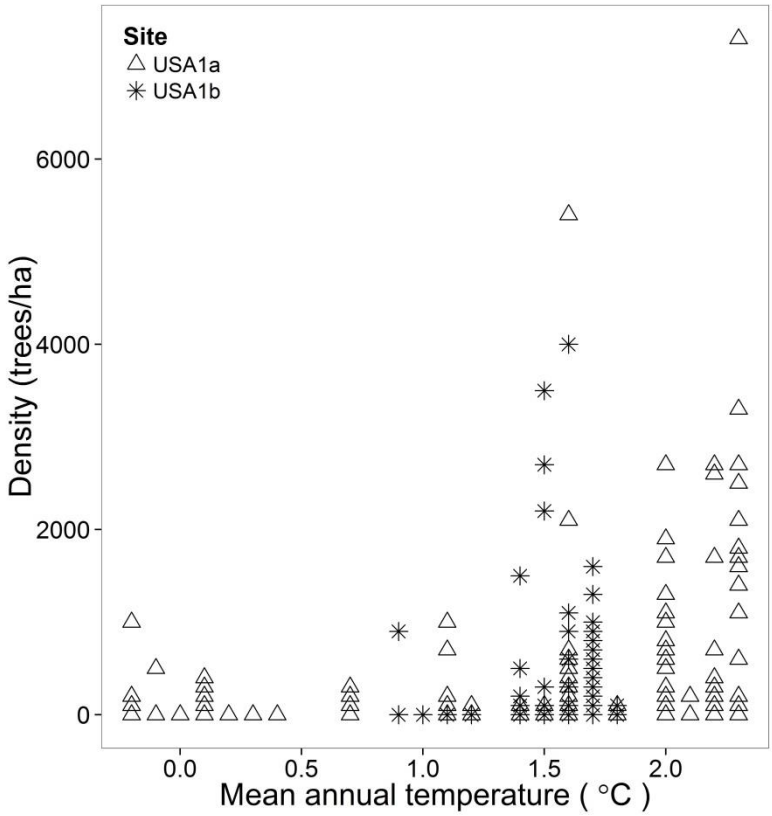

Figure A2. Density of *P. contorta* invasion in the native range USA ecoregion compared to the mean annual temperature of the plot (Hijmans et al. 2005; 30 arc-second resolution). Point shape differentiates the two sites (USA1a and USA1b).

Table A6. The top five most explanatory bioclimatic variables of invasion density in a model containing all density data from the native and introduced range and a model with just data from the introduced range. Due to collinearity between bioclimatic variables (Hijmans *et al*., 2005), mixed negative binomial models of *Pinus contorta* density were created with a single bioclimatic variable, vegetation type, and distance from source as fixed effects and site and cluster as random effects. The models were then ranked by AICc (Akaike information criterion corrected for small sample sizes). Abbreviations include temperature (temp.) and precipitation (precip.).

Native and introduced ranges		Introduced range	
Variable	deltaAICc	Variable	deltaAICc
Mean temp. coldest quarter	0	Mean temp. wettest quarter	0
Annual mean temp.	3.28	Precip. warmest quarter	17.16
Min temp. coldest month	6.04	Precip. seasonality	17.26
Temp. seasonality	25.42	Precip. driest quarter	18.02
Temp. annual range	38.22	Precip. driest month	18.88

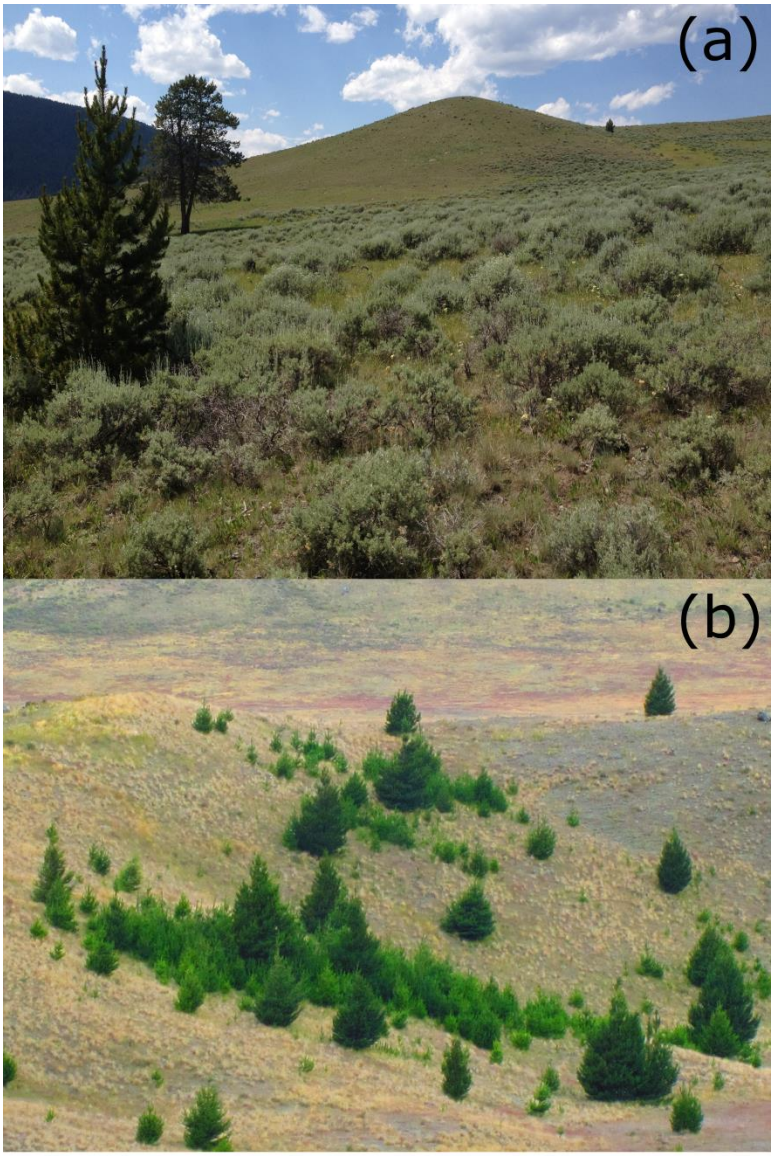

Figure A3. Photos exemplifying the lack of seedling establishment beneath *P. contorta* individuals growing in short shrub (i.e. sagebrush steppe) at the native range USA1a site (a), and the abundance of seedlings surrounding older individuals in grasslands of the introduced range at NZ1 more than 1.5 km from the source edge (b). See Table 2.1, Fig. A1, and Tables A1 and A2 for site descriptions.

APPENDIX B

SUPPORTING INFORMATION FOR CHAPTER 3

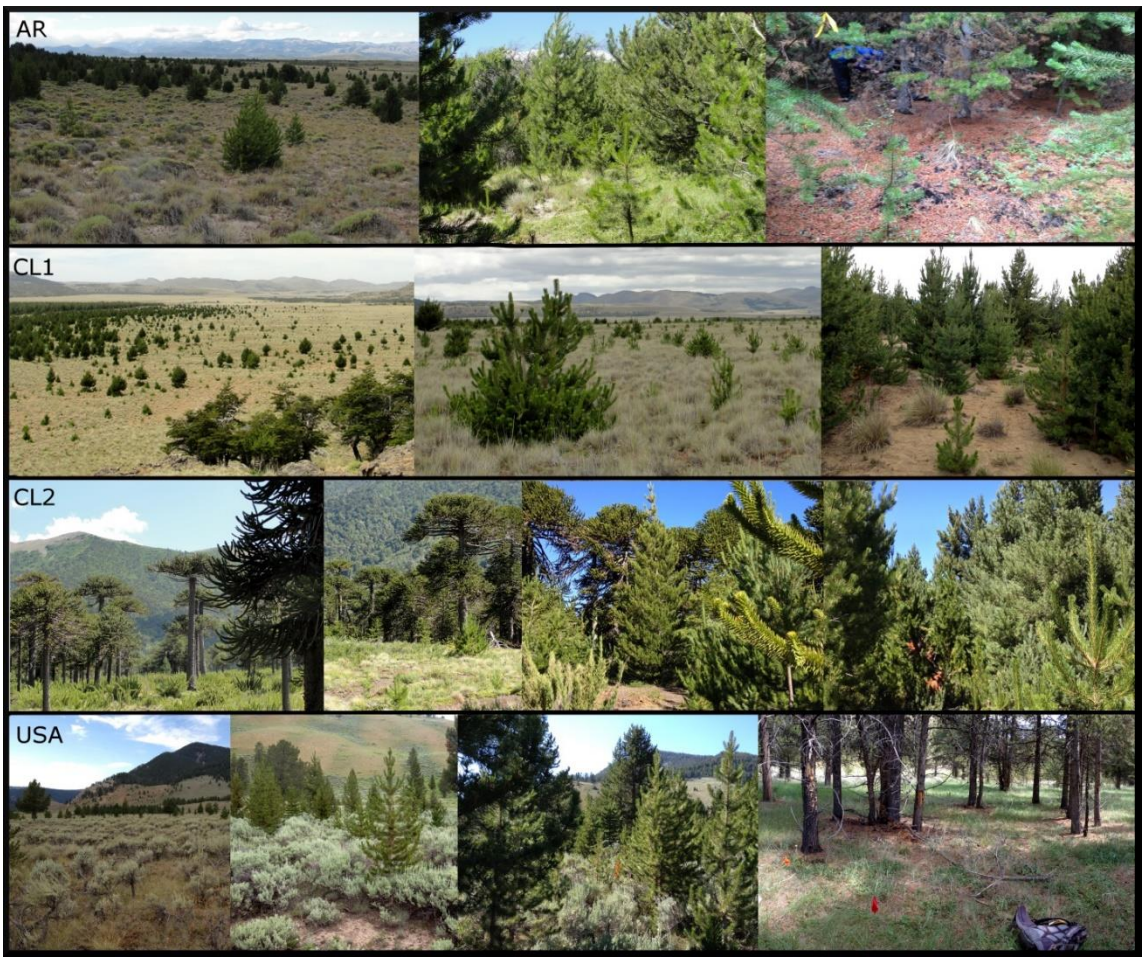

Figure B1. Photos of all sites with examples of increasingly dense *P. contorta* invasion at each site moving from left to right. Top row is site AR, second row from top is site CL1, third row from top is site CL2, and bottom row is site USA. The decrease in understory plant cover is clear in the photos farthest to the right.

Table B1. Description of study sites (AR, CL1, CL2, USA). Climate data obtained from the WorldClim database (Hijmans *et al.*, 2005). Abbreviations include temperature (temp.), precipitation (precip.), minimum (min.), maximum (max.), and coefficient of variation (CV).

Site	AR	CL1	CL2	USA
Longitude	-71.229	-71.702	-71.542	-111.14
Latitude	-41.148	-45.501	-38.424	45.064
Plots	13	20	19	21
Community type	Patagonian shrub steppe	Patagonian grass steppe	*Araucaria araucana* forest	*Artemisia tridentata* shrub steppe
Source type	Plantation	Plantation	Forestry trial plots	Native Forest
Source Age (years)	34	23	43	>100
Elevation (M.S.L)	835	745	1435	2060
Annual mean temp. (°C)	8.2	5.8	6.7	1.4
Mean max. temp. (°C)	21.9	16.3	22.1	23.7
Mean min. temp. (°C)	-1.6	-3	-2	-16
Annual precip. (mm)	846	715	1586	643
Precip. wettest quarter (mm)	417	290	810	192
Precip. driest quarter (mm)	81	108	123	135
Precip. warmest quarter (mm)	81	108	123	162
Precip. coldest quarter (mm)	397	262	767	164
Precip. seasonality (CV)	65	42	69	18
Mean temp. wettest quarter (°C)	3.5	1.1	2.6	5.3
Mean temp. driest quarter (°C)	13.8	10.6	11.5	8.4
Temperature annual range (°C)	23.5	19.3	24.1	40.0

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965-1978.

Table B2. The species found at each site, number of plots each species occurred in, frequency of that species (number of plots containing that species divided by total number of plots sampled), and status as native (N) or introduced (I). Species whose names appear in bold were found only in uninvaded plots and species whose names are underlined were found only in invaded plots. Note that at all sites sample sizes for invaded plots were significantly larger than sample sizes for uninvaded plots (especially at CL1 and CL2) due to our strategy of sampling continuously across the invasion gradient (rather than in invaded versus uninvaded plots). This likely inflates the number of species only found in invaded plots and decreases the number of species found only in uninvaded plots artificially.

Species	Plots	Frequency	Status
AR - Bariloche, Argentina			
Acaena splendens Hook. & Arn.	12	0.92	N
Festuca pallescens (St.-Yves) Parodi	10	0.77	N
Mulinum spinosum (Cav.) Pers.	10	0.77	N
Rumex acetosella L.	9	0.69	I
Acaena pinnatifida Ruiz & Pav.	8	0.62	N
Anemone multifida Poir.	7	0.54	N
Baccharis magellanica (Lam.) Pers.	7	0.54	N
Hordeum comosum J. Presl	7	0.54	N
Galium richardianum (Gillies ex Hook. & Arn.) Endl. ex Walp.	6	0.46	N
Koeleria sp.	6	0.46	
Agrostis capillaris L.	5	0.38	I
Euphorbia collina Phil.	5	0.38	N
Potentilla chiloensis (L.) Mabb.	5	0.38	N
Berberis microphylla G. Forst.	4	0.31	N
***Senecio sericeonitens* Speg.**	4	0.31	N
Senecio sp.	4	0.31	
***Adesmia corymbosa* Clos**	3	0.23	N
Pappostipa speciosa (Trin. & Rupr.) Romasch.	3	0.23	N
***Perezia recurvata* (Vahl) Less.**	3	0.23	N
Senecio bracteolatus Hook. & Arn.	3	0.23	N
Taraxacum officinale G. Weber ex F.H. Wigg.	3	0.23	I
***Valeriana clarionifolia* Phil.**	3	0.23	N
Danthonia sp.	2	0.15	
Holcus lanatus L.	2	0.15	I

Table B2 continued (AR species list).

Species	Plots	Frequency	Status
Hypochaeris radicata L.	2	0.15	I
***Lathyrus magellanicus* Lam.**	2	0.15	N
Nassauvia aculeata (Less.) Poepp. & Endl.	2	0.15	N
***Senecio neaei* DC.**	2	0.15	N
***Solidago chilensis* Meyen**	2	0.15	N
Viola reichei Skottsb.	2	0.15	N
Acaena platyacantha Speg.	1	0.08	N
Adesmia volckmannii Phil.	1	0.08	N
***Anarthrophyllum rigidum* (Gillies ex Hook. & Arn.) Hieron.**	1	0.08	N
Azorella trifoliolata Clos	1	0.08	N
Baccharis linearis (Ruiz & Pav.) Pers.	1	0.08	N
Berberis dawinii Hook.	1	0.08	N
Bromus setifolius J. Presl	1	0.08	N
Cerastium arvense L.	1	0.08	I
Chloraea magellanica Hook. f.	1	0.08	N
***Discaria articulata* (Phil.) Miers**	1	0.08	N
Euphorbia peplus L.	1	0.08	I
Fabaceae 1	1	0.08	
***Festuca pyrogea* Speg.**	1	0.08	N
Geranium magellanicum Hook. f.	1	0.08	N
Olsynium junceum (E. Mey. ex C. Presl) Goldblatt	1	0.08	N
***Oreopolus glacialis* (Poepp.) Ricardi**	1	0.08	N
Poa lanuginosa Poir.	1	0.08	N
Poa ligularis Nees ex Steud.	1	0.08	N
Rhodophiala mendocina (Phil.) Ravenna	1	0.08	N
***Sisyrinchium arenarium* Poepp.**	1	0.08	N
Unknown forb 1	1	0.08	
Unknown forb 2	1	0.08	

CL1 - Coyhaique, Chile

Anemone multifida Poir.	20	1.00	N
Baccharis magellanica (Lam.) Pers.	20	1.00	N
Rumex acetosella L.	20	1.00	I
Festuca pallescens (St.-Yves) Parodi	19	0.95	N
Acaena integerrima Gillies ex Hook. & Arn.	18	0.90	N

Table B2 continued (CL1 species list).

Species	Plots	Frequency	Status
Taraxacum officinale G. Weber ex F.H. Wigg.	16	0.80	I
Calceolaria biflora Lam.	12	0.60	N
Galium fuegianum Hook. f.	12	0.60	N
Agrostis capillaris L.	11	0.55	I
Sisyrinchium arenarium Poepp.	10	0.50	N
Erigeron imbricatus Vierh.	9	0.45	N
Lathyrus sp.	9	0.45	N
Loasa bergii Hieron.	9	0.45	N
Viola reichei Skottsb.	9	0.45	N
Acaena pinnatifida Ruiz & Pav.	8	0.40	N
Azorella ameghinoi Speg.	8	0.40	N
Cerastium arvense L.	8	0.40	I
Nassauvia darwinii (Hook. & Arn.) O. Hoffm. & Dusén	8	0.40	N
Senecio kingii Hook. f.	8	0.40	N
Senecio sericeonitens Speg.	8	0.40	N
Armeria maritima (Mill.) Willd.	7	0.35	N
Poaceae 1	7	0.35	
Chloraea magellanica Hook. f.	6	0.30	N
Festuca pyrogea Speg.	6	0.30	N
Leucheria candidissima D. Don	6	0.30	N
Mulinum spinosum (Cav.) Pers.	6	0.30	N
Noccaea magellanica (Comm. ex Poir.) Holub	6	0.30	N
Phacelia secunda J.F. Gmel.	6	0.30	N
Poa sp.	6	0.30	
Valeriana carnosa Sm.	6	0.30	N
Geranium sessiliflorum Cav.	5	0.25	N
Calceolaria lagunae-blancae Kraenzl.	4	0.20	N
Hypochaeris radicata L.	4	0.20	I
Luzula alopecurus Desv.	4	0.20	N
Oreopolus glacialis (Poepp.) Ricardi	4	0.20	N
Hordeum comosum J. Presl	3	0.15	N
Oxalis adenophylla Gillies ex Hook. & Arn.	3	0.15	N
Vulpia myuros (L.) C.C. Gmel.	3	0.15	I
Danthonia sp.	2	0.10	
Quinchamalium chilense Molina	2	0.10	N
Bromus sp.	1	0.05	

Table B2 continued (CL1 species list).

Species	Plots	Frequency	Status
Carex sp.	1	0.05	
Caryophyllaceae 1	1	0.05	
Dactylis glomerata L.	1	0.05	I
Hieracium sp. 1	1	0.05	
Hieracium sp. 2	1	0.05	
Microsteris gracilis (Hook.) Greene	1	0.05	N
***Silene magellanica* (Desr.) Bocquet**	1	0.05	N
Stipa sp.	1	0.05	

CL2 - Malalcahuello, Chile

Festuca scabriuscula Phil.	18	0.95	N
Rumex acetosella L.	15	0.79	I
Eleocharis melanostachys (d'Urv.) C.B. Clarke	14	0.74	N
Gaultheria poeppigii DC.	13	0.68	N
Baccharis magellanica (Lam.) Pers.	12	0.63	N
Chusquea culeou E. Desv.	11	0.58	N
Cerastium arvense L.	10	0.53	I
Potentilla chiloensis (L.) Mabb.	10	0.53	N
Galium fuegianum Hook. f.	9	0.47	N
Araucaria araucana (Molina) K. Koch	8	0.42	N
Discaria chacaye (G. Don) Tortosa	8	0.42	N
Berberis montana Gay	7	0.37	N
Gaultheria pumila (L. f.) D.J. Middleton	7	0.37	N
Poaceae 1	7	0.37	
Sisyrinchium arenarium Poepp.	7	0.37	N
Acaena pinnatifida Ruiz & Pav.	6	0.32	N
Baccharis concava (Ruiz & Pav.) Pers.	6	0.32	N
Lathyrus sp.	6	0.32	N
Quinchamalium chilense Molina	6	0.32	N
Adesmia emarginata Clos	5	0.26	N
Empetrum rubrum Vahl ex Willd.	5	0.26	N
Mulinum spinosum (Cav.) Pers.	4	0.21	N
Nothofagus antarctica (G. Forst.) Oerst.	4	0.21	N
Poa sp.	4	0.21	
Senecio chilensis Less.	4	0.21	N
Berberis empetrifolia Lam.	3	0.16	N
Pinus sylvestris L.	3	0.16	I

Table B2 continued (CL2 species list).

Species	Plots	Frequency	Status
Rhodophiala mendocina (Phil.) Ravenna	3	0.16	N
Berberis microphylla G. Forst.	2	0.11	N
Chloraea magellanica Hook. f.	2	0.11	N
Geranium magellanicum Hook. f.	2	0.11	N
Perezia fonkii (Phil.) Reiche	2	0.11	N
Poaceae 2	2	0.11	
Senecio baccharidifolius Poepp. ex DC.	2	0.11	N
Vicia sp.	2	0.11	
Viola reichei Skottsb.	2	0.11	N
Agrostis philippiana Rúgolo & De Paula	1	0.05	N
Anemone multifida Poir.	1	0.05	N
Berberis actinacantha Mart.	1	0.05	N
Calceolaria biflora Lam.	1	0.05	N
Danthonia sp.	1	0.05	
Hieracium sp.	1	0.05	
Hypochaeris apargioides Hook. & Arn.	1	0.05	N
Luzula alopecurus Desv.	1	0.05	N
***Nothofagus pumilio* (Poepp. & Endl.)** Krasser	1	0.05	N
Poaceae 3	1	0.05	
Poaceae 4	1	0.05	
Ribes cucullatum Hook. & Arn.	1	0.05	N
Senecio sp. 2	1	0.05	
Unknown forb 1	1	0.05	

USA - Greater Yellowstone Ecosystem, Montana

Festuca idahoensis Elmer	21	1.00	N
Carex sp.	19	0.90	N
Geum triflorum Pursh	19	0.90	N
Antennaria rosea Greene	18	0.86	N
Achillea millefolium L.	17	0.81	N
Artemisia tridentata Nutt.	17	0.81	N
Agropyron smithii Rydb.	16	0.76	N
Stipa richardsonii Link	15	0.71	N
Koeleria macrantha (Ledeb.) Schult.	13	0.62	N
Symphyotrichum foliaceum (Lindl. Ex DC.) G. L .Nesom	13	0.62	N
Taraxacum officinale F. H. Wigg.	13	0.62	I

Table B2 continued (USA species list).

Species	Plots	Frequency	Status
Eriogonum umbellatum Torr.	12	0.57	N
Arenaria congesta Nutt.	11	0.52	N
Fragaria virginiana Mill.	9	0.43	N
Lupinus sericeus Pursh	9	0.43	N
Penstemon procerus Douglas ex Graham	9	0.43	N
Potentilla gracilis Douglas ex Hook.	9	0.43	N
Agoseris glauca (Pursh) Raf.	8	0.38	N
Danthonia intermedia Vasey	8	0.38	N
Phlox hoodii Richarson	8	0.38	N
Stipa viridula Trin.	8	0.38	N
Linum lewisii Pursh	7	0.33	N
Phlox longifolia Nutt.	7	0.33	N
Viola sp.	7	0.33	N
Anemone multifida Poir.	6	0.29	N
Bromus porteri (J. M. Coulter) Nash	6	0.29	N
Erigeron sp. 1	6	0.29	N
Besseya wyomingensis (A. Nelson) Rydb.	5	0.24	N
Cirsium hookerianum Nutt.	5	0.24	N
Dasiphora fructicosa (L.) Rydb.	5	0.24	N
Galium boreale L.	5	0.24	N
Phleum pratense L.	5	0.24	I
Poa pratensis L.	5	0.24	I
Senecio streptanthifolius Greene	5	0.24	N
Juniperus communis L.	4	0.19	N
Noccaea fendleri (A. Gray) Holub	4	0.19	N
Orthocarpus tenuifolius (Pursh) Benth.	4	0.19	N
***Poa secunda* J. Presl**	4	0.19	N
Solidago missouriensis Nutt.	4	0.19	N
Boechera stricta (Graham) Al-Shebaz	3	0.14	N
Cerastium arvense L.	3	0.14	N
Chrysothamnus viscidiflorus (Hook.) Nutt.	3	0.14	N
Juncus sp.	3	0.14	N
Poa palustris L.	3	0.14	N
***Symphyotrichum campestre* (Nutt.) G. L. Nesom**	3	0.14	N
Symphyotrichum sp.	3	0.14	N
***Tragopogon dubius* Scop.**	3	0.14	I
Agropyron trachycaulum (Link) Malte	2	0.10	N

Table B2 continued (USA species list).

Species	Plots	Frequency	Status
***Arabis nuttallii* (Kuntz) B. L. Rob**	2	0.10	N
***Artemisia cana* Pursh**	2	0.10	N
Artemisia nova A. Nelson	2	0.10	N
***Astragalus miser* Douglas ex. Hook.**	2	0.10	N
Campanula rotundifolia L.	2	0.10	N
***Cymopterus nivalis* S. Watson**	2	0.10	N
Drymocallis arguta	2	0.10	N
***Erigeron* sp. 2**	2	0.10	N
Frasera speciosa Douglas ex Griseb.	2	0.10	N
Hieracium scouleri Hook.	2	0.10	N
Myosotis alpestris F. W. Schmidt	2	0.10	N
Oxytropis sericea Nutt.	2	0.10	N
Poa fendleriana (Steud.) Vasey	2	0.10	N
Poaceae 1	2	0.10	
***Potentilla pensylvanica* L.**	2	0.10	N
***Smilacina stellata* (L.) Desf.**	2	0.10	N
Unknown forb	2	0.10	
Agrostis scabra Willd.	1	0.05	N
***Allium cernuum* Roth**	1	0.05	N
***Arnica sororia* Greene**	1	0.05	N
***Artemisia frigida* Willd.**	1	0.05	N
Astragalus americanus (Hook.) M. E. Jones	1	0.05	N
***Astragalus kentrophyta* A. Gray**	1	0.05	N
Brassicaceae 1	1	0.05	
Bromus inermis Leyss.	1	0.05	I
***Cirsium undulatum* (Nutt.) Spreng.**	1	0.05	N
***Delphinium bicolor* Nutt.**	1	0.05	N
***Equisetum hyemale* L.**	1	0.05	N
***Ericameria nauseosa* (Pall. Ex Pursh) G. L. Nesom & G. I. Baird**	1	0.05	N
Gentiana affinis Griseb.	1	0.05	N
Geranium viscosissimum Fisch & C. A. Mey.	1	0.05	N
Micranthes odontoloma (Piper) A. Heller	1	0.05	N
Pyrola chlorantha Sw.	1	0.05	N
***Ribes* sp.**	1	0.05	N
***Salix geyeriana* Andersson**	1	0.05	N
***Salix wolfii* Bebb**	1	0.05	N
***Senecio pseudaureus* Rydb.**	1	0.05	N

Table B2 continued (USA species list).

Species	Plots	Frequency	Status
Shepherdia canadensis (L.) Nutt.	1	0.05	N
***Solidago rigida* L.**	1	0.05	N
***Sphaeralcea coccinea* (Nutt.) Rydb.**	1	0.05	N
***Symphyotrichum falcatum* (Lindl.) G. L. Nesom**	1	0.05	N
***Thalictrum occidentale* A. Gray**	1	0.05	N
***Thlaspi arvense* L.**	1	0.05	I
***Trifolium longipes* Nutt.**	1	0.05	N

Table B3. The slope and p-value for each species that had a relationship between their cover and *Pinus contorta* cover at all sites. N represents the number of plots that each species was found in. In the text significance is assumed at $P<0.05$ but here we display species whose relationship with *Pinus contorta* cover has a significance of $P<0.1$ to show the species that have weaker correlations with *Pinus contorta* as well.

Site	Species	Slope	p-value	N
AR	*Agrostis capillaris*	-0.0026	0.085	5
AR	*Koeleria* sp.	-0.0030	0.041	6
AR	*Mulinum spinosum*	-0.3715	0.004	10
AR	*Rumex acetosela*	-0.0029	0.090	9
AR	*Senecio sericeonitens*	-0.0007	0.046	4
AR	*Taraxacum officinale*	0.0034	0.084	3
CL1	*Agrostis capillaris*	-0.0086	0.013	11
CL1	*Armeria maritima*	-0.0022	0.025	7
CL1	*Calceolaria biflora*	-0.0030	0.006	12
CL1	*Chloraea magellanica*	-0.0008	0.005	6
CL1	*Erigeron imbricatus*	-0.0016	0.031	9
CL1	*Festuca pallescens*	-0.1555	0.029	19
CL1	*Festuca pyrogea*	-0.0082	0.018	6
CL1	*Loasa berghi*	-0.0008	0.020	9
CL1	*Luzula alopecurus*	-0.0006	0.026	4
CL1	*Mulinum spinosum*	-0.0049	0.020	6
CL1	*Nassauvia darwinii*	-0.0026	0.008	8
CL1	*Noccaea magellanica*	-0.0007	0.017	6
CL1	*Senecio kingii*	-0.0017	0.049	8
CL1	*Sisyrinchium arenarium*	-0.0008	0.010	10
CL1	*Viola reichei*	0.0009	0.005	9
CL2	*Acaena pinnatifida*	-0.0053	0.069	6
CL2	*Eleocharis melanostachys*	-0.0092	0.024	14
CL2	*Festuca scabriuscula*	-0.1790	0.009	18
CL2	*Lathyrus* sp.	-0.0036	0.059	6
CL2	*Quinchamalium chilense*	-0.0034	0.053	6
USA	*Agropyron smithii*	0.0151	0.093	16
USA	*Artemisia tridentata*	-0.2215	0.060	17
USA	*Besseya wyomingensis*	-0.0005	0.075	5
USA	*Juniperus communis*	0.0040	0.055	4
USA	*Poa palustris*	0.0033	0.039	3

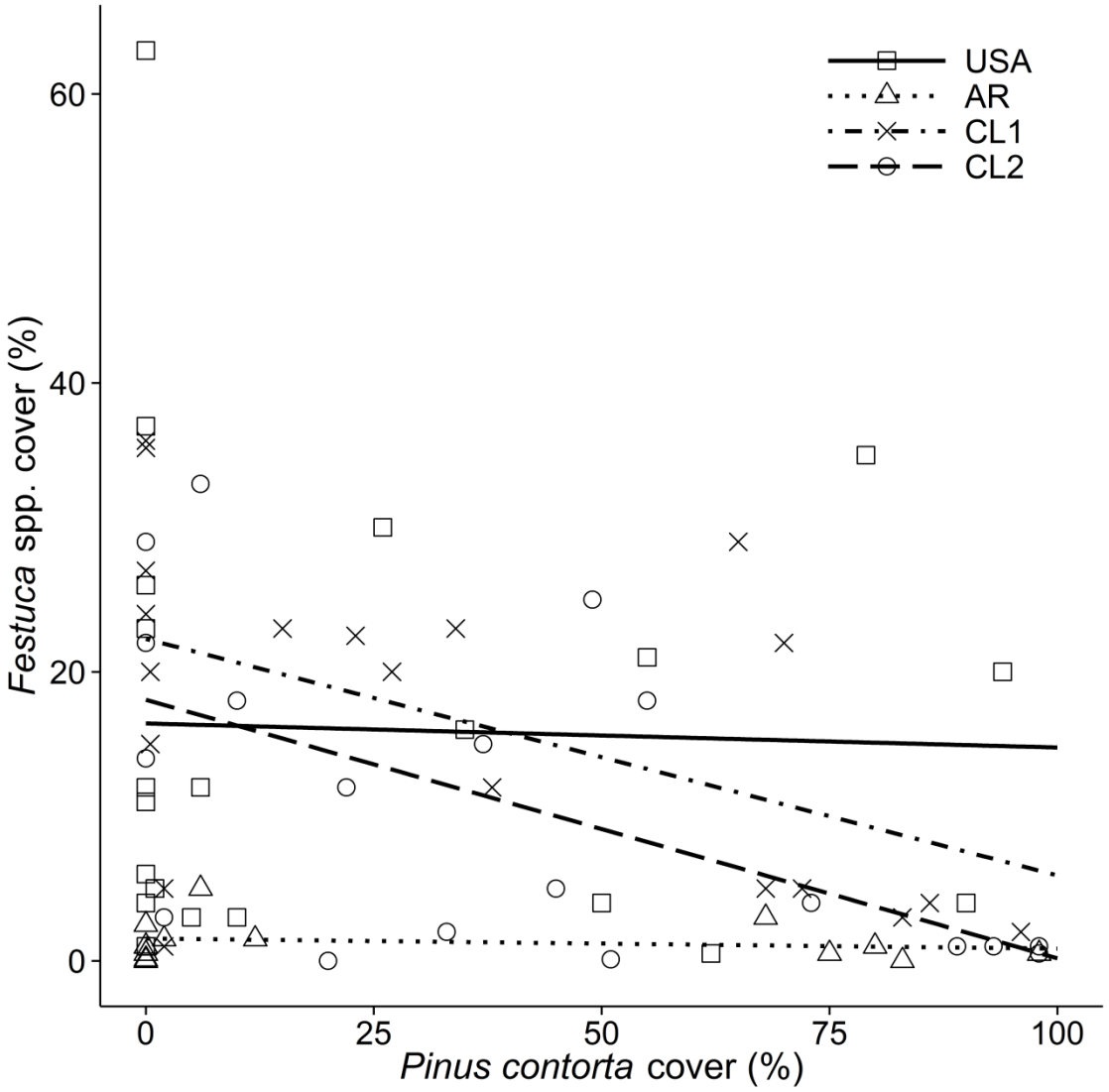

Figure B2. *Festuca* spp. cover against *Pinus contorta* cover at each site. The slope of the lines for USA and AR are not statistically different than zero, but the lines are still shown for comparison.

APPENDIX C

SUPPORTING INFORMATION FOR CHAPTER 4

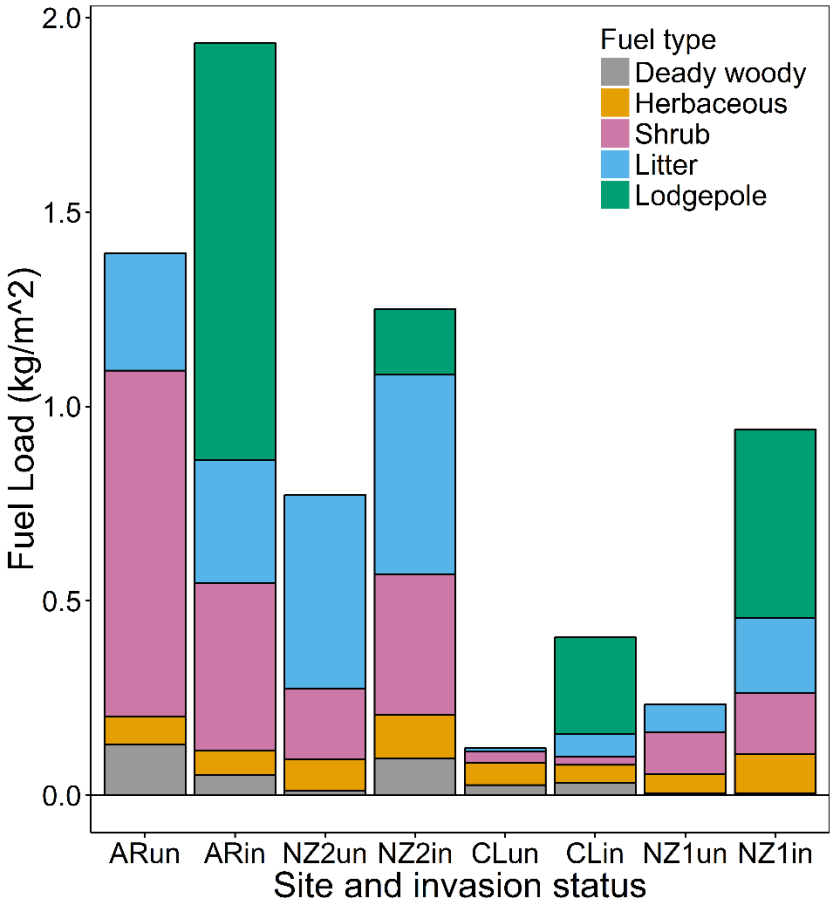

Figure C1. Mean fuel loads (kg/m^2) in each fuel class in invaded versus uninvaded plots at each site. “un” and “in” following site names stands for uninvaded and invaded, respectively. AR and NZ2 were shrublands and CL and NZ1 were grasslands.

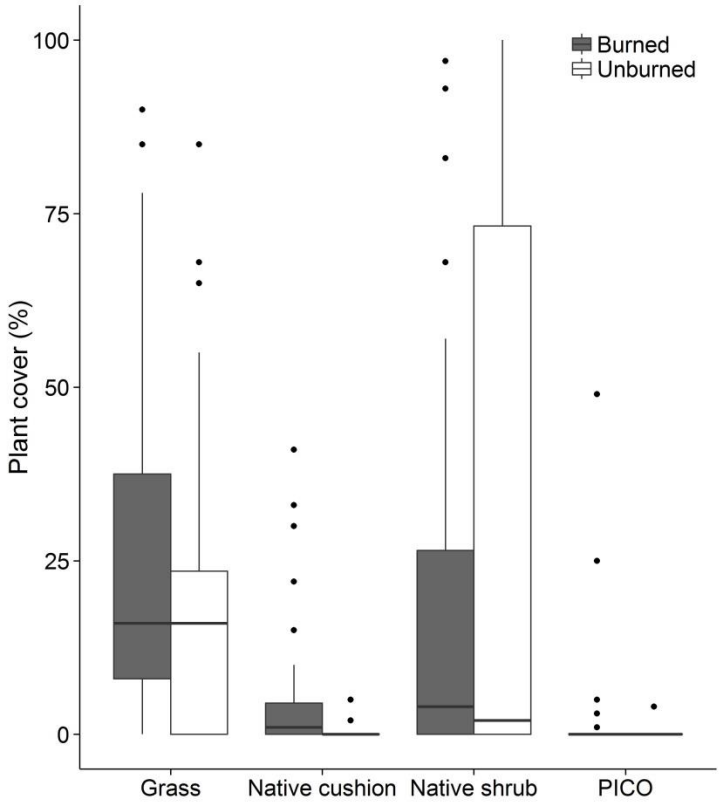

Figure C2. Cover of grass, native cushion plants, native shrubs, and *P. contorta* (PICO) in burned (gray fill) and unburned (white fill) one meter squared subplots at NZ2. Unburned plots fell within 100 meters of the fire boundary.

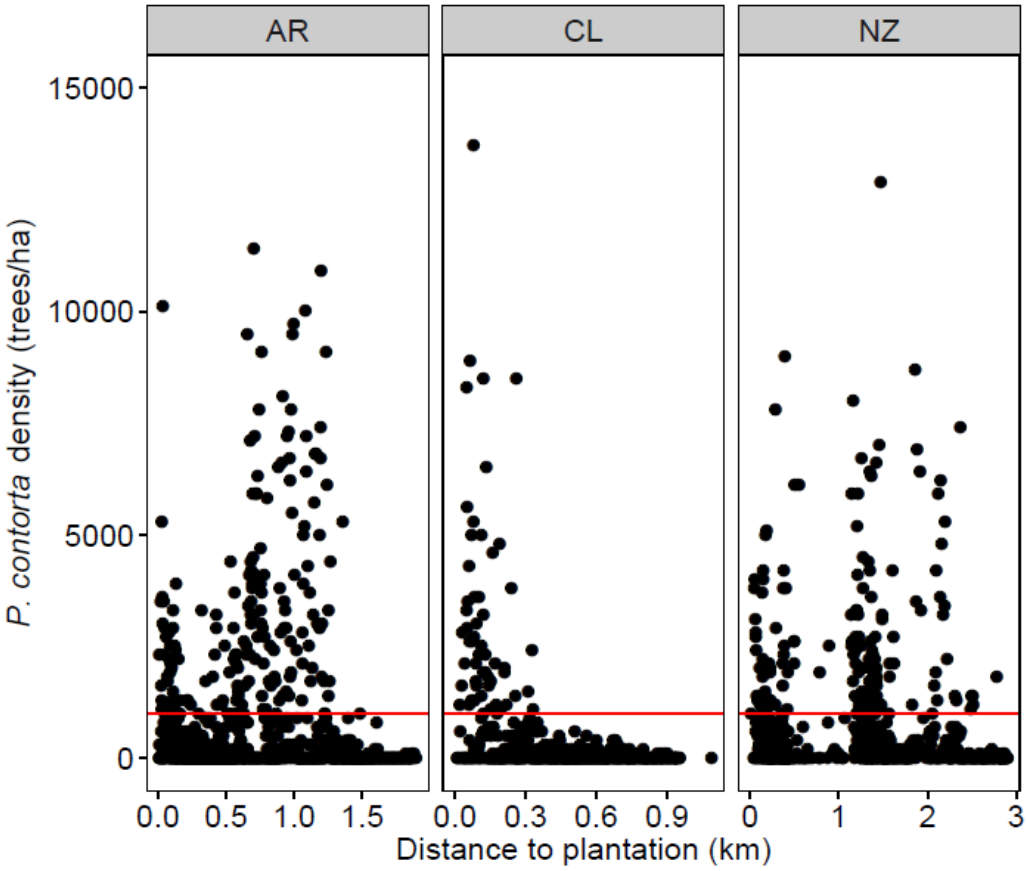

Figure C3. Density of *Pinus contorta* invasion with increasing distance from source plantation edge at sites AR (Bariloche, Argentina), CL (Coyhaique Alto, Chile), and NZ (NZ1 and NZ2 sites combined, Lake Pukaki and Craigieburn Forest Park respectively). The invasion threshold above which a positive feedback with fire can be expected (1000 trees/ha) is drawn in red. Each point represents a sample 100 m^2 plot (see Taylor et al. 2016a for details). This threshold was determined at the AR site and may vary by site depending on the native vegetation response to fire.

APPENDIX D

SUPPORTING INFORMATION FOR CHAPTER 5

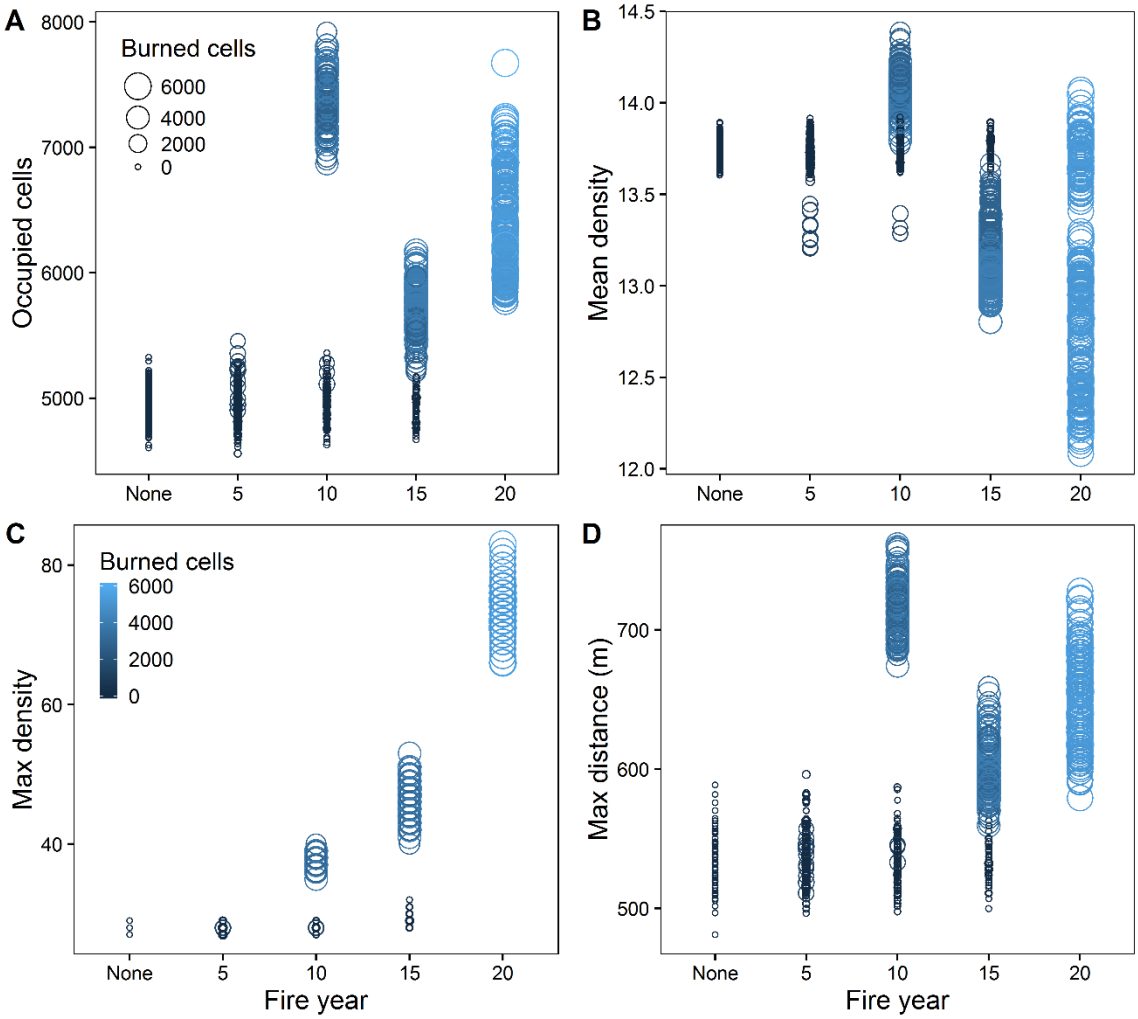

Figure D1. *Pinus contorta* occupied cells (A), mean density (B), maximum density (C), and maximum distance of an invading individual from the plantation (D) shown for each fire year treatment. The size and color of the points represent the size of the fire (number of burned cells) in that run. The larger and lighter colored points represent larger fires.