

THE LIFE CYCLE OF PLANT INVASIONS: A STUDY OF THE DRIVERS AND IMPACTS OF DOMINANT NON-NATIVE GRASSLAND SPECIES.

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DECLARATION OF CO-AUTHORED PUBLICATIONS

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2. **O'Reilly-Nugent, A.**, Wandrag, E. M., Catford, J. A., Gruber, B., Driscoll, D., & Duncan, R. P. (2019). Measuring competitive impact: joint-species modelling of invaded plant communities. *Journal of Ecology*, 1–11. <https://doi.org/10.1111/1365-2745.13280>
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Any data or code used in these chapters is available at <https://github.com/aornugent/>.

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Data collection	--	AO, DD	AO	AO, DB
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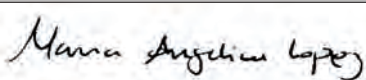
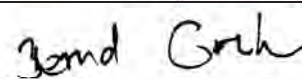
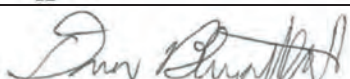
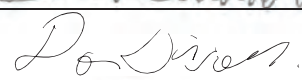
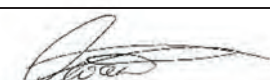

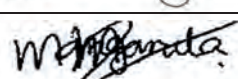
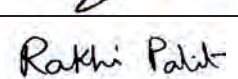
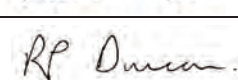
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ABSTRACT

Non-native plant species that become invasive can impact native communities and exclude native species. Understanding what drives the ongoing success of dominant non-native species is essential to mitigating the impacts of non-native species and predicting where mitigation will be successful. However, the key processes that determine invasion outcomes are context dependent and change throughout the life cycle of an invasion. Consequently, predicting invasion success and non-native species impact remains challenging. In this thesis I aim to identify dominant non-native species having significant negative impacts on grassland communities. I present four studies that span the major stages of an invasion: the spread and establishment of non-native species, the impacts of non-native species following establishment and the persistence of these impacts in the long term.

A common theme throughout is the need to disentangle the relative importance of site suitability and competitive interactions between non-native and resident species. We present a framework for understanding the landscape effects on the spread of non-native species. Long-distance dispersal events, coupled with the distribution of sites suitable for establishment, are the key determinants of non-native species spread. We also show that non-native species impact is determined by the conditions under which dominant non-native species maintain competitive superiority.

We develop a modelling approach for quantifying the impacts of dominant non-native species in a community context. We find that non-native species impact varied significantly under different conditions of resource availability and disturbance. Experimentally validating this analysis, we test the role of environmental and competitive conditions in determining these impacts. We also show that many non-native species can persist long-term. Our findings suggest that rehabilitation can be effective, but that interventions should target communities where the conditions facilitating non-native species impact are not expected to change.

Overall, this thesis highlights the difficulties in separating the different processes underlying invasion success and non-native species impact. Because environmental and

competitive drivers are both important, the relative importance of different processes can be confounded in observed patterns of species abundance. Combining observational and experimental data is essential, as neither approach is enough to conclusively identify which processes are most important at determining success and impact at different stages of the invasion lifecycle. The studies in this thesis demonstrate when models can fail and highlight the need for experiments that are both general and robust. The need to compare model and experiment is especially acute in ecology, where natural settings are often far from controlled, but managing the impacts of dominant non-native species requires action under uncertainty.

Keywords:

Invasion, non-native species, grasslands, dominance, spread, impact, joint-species modelling, rehabilitation, competition.

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1 INTRODUCTION

Author

Andrew O'Reilly-Nugent.

(2019).

1.1 General drivers of invasion, or a lack thereof

Invasion ecology focuses on the processes that allow new species to move between communities, finding space to settle and obtain the resources to reproduce and persist among established groups of species (Ehrenfeld, 2010; Mack et al., 2000). Research in invasion ecology often traces the path of conspicuous non-native species through a series of steps common to all invasions: introduction, establishment, impact and spread (Blackburn et al., 2011; Richardson et al., 2000). Conspicuous non-native species tend to be easily identifiable and often particularly damaging, diminishing the condition of invaded communities by outcompeting or excluding resident species (Vilà et al., 2011). Some non-native species can have severe impacts beyond community composition (Falk-Petersen, Bøhn, & Sandlund, 2006; Richardson et al., 2000), such as habitat transformers (organisms that change the condition, form or nature of a natural ecosystem) and ecosystem engineers (those that change the natural fluxes, feedbacks and availability of resources). The impacts of invasions are especially concerning when dominant, non-native species are pervasive across large geographic areas (Parker, Simberloff, & Lonsdale, 1999). Therefore, invasive species management typically involves targeting problematic invaders to limit their spread and impact through eradication. While this focus on problematic invaders is necessary, we do not fully understand the general drivers of invasion success, nor invasive species impact (Catford, Jansson, & Nilsson, 2009; Kueffer, Pyšek, & Richardson, 2013).

In many respects, the search for general drivers of invasion success mirrors the fundamental questions of community ecology (Gurevitch, Fox, Wardle, Inderjit, & Taub, 2011; Shea & Chesson, 2002). The mechanisms underlying species coexistence are central to understanding why diverse communities exist (Chesson, 2000; Vellend, 2016) and understanding how interactions between species within diverse communities can help explain how invasive species spread, establish, persist (Godoy, 2019; Shea & Chesson, 2002; Tilman, 2004). It is tantalising to think that the assembly of communities could be explained with a simple suite of rules using easily measurable indicators of environmental conditions and species traits (Adler, Fajardo, Kleinhesselink, & Kraft, 2013; Kraft, Godoy, & Levine, 2015), but while modern ecology has made great strides toward understanding the general principles that support diverse communities (Chesson, 2018; Ellner, Snyder, Adler, & Hooker, 2018; Letten, Ke, & Fukami, 2017), it

remains unclear which conditions lead these processes to explicable deterministic outcomes, or to chaotic systems where stochasticity rules (Adler, HilleRisLambers, & Levine, 2007; Grainger, Letten, Gilbert, & Fukami, 2019; Weiher et al., 2011).

Similarly, identifying general patterns that predict which non-native species become dominant and have large impacts is difficult because the drivers of invasion are likely context dependent (Catford et al., 2019; Gross, Liancourt, Butters, Duncan, & Hulme, 2015). A central theme of this thesis is therefore understanding when invasion success is driven by variation in environmental conditions, or by interspecific competitive interactions. A particularly compelling idea is that the relative importance of site suitability and competitive hierarchies within a community can be explained by a few dichotomous axes of plant functional traits (Díaz et al., 2015; Funk et al., 2017; Kunstler et al., 2015). Some species have traits that are suited to take advantage of disruption and opportunity, others have traits that advantageous under stable conditions (Westoby & Wright, 2006). Simply put, no one species can be good at everything (Tilman, 2011). Studying how site suitability and competitive interactions change with resource availability, disturbance and trophic structure can explain which community assembly processes enable dominant non-native species to invade, as well as inform the management of existing and future invasions (Colautti et al., 2014; Kueffer et al., 2013).

This thesis describes a series of studies covering the primary stages of an invasion: non-native species spread, establishment, impact, and long-term persistence in invaded communities. In the section that follows, I summarise the key processes and patterns of each stage and consider which mechanisms might be driving the impacts of dominant non-native species on communities of coexisting species. We use communities of grassland plant species as model systems throughout. Grassland and grassy woodland communities in Australia, South America and western North America have undergone massive compositional change since European settlement (Mack, 1989), with many now invasive species having been introduced intentionally to facilitate the conversion of native communities to pastoral ecosystems (Driscoll, Catford, et al., 2014). Because grassland species are sessile, numerous and well distributed, communities can be surveyed across square meters, hectares, or continents, making them useful candidates to study how environmental conditions and competition influence community assembly.

I conclude this introduction with an overview of the aims and structure of thesis before presenting our primary findings on dominant non-native grassland species.

1.2 The life cycle of an invasion

1.2.1 Introduction and spread:

Invasions begin when propagules arrive at an uncolonized site with conditions suitable to establish, reproduce and disperse. The large-scale distribution of non-native plant species can be predicted from environmental covariates, but also human activity (Pysek et al., 2010) which suggests that the original introduction of many non-native species is due to anthropogenic disruption. These introductions can be unintentional or intentional (Gravuer, Sullivan, Williams, & Duncan, 2008). Unintentional introductions occur when propagules are accidentally dispersed by vectors, including (but not limited to) cargo, tires, outdoor equipment, wildlife, livestock, and pets. Biosecurity efforts attempt to minimise the risk of unintentional introductions by intercepting foreign material in transport (Sikes et al., 2018). Intentional introductions differ in that propagules are transported *en masse* to new locations where they are cultivated, typically for economic benefit (Gravuer et al., 2008). Many non-native plants are introduced for pasture improvement, forestry, and ornamental trade. These economic activities are the primary driver of non-native species introductions in many countries (Dehnen-Schmutz, Touza, Perrings, & Williamson, 2007) and the rate of species introductions is expected to continue to increase with growing global connectivity (Hulme, 2009; Seebens et al., 2018).

Once introduced, some non-native species reproduce and disperse, driving further spread beyond the original point of introduction. Others, however, are only able to persist as isolated, often small populations. This variation in invasion success may be due to differences in propagule pressure (Levine, 2000). While some non-native species may depend on chance events and few introductions to colonize new areas (Shea & Chesson, 2002), others often invade established communities through sustained introduction of a large number of propagules (Colautti, Grigorovich, & MacIsaac, 2006), either through repeated introduction events or a large number of individuals per introduction (Lockwood, Cassey, & Blackburn, 2009). Difference in introduction outcomes can also be related to the compatibility of environmental conditions and introduced species niches

which can vary both spatially and temporally (Hastings et al., 2005). High rates of spread are often associated with habitat modification, altered disturbance regimes, and low levels of environmental stress, especially high resource availability, all of which facilitate opportunistic species that may be less suited to intensely competitive environments (Catford et al., 2012). However, dominant non-native species come in all shapes and sizes and often invade many different communities, which suggests that facilitation through introduction and disturbance may be less important in determining the success of their spread.

1.2.2 Establishment:

One reason propagule pressure is important to invasion success is that a greater number of introduction attempts increases the likelihood of establishment (Duncan, Cassey, Pigot, & Blackburn, 2019). But propagule supply alone does not explain successful establishment. Introductions to inhospitable sites can result in small founding populations that fail to establish due to demographic stochasticity and Allee effects (Duncan, 2016). Although large native ranges are typically indicative of tolerance to a wide range of environmental conditions, this has been shown to have poor predictive power of invasion success (Williamson, 2006), suggesting that there are other factors describing the establishment of non-native species. Some non-native species have mutualistic symbioses with specialist pollinators, rhizobial bacteria or mycorrhizal fungi and may face difficulty establishing if these facilitators are absent from newly colonized sites (Wandrag, Sheppard, Duncan, & Hulme, 2013). Warrington et al. (2019) show that these mutualisms can be maintained in non-native ranges if symbionts are co-introduced along with non-native plant species, further highlighting how establishment can depend on site conditions more specific than just coarse environmental indicators.

It is the interaction between site suitability and propagule abundance (the number of individuals that are introduced) that appear to be the primary drivers of establishment success (Duncan, 2016). The importance of site suitability for establishment is demonstrated in the positive relationship between native and non-native richness, because the processes favouring successful establishment favour both groups (Levine, 2000; Prober & Wiehl, 2012). Establishment in grassland communities is often facilitated by disturbance (HilleRisLambers, Yelenik, Colman, & Levine, 2010; MacDougall & Turkington, 2005). Disturbance in grasslands can lead to nutrient enrichment or the

temporary removal of competitors (J. C. Lake & Leishman, 2004; Prober, Thiele, & Speijers, 2013), thereby increasing the number of safe-sites where niches are vacant and available for both native and non-native species to establish (Wandrag, Catford, & Duncan, 2019). However, once colonised, disturbance must enable greater recruitment of individuals than are lost, lest established non-native populations decline (Buckley, Bolker, & Rees, 2007).

1.2.3 Impact:

Following establishment, invasion success is determined by the rate at which populations of dominant non-native species increase from rarity within existing communities (sensu Chesson, 2000). Here, invaders may face biotic resistance, where the expansion of newly established non-native species is prevented by the resident community (reviewed in: Levine, Adler, & Yelenik, 2004). Biotic resistance can be encountered where resident species share overlapping niches with the invading species, meaning that they must share access to common resources (Grainger, Levine, & Gilbert, 2019; Shea & Chesson, 2002).. Niche overlap is common among plants that all share common drivers of growth and mortality (Farrior et al., 2013; Mortensen et al., 2018) as they compete for space, water and nutrients during recruitment and reproduction. If the resident species are superior competitors, then established non-native species may be restricted to small, opportunistic populations. Alternatively, if the invader occupies an uninhabited niche, for example a deep-rooted plant establishing in a community of shallow-rooted residents, then it will experience no resistance and can expand within the community with no impact on residents (MacDougall, Gilbert, & Levine, 2009).

Impact occurs when competition between species with overlapping niches is decided by a fitness advantage of the invader, causing dominant non-native species to reduce the population growth of resident species more than they are impacted by resident species themselves (I. T. Carroll, Cardinale, & Nisbet, 2011; Tilman, 1988). In extreme cases, impact can lead to reduced local species richness when subordinate residents are excluded by dominant non-native species (Carmel et al., 2017; Catford, Bode, & Tilman, 2018). Invading species can impact communities in many ways, through resource competition, altered disturbance cycles, the accumulation of litter (Brooks et al., 2004; Crooks, 2002; Levine et al., 2003), and indirect effects such as the attraction of parasites or predators (Chesson & Kuang, 2008; Vilà et al., 2011). Mechanisms of impact that create

positive feedbacks can disproportionately affect resident species and community structure by favouring non-native species.

Andropogon gayanus (Gamba grass) provides a good example of how complex these effects can be (Buckley et al., 2007). *Andropogon gayanus* is a dominant non-native species, prevalent in Northern Australia where it was introduced to improve pasture for cattle. But because *Andropogon gayanus* produces a higher fuel load than the native savanna grasses, fires become more intense (Rossiter, Setterfield, Douglas, & Hutley, 2003), disrupting native communities and encouraging greater establishment arriving *Andropogon gayanus* individuals, thereby creating a grass–fire feedback that can result in native species exclusion (D’Antonio & Vitousek, 1992). Additionally, the litter produced by *Andropogon gayanus* is nitrogen rich, thereby tightly linking nutrient cycling to fire regime (Rossiter-Rachor, Setterfield, Douglas, Hutley, & Cook, 2008) and reducing available resources for competitors (Rossiter-Rachor et al., 2009). The dominance of *Andropogon gayanus* can impact larger landscape factors such as habitat structure for fauna (Parr, Ryan, & Setterfield, 2010) and ecosystem primary productivity (Beringer, Hutley, Tapper, & Cernusak, 2007), but this thesis focuses primarily on non-native impacts on community composition.

Luckily, only a subset of non-native species become dominant and have substantial impacts (Lai, Mayfield, Gay-des-combes, Spiegelberger, & Dwyer, 2015). Distinguishing between the contexts in which non-native species have minor effects and those where non-native species have large impacts is vital to prioritizing management efforts (Richardson et al., 2000). However, identifying these impacts can be difficult, particularly where they interact with other drivers of community change (Didham, Tylianakis, Gemmill, Rand, & Ewers, 2007). The per-capita impact of non-native species can change between native and non-native ranges (Parker et al., 1999) and be moderated by the presence or absence of other species in the community (Levine, Bascompte, Adler, & Allesina, 2017). If the dominance of non-native species facilitates the subsequent establishment of further invaders, a near total transformation of native to non-native communities can occur (Jeschke et al., 2012; Simberloff & Von Holle, 1999). This variation in invader effects means that impact can depend on both environmental and competitive contexts, which often frustrates simple comparisons between communities.

1.2.4 Persistence:

Once non-native species are identified as having large impacts, the major question becomes: how should we manage dominant non-native species that have established in invaded communities? The chronic effects associated with the persistence of these dominant non-native species represent the primary ecological (and economic) outcomes of species invasions, yet long-term effects are seldom studied (Strayer, Eviner, Jeschke, & Pace, 2006). Complete eradication is possible and recommended when established populations are small, (Simberloff, 2003), however the primary drivers of invasion must also be addressed, lest eradication leave a 'weed-shaped hole' (Buckley et al., 2007). In many cases, especially in heavily invaded communities, invader impacts are irreversible and eradication is impossible (S. P. Carroll, 2011). Here, the future impacts of non-native species can be controlled by manipulating the environmental and competitive components of community assembly to limit abundance of dominant species. Declines in non-native dominance can be brought about by passive regeneration of resident communities (Bellingham, Peltzer, & Walker, 2005; Fensham, Butler, Fairfax, Quintin, & Dwyer, 2016). More intensive interventions may be required to facilitate recovery if native species are unable to re-establish (Derham, Duncan, Johnson, & Jones, 2018). Knowing which interventions and when they are required relies on being able to identify and predict the impacts of dominant non-native species and understand how they may change in the future (D'Antonio, Jackson, Horvitz, & Hedberg, 2004).

1.3 Summary

The key processes that determine invasion success and invasive species impact are context dependent and changes throughout the life cycle of an invasion. Species introductions typically occur due to human driven propagule pressure, but less is known about how variation between species and among introduction sites causes some non-native species to spread of their own accord. The interaction between propagule pressure and site suitability is particularly important for driving establishment, whereas competitive resistance from the resident community is not. However, competitive differences do describe how non-native species interact within a community and are central to understanding the impacts of established non-native species. The difficulty in predicting this impact stems from changes in species interactions in different environmental and community contexts. The impacts of some dominant non-native

species appear to persist for long time periods, whereas other species may only be transient. Management needs to understand what determines the ongoing success of dominant non-native species, where their removal most often results in reinvasion.

1.4 Aims

We suggest that viewing invasion in the context of environmental and competitive drivers of community assembly could act as a basis for better empirical studies and monitoring programs. This thesis aims to improve the effectiveness of our response to invasive species by contributing to fundamental research in three main areas: 1) the development of methods to identify potentially invasive plants; 2) the assessment of the impacts of invasive plants that have already arrived in native communities; and 3) the development of ecological restoration strategies for managing invasive plant impacts in the future.

1.5 Chapter descriptions

In **Chapter 2 (*Landscape effects on the spread of invasive species*)** my co-authors and I conduct a selective review of research focused on how landscape factors contributed to the spread of invasive species, both plant and animal, in the last 5 years (2010-2015). We organise this research in terms of the composition and configuration of habitats and explore how heterogeneity in either can influence the pattern of invasive species spread in complex ways. Studying how landscape composition and configuration influences dispersal behaviour and how local population growth varies across landscapes can help to understand how species spread. Interactions between species demographic processes and landscape heterogeneity can then be used to identify potential invaders and areas at risk.

In **Chapter 3 (*Measuring competitive impact: joint species modelling of invaded plant communities*)** we explore methods to quantify the impacts of non-native species that dominate native plant communities by competitively displacing native species. Joint-species distribution models (JSDMs) can potentially disentangle the relative mechanisms of invasive species dominance by simultaneously modelling how species respond to environmental variation and to changes in community composition. We use a JSDM to model variation in plant cover of an invaded grassland community in Canberra, Australia

to identify impactful invaders that cause other species to decline in abundance. In combination with experimental manipulations and analyses of species functional traits, we explain how the impact of two dominant non-native species occurs at high fertility sites, in the absence of herbivores, primarily through light competition, and suggest how these non-native species could be managed to reduce their impacts.

However, the inferences of our JSDM analysis are primarily phenomenological, meaning that although our model captured the observed patterns of abundance well, it lacked an ability to explain how they were generated. We attempted to validate these findings experimentally in **Chapter 4 (*Inferring the strength of plant competition from field data: reconciling field and experimental results*)**. We found that while our JSDM correctly identified the strong competitive interactions of dominant invasive species, it suffered a flaw common to studies of observational data and underestimated the strength of competition. In the glasshouse, all species had strong positive responses to increasing soil fertility, where our phenomenological model mis-predicted that many native and non-native species would decrease in abundance at high fertility sites. This means that the competitive effect of dominant species remained confounded with environmental variation, demonstrating a very real pitfall of estimating the competitive impact of invasive species, especially where species have been excluded.

Lastly, **Chapter 5 (*Can rehabilitation alter long-term trajectories of vegetation change in degraded grasslands?*)** investigates how the invaded communities may be managed in the future, by seeking to answer whether rehabilitation interventions have net positive, long-term effects on community structure or whether these effects are overridden by deterministic successional change. We present a case-study from Minnesota, USA where seed addition had small, positive effects on native species abundance after 25-years, but importantly, separating this effect from natural variation in the succession of degraded old fields was only possible with an extensive dataset of reference communities. Finding suitable control plots to evaluate the rehabilitation of invaded communities is a challenging problem that requires greater consideration when testing and evaluating courses of invasive species management.

1.6 Thesis outline

While these chapters follow a common thread of invasive species research, they are presented herein as standalone scientific articles, each accompanied by their specific background, aims and findings. I summarise the combined contribution of my research with a summary and suggestions on the common futures of community and invasion ecology may hold. Finally, acknowledgements of support, a bibliography and several appendices are included at the end of this thesis. These appendices that include additional detail, figures, and tables to support each article, and referred to in text with the letter of the appendix heading.

2 LANDSCAPE EFFECTS ON THE SPREAD OF INVASIVE SPECIES

Authors

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Landscape heterogeneity, dispersal, invasion, population growth, stochasticity, density-dependence

2.1 Abstract

Landscapes differ in the composition and configuration of habitats, and this heterogeneity can influence the manner in which invasive species spread in complex ways. To understand this complexity, we outline a framework that identifies how landscape heterogeneity influences spread by causing dispersal behaviour and local population growth to vary across the landscape. We use this framework to review progress over the last 5 years in understanding landscape effects on invasive spread, focussing on the role of interactions between landscape heterogeneity, dispersal, and population processes.

2.2 Introduction

Species introduced to regions outside their native range become invasive when they spread away from the site of initial introduction to establish self-sustaining populations in new locations (Richardson et al., 2000). Understanding the processes that control the pattern and rate at which invasive species spread is key to forecasting and managing their potential impacts (Caplat, Coutts, & Buckley, 2012; Letnic, Webb, Jessop, & Dempster, 2015; Tingley et al., 2013).

Much of our understanding of spread dynamics comes from mathematical models of populations expanding across homogeneous landscapes (Hastings et al., 2005; Skellam, 1951; van den Bosch, Hengeveld, & Metz, 1992). However, invasions typically unfold across more complex landscapes, and attention has shifted toward understanding how landscape heterogeneity (the composition and configuration of habitats) can influence the pattern and rate of invasive species spread (Higgins, Richardson, & Cowling, 1996; Marco & Páez, 2000; Shigesada & Kawasaki, 1997; With, 2002). Perhaps the dominant theme to emerge from this research is the wide variation in outcomes obtained from relatively simple spread models, with this complexity arising for three key reasons. The first is that the pattern and rate of species spread is context specific, depending on both the traits of the species concerned and individual landscape composition and configuration. Second, theoretical studies show that the key demographic processes driving spread, including rates of dispersal and local population growth, can have non-linear responses and both interact and feedback on one another, leading to highly variable outcomes given slight changes to demographic parameters, landscape configuration or starting conditions (Coutts, van Klinken, Yokomizo, & Buckley, 2011). Finally, recent work has highlighted the role that demographic and environmental stochasticity can play in affecting spread rates, with their influence mediated by interactions with other demographic processes (Jongejans, Shea, Skarpaas, Kelly, & Ellner, 2011; Pachevsky & Levine, 2011). These complex interactions and the varied outcomes they generate make it difficult to identify general principles governing the effect of landscape structure on invasive spread (Melbourne & Hastings, 2009; Schreiber & Lloyd-Smith, 2009).

Our aim in this review is twofold. First, to illustrate the potentially complex interactions that can drive spread we develop a framework that aims to capture the key processes underlying spread and use this framework to identify the ways in which landscape heterogeneity can influence the spread of invasive species. Second, using this framework we review progress over the last five years in understanding landscape effects on invasive spread.

To do this, we conducted a systematic review of studies published since 2010 as indexed by Web of Science and Google Scholar, using the following Web of Science keywords:

TOPIC: ((invas* OR alien OR exotic) AND (land*)) AND (spread OR expansion) AND YEAR PUBLISHED: (2010 - 2015).

This returned 809 articles, which we refined to 503 by specifying the following Web of Science fields:

Environmental Sciences Ecology OR Plant Sciences OR Biodiversity Conservation OR Zoology OR Agriculture OR Marine Freshwater Biology.

These 503 articles were further narrowed to 180 based on their title. We reviewed the abstracts of these 180 articles and identified a subset we considered most relevant to the aims of this review. Our choice was selective: there have been several excellent reviews of landscape effects on invasive spread (Hastings et al., 2005; Vilà & Ibáñez, 2011; With, 2002), and rather than covering much of the same ground, we focus on recent developments in understanding how landscape heterogeneity and interactions between spread processes generate variation in spread dynamics, using the framework we develop

2.3 Conceptual framework for spread

Spread involves an increase in the number of locations or area occupied by a species (Coutts et al., 2011). At its core, spread is a population process that can be understood as a repetitive sequence of events (Figure 2.1): individuals arrive and settle at a location, with settlement implying that arriving individuals persist at that location. Given conditions suitable for reproduction, those individuals then produce propagules that either contribute to local population growth or disperse to new locations. If conditions

are suitable at these new locations, dispersed propagules settle and reproduce, producing propagules that are dispersed to further locations, and so forth (Hodgson, Thomas, Dytham, Travis, & Cornell, 2012). Figure 2.1 illustrates these events, with arrows identifying the steps between dispersal, settlement and local population growth that result in spread.

We include settlement and local population growth as separate events to accommodate sink habitats: locations where arriving individuals can survive (settle) but local reproduction is insufficient for positive population growth, and occupancy relies on the continued arrival of individuals from elsewhere (Pulliam, 2000). This distinction is important when considering the spread of invasive species, because sink habitats will usually be included in the area an invader has occupied, and thus contribute to measures of spread, although in reality it is difficult to distinguish sink from non-sink locations (Meffin, Duncan, & Hulme, 2015). The transition from settlement to population growth implies that conditions are suitable for the establishment of a self-sustaining population at a given locality.

A large body of theory shows that in homogeneous landscapes, the rate at which an invasive species spreads is critically dependent on its dispersal capability and its rate of population growth when rare (Kot, Lewis, & van den Driessche, 1996; Skellam, 1951; van den Bosch et al., 1992). Real landscapes are not homogeneous, and typically comprise a variety of habitats with different characteristics. For a given species, habitats can differ both in their suitability for movement, with some habitats facilitating and others impeding dispersal (Bullock, Moy, Coulson, & Clarke, 2003), and in their suitability for survival and reproduction, leading to spatial variation in local population growth rates (Pulliam, 1988). Landscape heterogeneity can thus directly affect spread through variation in habitat suitability that results in varying rates of dispersal, settlement, and local population growth across the landscape. The direct effects of habitat suitability on these demographic processes are shown as arrows in Figure 2.1.

Although habitat variation can affect spread directly by causing dispersal and local population growth rates to vary, complex spread dynamics often arise through interactions between these processes, creating the potential for non-linear responses, feedback and thresholds in spread behaviour, leading to highly variable outcomes (Coutts et al., 2011). While the arrows in Figure 2.1 identify the direct effects of one process on

another, multiple arrows pointing to the same process identify the potential for interactions, meaning outcomes could exhibit greater variability because they depend on the joint effects of two processes whose effects may not be additive. Settlement and the transition to population growth, for example, depend on both dispersal and habitat suitability for survival and reproduction (Figure 2.1). Rather than acting independently, however, it is the interaction between these processes that determines the probability that a population will establish at a new location (Duncan, 2016; Duncan, Blackburn, Rossinelli, & Bacher, 2014). Low rates of dispersal, for example, may allow populations to settle in patches of suitable habitat, but may not provide sufficient propagules for establishment in patches of less suitable habitat (Duncan, 2016), resulting in spread being strongly influenced by the make-up of habitat patches that differ in their suitability for population growth. In contrast, high rates of dispersal may provide sufficient propagules to overcome establishment barriers (Von Holle & Simberloff, 2005), meaning spread is much less affected by differences among habitat patches in their suitability for population growth. As a consequence, while landscape heterogeneity may cause dispersal behaviour and local population growth to vary across the landscape somewhat independently, spread is critically dependent on how these processes interact to jointly determine outcomes. Here we use the framework shown in Figure 2.1 to review progress over the last 5 years in understanding how landscape-level heterogeneity in dispersal behaviour and population growth can influence spread dynamics, first by considering the direct effects of heterogeneity on each of these processes separately, and second by examining the importance of interactions.

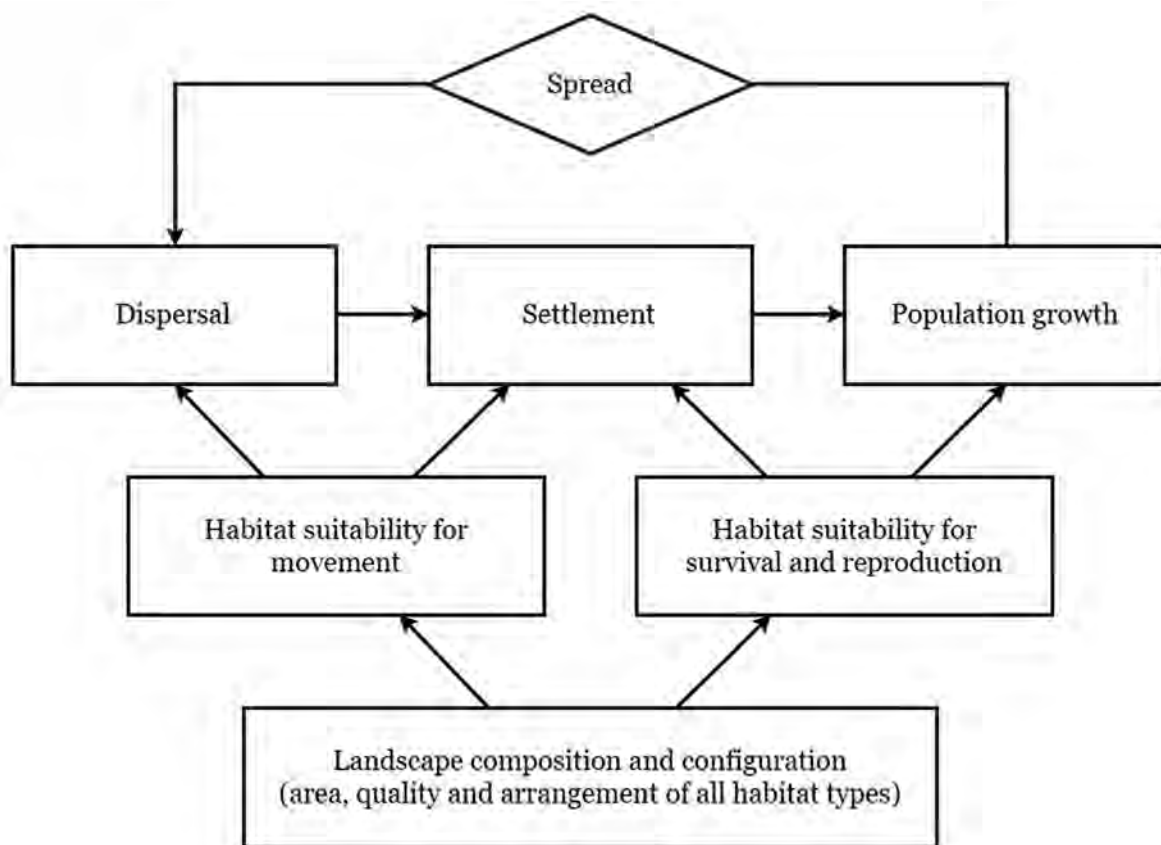


Figure 2.1. Conceptual framework for understanding landscape effects on the spread of invasive species. Landscapes differ in the composition and configuration of habitats. For a given invader, landscapes comprise habitats of varying suitability for movement, survival and reproduction, which influences spread by generating spatiotemporal heterogeneity in both dispersal behaviour and local population dynamics (settlement and population growth)

2.4 Direct effects of landscape heterogeneity on dispersal behaviour

The rate at which invasive species spread is known to be highly sensitive to variation in dispersal parameters, with spread rate increasing as both mean dispersal distance and the frequency of long-distance dispersal events increase (Coutts et al., 2011; Kot et al., 1996). Nevertheless, for a given species, spread is often modelled assuming a fixed dispersal kernel that does not vary across the landscape. Relative to this, patterns of spread are likely to differ if, instead, a landscape comprises habitats or has features that differentially affect the movement of individuals, leading to spatial and/or temporal heterogeneity in dispersal behaviour. Spatially, dispersal behaviour may vary if

propagule movement is facilitated in some habitats but not others, resulting in more propagules able to move a greater distance through some parts of the landscape (Bullock et al., 2003). If the mean dispersal distance remains the same, introducing spatial heterogeneity in dispersal behaviour should increase invasion speed, because this will increase the frequency of longer-distance dispersal events, which have a disproportionate influence on spread rates (Ellner & Schreiber, 2012; Kot et al., 1996). Ellner and Schreiber (2012) have shown that this is the case for temporal variation, with increasing variation in dispersal rates accelerating invasive spread because this results in an increase in the frequency of longer-distance dispersal events. We expect the same outcome given spatial heterogeneity, whereby the addition of landscape features or vectors that facilitate long-distance dispersal will increase invasion speed. Human-assisted dispersal can play a key role in this regard, with even occasional long-distance movements by humans substantially accelerating the spread of invasive species (Carrasco et al., 2010).

Empirical studies of invasive spread highlight the importance of landscape features that influence propagule movement. Caplat et al. (2012) and Jongejans et al. (2011), for example, show that invasion speed in two wind-dispersed species is highly sensitive to variation in wind speed, implying that the strength and direction of wind patterns across the landscape are likely to be critical determinants of spread dynamics (Cousens et al., 2012). Data on how wind patterns vary across the landscape can be used to identify areas connected by high rates of dispersal, which is where management may be most effective in limiting spread (N. S. G. Williams, Hahs, & Morgan, 2008). Similarly, Miller et al. (2015) show that variation in local vegetation structure affects spread by creating barriers to movement. They show a steeper decline in the density of the wind-dispersed invasive herb *Hieracium lepidulum* away from stream habitat, which acts as a propagule source, when the surrounding vegetation is forest rather than grassland. The ability of *Hieracium lepidulum* to spread more rapidly into grassland habitat is most likely due to greater dispersal distances across low-growing grassland vegetation relative to forest, which creates a taller barrier (see also: Gelbard & Harrison, 2003). This suggests that management to reduce spread would be most effective if it targeted control in parts of the landscape acting as a source for rapid dispersal into surrounding areas (in this case grassland stream habitat; A. L. Miller et al., 2015).

Nevertheless, relative to settlement and population growth, which we discuss below, few invasion studies have quantified the extent to which landscape heterogeneity affects dispersal behaviour, and fewer still have explored the consequences of such heterogeneity for spread dynamics (Driscoll, Banks, et al., 2014). This is most likely due to the difficulty in measuring dispersal but highlights an important gap in understanding. The increasing availability of genetic data allowing the spatial locations of parents and their offspring to be matched (Manel, Gaggiotti, & Waples, 2005) provides a way of quantifying rates of dispersal across the landscape and identifying landscape features that act as barriers or facilitate movement (Zeller, McGarigal, & Whiteley, 2012). Such approaches are starting to be applied to invasion questions (Medley, Jenkins, & Hoffman, 2015).

2.5 Direct effects of landscape heterogeneity on local population processes

In simple spread models across homogeneous landscapes, rate of spread depends on population growth rate when rare: all else being equal, higher rates of population growth result in faster spread (Fisher, 1937), because more rapidly growing local populations are able to supply greater numbers of propagules that then disperse and settle (Figure 2.1). Variation across the landscape in local population growth rates should therefore directly affect spread dynamics.

Many studies that have explored how heterogeneity in local population processes affect invasive spread have employed spatially explicit simulation models, because the added complexity of allowing population processes to vary means analytical approaches are less tractable or require strongly simplifying assumptions (Keeling et al., 2001; Pitt, Worner, & Suarez, 2009; Sebert-Cuvillier et al., 2008). While simulation models are informative, it is not always clear whether the findings from modelling a given scenario are system-specific or provide more general insights. Significant progress has been made recently, however, in deriving analytical solutions for spread dynamics across landscapes where population growth rates vary spatially. Perhaps the most accessible treatment is by Dewhurst and Lutscher (2009), who derive several important results that generalise findings from earlier simulation studies. A key outcome is that the relationship between landscape heterogeneity and rate of spread can be highly non-linear. Simulation models, for example, have previously identified the existence of ‘invasion thresholds’ whereby

invasive spread occurs most rapidly and extensively across landscapes with some minimum proportion and distribution of suitable habitat (With, 2002). Dewhurst and Lutscher (2009) show that, as a rule of thumb, in a landscape comprising suitable and less-suitable habitat patches, the minimum proportion of suitable habitat, p_{min} , required for an invader to spread is:

Equation 2.1

$$p_{min} = \frac{1 - r_2}{r_1 - r_2}$$

where r_1 and r_2 are the population growth rates when rare in suitable and less suitable habitat patches, respectively (assuming $r_2 < 1$). When $r_2 = 0$ (i.e. populations are unable to establish in unsuitable patches,) the proportion of suitable habitat required for spread is $(1 / r_1)$, implying that much larger areas of suitable habitat are required for invasive spread if that suitable habitat has relatively low rates of population growth. These outcomes depend on the shape of the invader species' dispersal kernel, and the above rules apply when the variance, and hence the mean dispersal distance, is large relative to the average distance between suitable habitat patches, meaning that suitable patches are well connected by dispersal. As the mean dispersal distance declines relative to the distance between habitat patches, the probability that some suitable patches may not be colonised increases, and p_{min} also increases.

Dewhurst and Lutscher (2009) also show that, in the absence of Allee effects, the rate of invasive spread across a landscape comprising habitat patches that differ in suitability for population growth is a function of the spatially weighted average population growth rate of the different patches. This confirms the intuitive idea that increasing the area of habitat unsuitable for population growth should slow invader spread by creating habitat sinks that effectively act as dispersal barriers. Rigot et al. (2014) provide a recent demonstration, showing that the rate of spread of the pine bark scale *Matsucoccus feytaudi* is slower in diverse landscapes having patches of suitable and unsuitable habitat, relative to more homogeneous landscapes.

What remains less well understood analytically is how the spatial arrangement of habitat patches, as opposed to the proportion of suitable habitats or degree of fragmentation, affects spread (but see: Kinezaki, Kawasaki, & Shigesada, 2010). Spatial simulation

models reinforce what we might anticipate: that spatial aggregation of suitable habitat can slow the rate of spread, with more spread occurring across greater distances where suitable habitat forms corridors or stepping stones that allow rapid movement or jumps through unsuitable habitat (Hodgson et al., 2012). This highlights the importance of habitat corridors and stepping stones in facilitating invasive spread, and the potential for management to slow spread by targeting populations in these habitats (Letnic et al., 2015; Resasco et al., 2014; Tingley et al., 2013).

A further source of heterogeneity in population processes are temporal fluctuations due to demographic and environmental stochasticity. Recent work has identified two important consequences of temporal stochasticity. First, while theoretical studies have shown that temporal variability in dispersal can lead to increased rates of invasive spread (Ellner & Schreiber, 2012), the opposite is true for population growth, where temporal variation in growth rates causes spread to slow relative to a temporally stable landscape (Ellner & Schreiber, 2012). This occurs because long-term mean population growth rates at localities will decline with increasing variance in local population growth rates (Dennis, Munholland, & Scott, 1991), meaning invasion speed will slow as temporal variability increases. Fitzpatrick et al. (2012), for example, show that spread of the hemlock woolly adelgid *Adelges tsugae* is slowed substantially by cold winter temperatures, and that regions with greater temperature variability, leading to extremes lethal to populations, have slower spread rates.

Second, temporal stochasticity means that invasive spread is not a deterministic process: any real-life invasion represents one outcome contingent on a series of probabilistic events, such that we could see a different outcome if we reran the process. How important is this variation? Melbourne and Hastings (2009) show that spread of the flour beetle *Tribolium castaneum* is remarkably variable in replicate landscapes comprising identical habitat patches. This variability arises in part through demographic stochasticity, but also through other stochastic processes perhaps related to the initial conditions in small founding populations (Melbourne & Hastings, 2009). The implication is that stochasticity makes it inherently difficult to predict the trajectory of any given invasion, even under laboratory controlled homogeneous conditions. In contrast, Giometto et al. (2014) show much higher levels of repeatability in the spread of the freshwater ciliate *Tetrahymena*

sp. Under similar controlled conditions, although any uncertainty will almost certainly be magnified in heterogeneous landscapes (e.g. Fitzpatrick et al., 2012).

2.6 Interactions between landscape heterogeneity, dispersal, and population processes

The previous two sections considered how landscape-induced variation in dispersal and population processes can independently affect spread dynamics. While heterogeneity in these processes alone can generate substantial variation in patterns of spread, recent work has emphasised that interactions between these processes have the potential to generate even greater complexity.

Central to understanding the variability in outcomes that can result from interactions between dispersal and population processes is the role of stochasticity. While deterministic models treat population density and spread as continuously varying, in reality, spread involves the dispersal of a discrete number of individuals. When only a few individuals disperse to a new locality, the resulting small founding population will be prone to extinction through fluctuations in size due to demographic and environmental stochasticity (Duncan et al., 2014). As a consequence, spread via the establishment of new populations is a probabilistic process, with the probability of a new population establishing jointly dependent on the number of individuals that disperse and settle (the size of the founding population) and the suitability of the locality for survival and reproduction (see: Figure 2.1; Duncan, 2016; Duncan et al., 2014; Warren, Bahn, & Bradford, 2012).

Relative to a deterministic spread model, the inclusion of stochasticity should slow the spread of an invasive species, because small founding populations just beyond the edge of the invasion front can go extinct in even suitable localities. Eventually, however, these localities should be colonised as populations at the edge of the invasion front grow and supply a greater number of propagules, leading to more frequent colonisation events and larger founding populations, resulting in higher probabilities of establishment. The potential to colonise beyond the invasion front, however, depends on the ability of established populations near the front to produce sufficient propagules, and hence on the degree to which reproductive output is density dependent.

In homogeneous landscapes, the combined effects of density dependence and demographic stochasticity have been shown to result in only a modest slowing of invasion speed (Snyder, 2003). In heterogeneous landscapes, however, these processes can interact to have large effects on spread rates (Pachepsky & Levine, 2011). In a fragmented landscape comprising patches that are both suitable and unsuitable for population growth, spread will slow if populations on the edge of the invasion front cannot produce enough dispersing propagules to successfully colonise suitable habitat patches that are sufficiently far away. Without density-dependent regulation, initially small populations at the invasion front will grow and increase their propagule output, eventually producing sufficient numbers of propagules that disperse across a habitat gap to ensure colonisation of distant patches. However, if density-dependent regulation causes per capita reproductive output to decline as populations increase in size, total propagule output may not increase greatly as edge populations grow, meaning distant patches continue to receive few propagules, resulting in a low probability of colonisation and greatly slowing the rate of spread (Pachepsky & Levine, 2011).

While we are not aware that this effect has been demonstrated in real populations, Warren et al. (2012) have shown that the relevant conditions arise in the invasive grass *Microstegium vimineum*. This species shows variable recruitment across the landscape (equivalent to settlement in Figure 2.1) that is jointly dependent on the number of seeds arriving at a locality and the suitability of that locality, such that the probability of colonisation increases with greater seed supply and in more favourable habitats. Subsequent reproductive output, however, is strongly density-dependent, with low-density populations producing roughly the same number of seeds as high-density populations. While the number of seeds produced by an initially low-density population is sufficient for positive local population growth (Warren et al., 2012), strong density dependence then limits the number of seeds available for dispersal as the population grows, potentially limiting its ability to provide sufficient seeds to colonise more distant localities. This potential for density dependence to interact with heterogeneity in suitability for population growth has implications for the traits we associate with species having high rates of invasive spread. While previous work has emphasised the importance of traits linked to rapid population growth rate when rare, Pachepsky and Levine (2011) show that traits associated with reproduction at both high and low densities may be important.

The importance of interactions between landscape heterogeneity, dispersal and population processes is likely to depend on the extent to which rates of dispersal and population growth are correlated across the landscape, with strong correlations potentially accelerating rates of spread through positive feedback between dispersal and population growth. For example, while Ellner and Schreiber (2012) showed that temporal variation in population growth rate slows spread, such variation will increase the rate of spread if it is positively correlated with dispersal variability. In other words, invasive spread will accelerate if favourable years for local population growth are also associated with favourable years for dispersal. Similarly, Schreiber and Lloyd-Smith (2009) show that spread rates increase when dispersal and population growth rates are positively correlated in spatially heterogeneous landscapes, and slow when they are negatively correlated. These findings are important because it may be relatively common for good years or good habitat patches to provide conditions favourable for both population growth and dispersal. Many animal species, for example, exhibit density dependent dispersal (Matthysen, 2005), such that patches of higher population growth may lead to greater dispersal distance among animals to avoid crowding effects. Similarly, roadsides are often identified as conduits for the rapid spread of invasive species because they provide corridors of suitable habitat, but also because human-mediated transport along road corridors can facilitate long distance dispersal (Medley et al., 2015; Warren, Ursell, Keiser, & Bradford, 2013).

The implication is that spatiotemporal heterogeneity in environmental conditions can result in windows of opportunity where conditions are particularly favourable for both population growth and dispersal (Johnstone, 1986), and that even brief windows of opportunity could play a critical role in accelerating the spread of invasive species. Such heterogeneity also provides a plausible mechanism for the widely observed time lag between establishment and the start of rapid population growth and spread in invasive species (Aikio, Duncan, & Hulme, 2010; Schreiber & Lloyd-Smith, 2009).

If spatial variation in dispersal and population growth are positively correlated, then management aimed at reducing spread may be most effective if it targets habitats with high suitability for both (N. S. G. Williams et al., 2008). Without detailed knowledge of how dispersal and population growth vary across the landscape, it is less clear which should be targeted. Coutts et al. (2011) found that dispersal was the main factor driving

spread in a spatially explicit invasive plant simulation model, implying that management aimed at limiting dispersal at key locations in the landscape may be the most effective way to slow invasions. Nevertheless, they also found that interactions between drivers could result in habitat manipulations having highly variable and unpredictable outcomes. Indeed, we suspect there is no universal answer as to the relative importance of dispersal versus population growth in influencing spread, given the potential for these processes to both interact and covary across the landscape. In pine species, for example, Caplat et al. (2012) found that intraspecific variation in seed terminal velocity had the largest effect on spread rate via wind, while Nathan et al. (2001), using a similar approach, found that wind velocity was more important. The differing results were attributed to stronger mean wind velocity in the Nathan et al. (2001) study, emphasising the importance of landscape context and highlighting that spread dynamics result from interactions between landscape conditions and demographic processes.

2.7 Conclusion

Figure 2.1 provides a framework identifying how landscape heterogeneity affects invasive spread, both as a direct consequence of variations in dispersal, settlement and population growth across the landscape, and because the joint effects of these processes are not additive, resulting in interactions that increase the range of possible outcomes. Our review has identified areas of recent progress in understanding how these processes combine to determine invasive spread, but has also highlighted gaps in our understanding that provide avenues for further research:

1. Relative to understanding how variation in population processes affect spread, we understand less about how dispersal behaviour varies across the landscape and the implications of this for spread dynamics.
2. Interactions between landscape heterogeneity, dispersal and population processes appear key to understanding spread, and demographic and environmental stochasticity play a central role in these interactions.

Spread dynamics should be influenced by the degree to which variation in dispersal behaviour and population processes are correlated across the landscape, because this can result in positive feedback that disproportionately drives spread.

3 MEASURING COMPETITIVE IMPACT: JOINT SPECIES MODELLING OF INVADED PLANT COMMUNITIES

Authors

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Keywords:

Invasive species, impact, biotic interaction, tobit regression, joint species distribution model (JSDM), grasslands, light competition, grazing, nutrient addition.

3.1 Abstract

1. Non-native species can dominate plant communities by competitively displacing native species, or because environmental change creates conditions favourable to non-native species but unfavourable to native species. We need to disentangle these mechanisms so that management can target competitively dominant species and reduce their impacts.

2. Joint-species distribution models (JSDMs) can potentially quantify competitive impacts by simultaneously modelling how species respond to environmental variation and to changes in community composition. We describe a JSDM to model variation in plant cover and show how this can be applied to compositional data to detect dominant competitors that cause other species to decline in abundance.

3. We applied the model to an experiment in an invaded grassy-woodland community in Australia where we manipulated biomass removal (through slashing and fencing to prevent grazing by kangaroos) along a fertility gradient. Non-native species dominated plant cover at high fertility sites in the absence of biomass removal. Results from the JSDM identified three of the 72 non-native plant species (*Bromus diandrus*, *Acetosella vulgaris* and especially *Avena fatua*) as having a strong competitive impact on the community, driving changes in composition and reducing the cover of both native and non-native species, particularly in the absence of grazing. The dominant non-native grasses *Bromus diandrus* and *Avena fatua* were among the tallest species in the community and had the greatest impact on shorter-statured species, most likely through competition for light under conditions of high fertility and low grazing.

4. *Synthesis.* We demonstrate a method to measure competitive impact using a JSDM, which allowed us to identify the species driving compositional change through competitive displacement, and where on the landscape competitive impacts were greatest. This information is central to managing plant invasions: by targeting dominant non-native species with large competitive impacts, management can reduce impacts where they are greatest. We provide details of the modelling procedure and reproducible code to encourage further application.

3.2 Introduction

Dominance by non-native plant species is frequently associated with declines in the abundance and diversity of native species (Vilà et al., 2011). These changes can occur if non-native species are superior competitors, such that increasing abundance of non-natives directly drives declines in native species through competitive displacement (Levine et al., 2003; MacDougall et al., 2009). Alternatively, increasing dominance by non-native species could be a consequence of changing environmental conditions that favour non-natives over natives due to species in each group having different environmental tolerances (HilleRisLambers et al., 2010; Shea & Chesson, 2002). As plant invasions are frequently accompanied by environmental perturbations (Pysek et al., 2010; Vellend et al., 2017), it can be difficult to determine when non-native dominance is driven by competitive impact (Godsoe, Franklin, & Blanchet, 2017; Soberón, 2010). In fact, many non-native species appear to have little impact on the communities they invade (Lai et al., 2015; Williamson & Fitter, 1996). In order to manage non-native species appropriately, we need ways to identify which non-native species, if any, are having strong competitive impacts, and where those impacts are greatest (Gallien, Münkemüller, Albert, Boulangéat, & Thuiller, 2010; Ricciardi, Hoopes, Marchetti, & Lockwood, 2013).

Joint species distribution models (JSDM) are extensions of standard species distribution models that have the potential to measure both competitive impact and species responses to environmental conditions using community composition data from sites along known environmental gradients (Kissling et al., 2012; Nieto-Lugilde, Maguire, Blois, Williams, & Fitzpatrick, 2018). JSDMs use data on species composition across multiple sites to jointly model individual species responses to environmental variation, interpreting residual among-species covariation as potentially resulting from interactions such as competition (Latimer, Banerjee, Sang, Mosher, & Silander, 2009; Ovaskainen, Hottola, & Shtonen, 2010; Pollock et al., 2014; Warton et al., 2015). To date, JSDMs have mostly been used to model presence-absence data, where large negative residual covariance between two species could be interpreted as the competitive displacement of one species from sites that both could occupy. However, presence-absence data can only detect competitive impacts that result in complete exclusion from a site, yet dominance without exclusion is an important component of species impact (Levine et al., 2003; Seabloom et al., 2013). Here we use a method proposed by Clark et

al. (2017) to model cover data in a JSMD that overcomes the problem of zero-inflation that is typically inherent in these data (see: *Joint-species tobit modelling in Methods*; Figure 3.1). With this approach, we can detect declines in species abundance associated with the presence and abundance of competitors, which should provide greater resolution in quantifying competitive impacts.

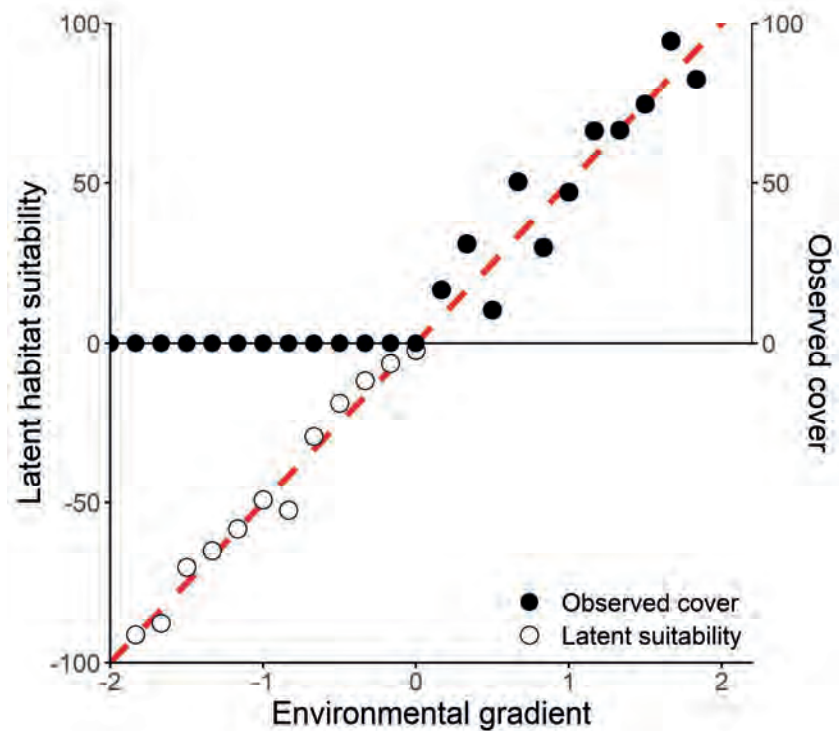


Figure 3.1. A simulated example of tobit regression. Black circles show observed cover for a species measured at points along an environmental gradient. Cover declines as environmental suitability decreases, eventually reaching a point where the environment is unsuitable for the species and cover is zero. Beyond that point, environmental suitability continues to decline but cover remains at zero. These zero values are censored in that zero cover provides partial information about the latent suitability (open circles): it tells us a site is unsuitable but, beyond that, does not measure how unsuitable. Tobit regression aims to estimate latent suitability (the open circles, which are uncensored) by fitting a regression line (red) to the cover data, treating the zero values as censored.

Even with these improvements to JSMDs, separating environmental responses from competitive impacts is challenging (Adler, Kleinhesselink, et al., 2018), suggesting we

should apply JSDMs to systems where the primary environmental drivers of species abundances are well understood (Giannini, Chapman, Saraiva, Alves-dos-Santos, & Biesmeijer, 2013; Wisz et al., 2013; Zurell, Pollock, & Thuiller, 2018). In grasslands around the world, non-native plant species often increase in dominance at higher fertility sites and when grazing is excluded (Seabloom et al., 2015). This shift in dominance has been attributed to the competitive displacement of native species by non-native species that are competitively superior under conditions of high resource availability and low grazing. This competitive superiority arises because, relative to native species, many non-native grassland species have traits associated with rapid growth and high biomass (Ordonez, Wright, & Olf, 2010; M Van Kleunen, Weber, & Fischer, 2010), traits that are likely beneficial when there is little above ground disturbance and competition for light is intense (Borer et al., 2014; Hautier, Niklaus, & Hector, 2009). These trait differences between native and non-native species should be less important under herbivory where biomass removal may reduce any competitive advantage of fast growth (Lind et al., 2013).

We aim to test these ideas using data from a 7-year experiment that tracked changes in plant cover over time following herbivore exclusion (Driscoll, 2017). Sites were arrayed along a fertility gradient and we predicted that non-native species would dominate under high fertility and would increase in dominance following herbivore exclusion. We used JSDMs to model how species cover varied with fertility, grazing and rainfall, and identified species with strong negative residual covariances, suggestive of strong competitive impacts on the community. We predicted that: 1) competitive impacts, and hence the magnitude of negative residual covariances, would increase in the absence of grazing where competition for light would be most intense; and 2) if competition for light caused competitive displacement, the strength of negative covariances between species (reflecting the strength of competitive interactions) should correlate with trait differences associated with growth and light capture.

3.3 Methods

3.3.1 Study system:

This study was carried out in a box-gum grassy woodland reserve in south-eastern Australia (Pinnacle Reserve, ACT. 35° 15' S, 149° 02' E; 620 – 708 m a.s.l.). The vegetation of the reserve comprised a scattered overstorey of trees, predominantly *Eucalyptus*

blakelyi and *E. melliodora*, with a dense understorey of grasses and forbs. The vegetation has been extensively modified over the last 150 years, primarily by tree clearance and livestock grazing. Livestock grazing ceased in the reserve in 1993 and the dominant herbivore is now the native eastern grey kangaroo (*Macropus giganteus*), which was at moderately high density over the course of the study (1.8 – 2.2 ha⁻¹; Driscoll 2017). The understorey vegetation was dominated by a mix of native and non-native species, with many non-native species introduced for pasture improvement (e.g. *Dactylis glomerata* and *Trifolium subterraneum*) or as pasture contaminants (e.g. *Avena fatua* and *Bromus diandrus*). Mean annual precipitation in the area is ~660 mm year⁻¹ and daily maximum temperatures range from 9 °C to 33 °C during the spring growing period and as low as 4 °C in the preceding winter months (Australian Government Bureau of Meteorology, 2017). Soils are typically of relatively low fertility, shallow and rocky, although some deeper soils occur on slopes and in depressions.

3.3.2 Data collection:

We used data from an experiment that tested whether different management interventions can increase native grassland species richness (Driscoll, 2017). In 2010, ten sites were established in open, unshaded areas along a natural fertility gradient (see below). Sites ranged from relatively uninvaded communities to communities dominated by non-native species. Each site contained 10 permanently marked 5 m x 5 m plots separated by at least 1 m. One of 10 different experimental treatments was applied to each plot, but we use only a subset of the treatments in this study (see Appendix A1, Figure A4-S1). From 2011, five plots at each site were fenced in a single enclosure to exclude mammalian herbivores (predominantly kangaroos but also rabbits). One plot inside and one plot outside the fence had its above-ground biomass removed each year by slashing, and one plot inside and one plot outside the fence was left unmanipulated (unslashed). We analysed these four treatments at each site (grazed, unslashed; grazed, slashed; fenced, unslashed; and fenced, slashed), allowing us to test whether the competitive impact of non-native species was stronger in the absence of biomass removal by grazing and/or slashing, and to assess whether uniform biomass removal by slashing had similar effects to herbivore grazing.

Vegetation surveys were conducted every year from 2010 to 2016, except for 2014. In late spring (October) of each year, the percent cover of all vascular plant species was

visually estimated in four 1 m x 1 m quadrats placed in the corners of each plot (only three quadrats per plot were surveyed in 2013 due to time constraints). We use plant cover as a proxy for abundance. Our dataset thus comprised six years of vegetation cover data from 160 quadrats across 40 plots. In total, we had 920 quadrat level vegetation measurements, comprising 10,780 cover estimates for 142 species (70 native and 72 non-natives; see Appendix A1, Figure A4-S2 for more details). In 2015 and 2016, we measured the traits of abundant species, defined as those comprising the first 80% of total recorded cover at each site. At each site, we measured traits associated with growth rate and light capture on 5-10 adult individuals in each of the unslashed plots following standard protocols (Pérez-Harguindeguy et al., 2013). These traits included canopy height (m), maximum height (m), canopy width (m), leaf length and width (cm) and specific leaf area ($\text{mm}^2 \text{mg}^{-1}$; SLA). To avoid the influence of outliers, we used 90th quantile values from all measured plants to estimate species maximum potential for each trait.

Total extractable nitrogen at sites along the fertility gradient ranged from 615 ppm to 2420 ppm (Driscoll & Strong, 2017). Total soil carbon, nitrogen, and phosphorus levels, as well as extractable nitrogen and phosphorus, all covaried strongly across the 10 sites (Appendix A1), and we used total extractable nitrogen as a proxy for overall soil fertility. Grasslands in this region also respond strongly to variation in annual rainfall (Figure A4-S3; Prober et al., 2013). We obtained data on total rainfall for the four months prior to each survey (August – November) from the Australian Bureau of Meteorology (Appendix A1) as a proxy for water availability. Total rainfall during these four months ranged from 185 – 414 mm over the seven years of the study. Both total nitrogen and spring rainfall were centred and scaled prior to model fitting.

3.3.3 Analyses:

Relative dominance of non-native species

We examined how the dominance of non-native species changed over time, in relation to soil fertility and rainfall, and in response to the experimental treatments (fencing and slashing). Our response variable was the proportion of non-native species cover in each plot in each year. This was calculated by taking the average cover of each species across quadrats in each plot in each year, summing these averages to get the total average cover of all species in each plot in each year, and calculating the proportion of total cover

comprising non-native species. We logit-transformed this proportion and modelled it as a linear function of soil fertility, fitting a separate intercept and slope for each experimental treatment (grazed/fenced and slashed/unslashed) and for each year. We included rainfall by specifying a single coefficient for the effect of inter-annual rainfall variation on the proportion of non-native cover. The model structure is described in detail in Appendix A2.

Joint-species tobit modelling

To test if dominance by non-native species was a consequence of environmental responses or competitive displacement, we specified a JSJM that modelled the cover of each species in response to variation in soil fertility, rainfall, and experimental treatment (JSJM1). This model included a single covariance matrix to capture unexplained residual variation, with negative residual covariances potentially indicating competitive impacts. We fitted a second model (JSJM2) to test whether competitive impacts varied with grazing and slashing treatments. JSJM2 had the same structure as JSJM1, but we fitted separate residual covariance matrices for each experimental treatment, which allowed us to test if the magnitude of negative residual covariances were greater in the absence of biomass removal where light competition should be most intense. We analysed data for the years 2013-2016, which were the years during which the experimental treatments showed clear effects (see: Figures 2 & S4b), and restricted our analyses to species present in >20% of plots measured between 2013 and 2016 (N = 30, 14 native and 16 non-native species; Figure A4-S2.) These species were present at >50% of sites in each year and were thus sufficiently widespread that absences were more likely due to unsuitable environmental conditions or competitive displacement rather than dispersal limitation. We analysed cover data at the quadrat level because we expected species interactions to be most evident at this scale. Zero cover was recorded when a species was absent from a quadrat. Even after restricting our analysis to the 30 most common species, most of our data comprised zero values (~69%; 4,396 cover estimates, 10,004 absences).

We used tobit regression to accommodate zero inflation by treating absences as censored data (J. S. Clark et al., 2017; Tobin, 1958). Censored data occur when it is not possible to observe a value beyond some limit. In this case, we assume there is an unobserved latent variable that measures the 'suitability' of each quadrat for each species, where suitability encompasses all biotic and abiotic factors that might influence species cover. When a

species is present in a quadrat, we equate the latent suitability with cover, assuming that higher cover indicates higher suitability (Figure 3.1). Quadrats where species are absent can be thought of as sufficiently low suitability that a species cannot persist but quadrats with zero cover can still vary in their underlying suitability. We model observations of zero cover as censored data arising from this latent suitability distribution, which can take values less than zero:

Equation 3.1

$$y = \begin{cases} y^*, & \text{if } y^* > 0 \\ 0, & \text{if } y^* \leq 0 \end{cases}$$

where y is the observed cover and y^* is the corresponding latent suitability value. To complete the model, we need to specify a distribution for the underlying latent variable. We specified the underlying distribution as multivariate normal with 30 dimensions, one for each species.

We regressed latent suitability (y^*) against the environmental variables soil fertility and rainfall, with residual variation captured in a single covariance matrix (JSDM1). We specified different regression coefficients for each experimental treatment, modelled hierarchically, and included normally distributed random effects to account for repeated measurements of plots nested within sites. The structure of JSDM1 was:

JSDM1:

Equation 3.2

$$\mathbf{y}_{[ijkl]}^* \sim \text{MultiNormal}(\boldsymbol{\mu}_{[ijkl]}, \boldsymbol{\Sigma})$$

$$\boldsymbol{\mu}_{[ijkl]} = \begin{pmatrix} \mu_{1[ijkl]} \\ \mu_{2[ijkl]} \\ \vdots \\ \mu_{N[ijkl]} \end{pmatrix}$$

$$\mu_{s[ijkl]} = \beta_{\text{intercept}_{s[j]}} + \beta_{\text{slope}_{s[j]}} \cdot \text{fertility}_{[jk]} + \beta_{\text{rain}_{s[j]}} \cdot \text{rainfall}_{[i]} + \beta_{\text{plot}_{[jk]}}$$

$$\beta_{\text{plot}_{[jk]}} \sim \text{Normal}(\beta_{\text{site}_{[k]}}, \sigma_{\text{plot}}^2)$$

$$\beta_{\text{site}_{[k]}} \sim \text{Normal}(0, \sigma_{\text{site}}^2)$$

where $\mathbf{y}_{[ijkl]}^*$ is an N -length vector of latent suitability values in year \mathbf{I} (1-3), under treatment \mathbf{j} (1-4), at site \mathbf{k} (1-10) in quadrat \mathbf{l} (1-4). \mathbf{S} indexes species ($\mathbf{s} = 1 \dots N$) with

intercept terms measuring average site suitability for each species in each treatment, and slope and rain terms measuring how site suitability varied with soil fertility and rainfall for each species in each treatment. Σ is an $N \times N$ covariance matrix with the diagonal containing the residual variances in suitability for each species, σ^2 , and the off-diagonals containing the residual covariances between each species pair, conditional on the value of $\mu_{[ijkl]}$. This matrix has $N * (N - 1) / 2 = 435$ unique elements, with the covariance between two species defined as: $\Sigma_{12} = \sigma_1 \sigma_2 \rho_{12} = \Sigma_{21}$.

The covariances describe how residual variation in the cover of one species is related to residual variation in the cover of a second species. If, having accounted for environmental effects, the cover of one species declined in quadrats when the cover of a second species increased, the residuals of the two species would covary negatively. We interpreted negative covariances as due to competition on the grounds that we had modelled species responses to the major environmental gradients in these grasslands (fertility and water availability; Leishman & Thomson, 2005; Morgan et al., 2016; Prober, Thiele, & Speijers, 2016). Large negative covariances imply potentially strong competitive impacts, while species with low cover, or where cover is well explained by environment variables, will have smaller covariances because there is less residual variation that could be associated with co-occurring species. Moreover, if a dominant species caused several species to decline in cover, resulting in strong negative covariances, this is likely to induce a pattern of positive covariances among the impacted species because they would all tend to have lower cover at sites where the dominant species was present and higher cover at sites where it was absent.

Change in species covariances by treatment

Specifying a single covariance matrix in JSMD1 meant the covariances were estimated from the data in all treatments. In JSMD2, we specified a separate covariance matrix for each of the four treatments:

JSMD2:

Equation 3.3

$$y_{[ijkl]}^* \sim \text{MultiNormal}(\mu_{[ijkl]}, \Sigma_{[j]})$$

$$\mu_{s_{[ijkl]}} = \beta_{intercept_{s[j]}} + \beta_{slope_{s[j]}} \cdot fertility_{[jk]} + \beta_{rain_{s[j]}} \cdot rainfall_{[i]} + \beta_{plot_{[ijkl]}}$$

where both the coefficients for species s and the covariances Σ varied with treatment j (1-4). Comparing the covariance matrices for different treatments in JSMD2 allowed us to evaluate whether competitive interactions were stronger in plots without slashing or grazing.

Predicting competitive impact from functional traits

We predicted that competitive impacts, measured as the magnitude of negative covariance between species, should be linked to differences in traits associated with growth and light capture. To test this, we regressed the posterior mean of the negative covariance parameters estimated in JSMD2 against the absolute difference in measured trait values for each species pair. Trait values were normalised prior to analysis so that traits measured using different units could be compared directly. For the regression models, we specified separate intercept and slope coefficients for the covariance-trait relationships in each experimental treatment, with the slopes and intercepts modelled as drawn from normal distributions for each trait.

All models were fitted to the data in a Bayesian framework using adaptive Hamiltonian Monte Carlo with the probabilistic programming language Stan (Carpenter et al., 2017) and the rstan interface (Guo et al., 2016) in R, version 3.4 (R Core Team, 2018). Details of model fitting and prior specification are in Appendix A2 and online at <https://github.com/aornugent/impact2>. We took a conservative approach to identifying interactions in the data by specifying that we *a priori* expected covariances to be weak (see prior specification in Appendix A2), meaning that strong residual covariances required strong support from the data.

3.4 Results

3.4.1 Relative dominance of non-native species:

Overall, the proportion of total cover that comprised non-native species increased with increasing soil fertility (Figures 2, S4a). Prior to and immediately after fencing (2010 & 2011), the relationship between fertility and proportion of non-native cover was similar in the fenced and grazed, and in the slashed and unslashed treatments. However, from 2012 onwards the proportion of non-native cover increased substantially at higher fertility sites in the fenced, unslashed plots (i.e., in the absence of biomass removal).

There was no clear change over time in the proportion of non-native cover along the fertility gradient in plots that were grazed, slashed or both (Figure 3.2, Figure A4-S4b). The proportion of non-native cover was higher in years with higher spring rainfall (Figure A4-S3, inset)

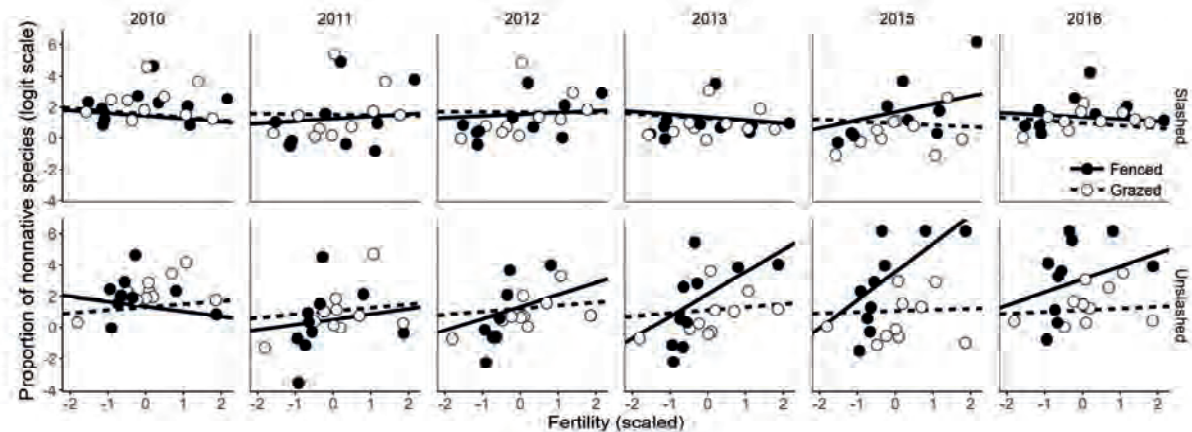


Figure 3.2. Proportional cover of non-native species (logit-transformed) as a function of soil fertility at 10 sites measured over 7 years (2010-2016 with no measurement in 2014). There were four treatments at each site, which are plotted separately. Slashed plots are shown on the top line and unslashed plots on the lower line, with filled circles and solid lines for fenced plots, and open circles and dashed lines for grazed plots. Fertility is scaled and standardized as described in Appendix A1.

3.4.2 Joint species tobit modelling:

Species responded differently to changes in soil fertility, with latent site suitability increasing strongly with higher soil fertility (i.e. total extractable nitrogen) for two native and five non-native species (95% credible intervals above zero in at least one treatment; Figure 3.3). The remaining species, both native and non-native, declined in cover with increasing fertility. Relationships between cover and fertility did not vary much between experimental treatments with three exceptions: relative to other species, the cover of the non-native species *Avena fatua*, *Bromus diandrus* and *Acetosella vulgaris* increased more strongly with fertility in the fenced, unslashed treatment. At high fertility, several fenced, unslashed plots were completely dominated by one or more these species. For most species, cover was positively related to rainfall across years (Figure A4-S3).

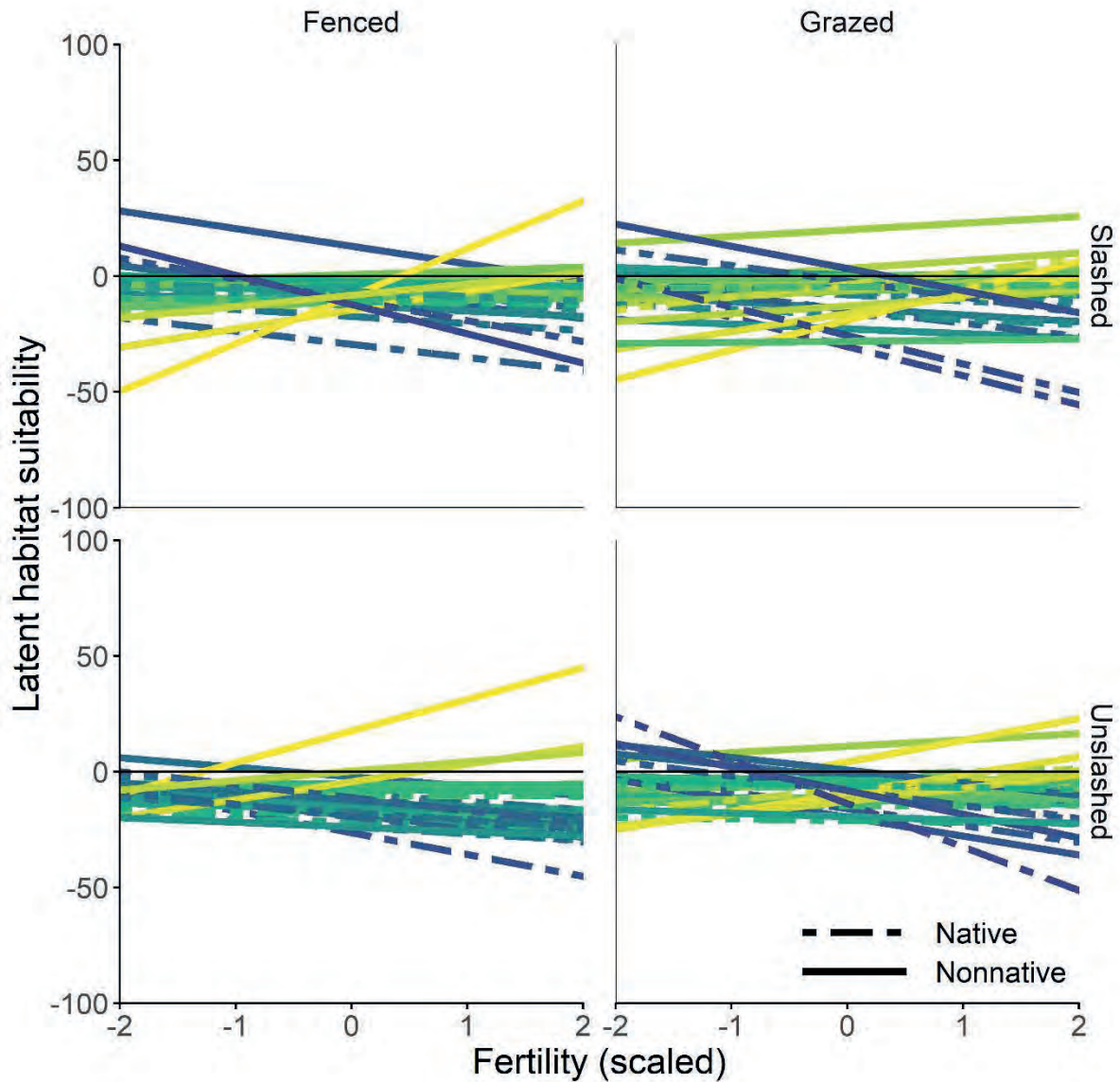


Figure 3.3. Latent suitability with respect to soil fertility for 30 species estimated using a joint-species-distribution model and tobit regression (see text). Separate relationships were fitted for each species in each of four treatments, shown as different panels. Native species are drawn with dashed lines ($n = 14$) and non-native species with solid lines ($n = 16$). Lines are coloured from dark blue to light yellow corresponding to a shift from negative to positive slopes, respectively.

Figure 3.4 shows species' residual covariances from JSDM1 as a pairwise covariance matrix (Figure 3.4a) along with the median covariance for each species across all pairwise interactions (Figure 3.4b). We report the median covariance because covariance values

could be highly skewed. One species, *Avena fatua*, stood out as having strong negative covariances, with high cover of *Avena fatua* often associated with reduced cover of other species. Median covariance for the native grass *Themeda triandra* was the second most negative but of much smaller magnitude than *Avena fatua*. Moreover, *Themeda triandra* covaried negatively with *A. fatua* (Figure 3.4a), such that high cover of *A. fatua* was associated with low cover *Themeda triandra* and vice versa. Small-statured species, such as those in the genera *Aira*, *Vulpia* and *Hypochaeris*, tended to covary positively.

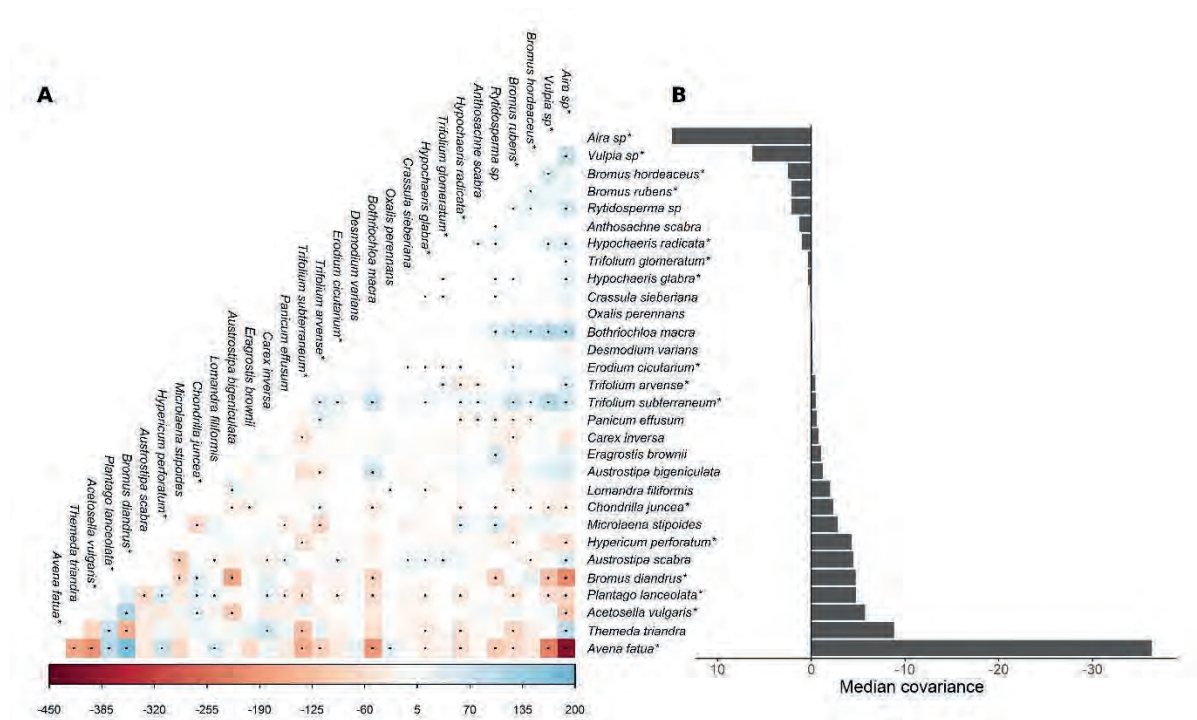


Figure 3.4. Species associations estimated by JSDM1. **a)** The full residual covariance matrix for JSDM1 and **b)** the median residual covariance from all pairwise interactions for each species, with negative covariances indicative of competitive displacement (see text). The full matrix shows mean covariances from the posterior distributions shaded by magnitude and direction, ranging from large negative covariances (deep red) to large positive covariances (blue). A black dot indicates the 95% credible intervals for a covariance did not include zero. Non-native species are marked with asterisks.

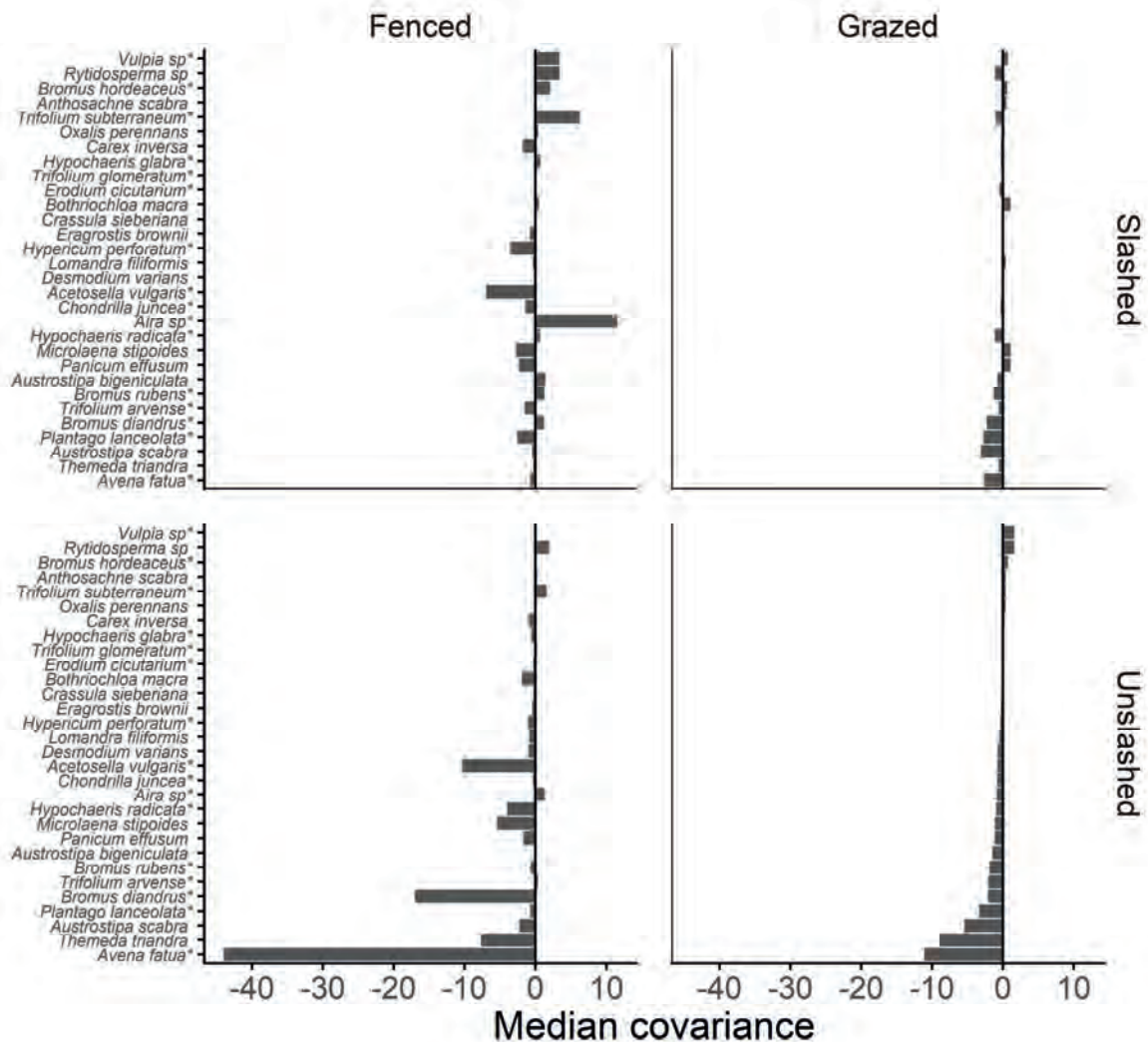


Figure 3.5. The median residual covariance from all pairwise interactions for each species from JSMD2, where a separate covariance matrix was fitted for each treatment (shown as separate panels). The median covariance summarises the magnitude of competitive displacement between a single species and the rest of the community. Names of non-native species are shown in black and native species in grey. Non-native species are marked with asterisks.

3.4.3 Change in species covariances by treatment:

JSMD2 revealed that species' residual covariances varied by grazing and slashing treatment (Figure 3.5), suggesting that competitive interactions were altered by biomass removal. Covariances were weakest in the grazed, slashed treatment with the median close to zero for most species (mean median covariance with 95% confidence intervals =

-0.4, CI = [-2.2, 1.3]), implying weak interactions. Covariances were larger but still relatively weak in the fenced, slashed treatment (mean = 0.2, CI = [-1.5, 2.0]). Median covariances were most negative in the grazed, unslashed treatment (mean = -1.3, CI = [-3.0, 0.5]) and especially the fenced, unslashed treatment (mean = -3.2, CI = [-4.9, -1.5]), suggesting stronger competitive interactions in the absence of slashing, and especially in the absence of both grazing and slashing. Relative to the natural situation in these grasslands (the grazed, unslashed treatment), the three species whose cover increased most strongly with fertility in the fenced, unslashed plots (*Avena fatua*, *Bromus diandrus* and *Acetosella vulgaris*) showed a marked shift to more negative covariances in the same treatment, especially *A. fatua* (Figure 3.5). This implies these species had a greater competitive impact on other species in the absence of biomass removal.

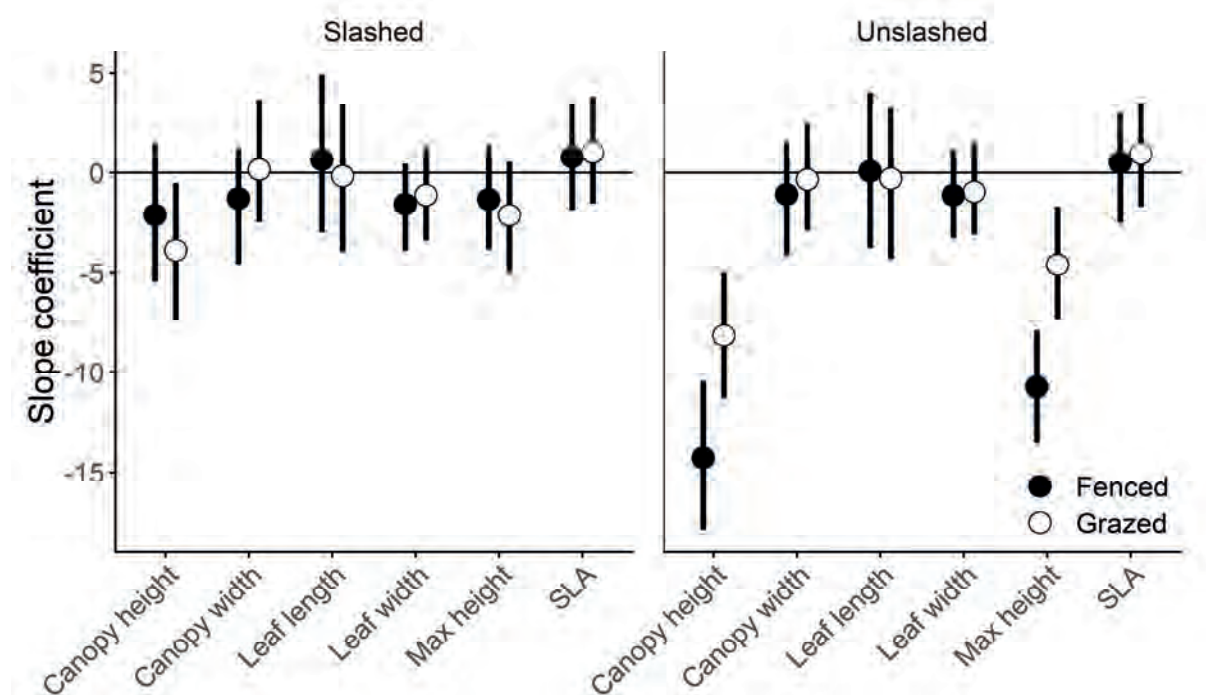


Figure 3.6. The relationship between covariance and trait differences among species (mean and 95% credible intervals). Negative values indicate that competitive displacement is associated with greater difference in trait values between species. The relationships are plotted separately for the four treatments, with filled circles for fenced plots, open circles for grazed plots, and slashed and unslashed plots in different panels.

Trait differences were normalized before analysis to allow direct comparison of slope estimates for traits measured in different units.

3.4.4 Predicting impact from functional traits:

In the fenced, unslashed treatment, stronger negative covariances between species were associated with greater differences in plant height (Figure 3.6). This relationship was evident, though weaker, in the grazed, unslashed treatment but largely absent in both slashed treatments. Covariances were less negative between species that had greater differences in SLA in all treatments, but the strength of this relationship was much weaker than for height. None of the remaining trait differences (canopy width and leaf dimensions) showed strong relationships with covariances.

3.5 Discussion

Measuring the strength of species interactions when these are confounded with environmental variation remains a major obstacle to studying the impact of non-native species in plant communities (HilleRisLambers et al., 2010; Levine et al., 2003; MacDougall & Turkington, 2005). We have shown how a joint-species-distribution model can be adapted to model plant cover and, when applied to our case study, could identify the non-native species having large competitive impacts on the community, along with the conditions under which those impacts were greatest. Globally, non-native species frequently dominate grasslands under conditions of high fertility in the absence of grazing (Seabloom et al., 2013, 2015). Our findings show this can result from displacement of native species by one or more competitively dominant non-native species. In our study, greater cover of three non-native species (*Bromus diandrus*, *Acetosella vulgaris* and especially the annual grass *Avena fatua*) was associated with strong declines in the cover of native species after accounting for differences in environmental responses. This outcome is consistent with previous studies that have measured the impact of non-native species in Australian temperate grasslands (Driscoll & Strong, 2017; Prober, Thiele, Lunt, & Koen, 2005) and in grasslands globally (Chang & Smith, 2014; Flores-Moreno et al., 2016; Harpole et al., 2016).

Our results support the predictions outlined in the Introduction. First, competitive impacts, as revealed by the strength of negative covariances, were much stronger in the

absence of biomass removal (Figure 3.5). Second, under low or no biomass removal, the strength of negative covariances were linked to differences in plant height: in unslashed plots, taller species had greater impact on shorter species, implying a strong competitive advantage associated with plant height under these conditions (Figure 3.6). This outcome most likely results from competition for light, which should favour taller, higher biomass species (Borer et al., 2014; Hautier et al., 2009). While negative covariances were linked most strongly to height differences, negative covariances were smaller among species with greater differences in specific leaf area (Figure 3.6). This implies that, while competitive dominance was due primarily to a trait advantage in height, this was partly offset by trait dissimilarity in SLA, potentially indicative of reduced competitive impact through niche differentiation (Gross, Börger, Duncan, & Hulme, 2013).

Results from the JSDBMs provide additional insights into interactions in these grasslands. For example, negative covariances, and hence competitive interactions, were weaker in the slashing treatments (Figure 3.5). Annual biomass removal by slashing may prevent species from attaining cover sufficient to have a strong competitive impact (Mortensen et al., 2018). Grazing may also prevent competitive dominance, although interactions were stronger under grazing alone than when plots were slashed (Figure 3.5), suggesting grazing removes less biomass than slashing, or selectively removes certain species allowing others to attain cover sufficient to have measurable impact (Evju, Austrheim, Halvorsen, & Myrnes, 2009). The most dominant species, *Avena fatua* had the greatest competitive impact, but also covaried negatively with two other species that had relatively high impact overall: the native grass *Themeda triandra* and non-native forb *Acetosella vulgaris* (Figure 3.4). *Avena fatua* and *Acetosella vulgaris* both increased in cover at higher fertility in the absence of biomass removal, suggesting these species competed for site occupancy under those conditions. The ability of *Acetosella vulgaris* to form dense rhizomatous mats may have excluded *Avena fatua* from some sites (Fan & Harris, 1996). *Themeda triandra*, in contrast, had higher cover at lower fertility. *Themeda triandra* is known to dominate more intact native grasslands (Prober & Lunt, 2009), suggesting that *Avena fatua* may be displacing an otherwise competitively dominant native grass at higher fertility sites.

Other non-native species were abundant in these grasslands but had little or no competitive impact. Short-statured annual grasses in the genera *Aira* and *Vulpia*, for

example, were widespread (Figure A4-S2) and had high average cover where they occurred (15% and 24% for *Aira* and *Vulpia*, respectively, compared with 30% for *Avena fatua*). Both *Aira* and *Vulpia* strongly negatively covaried with *Avena fatua* and *Bromus diandrus*, and both covaried positively with other, typically short-statured, species that were also impacted by the competitive dominants. Hence, in addition to identifying the drivers of change in this community, we can identify non-native species that achieve moderate to large cover without impacting the community, most likely because they are ruderal-like species that exploit more marginal habitats.

We have demonstrated how a JSJM can be applied to field data to measure impact and identify the species driving compositional change in a plant community. We emphasise that interpreting negative residual covariation as due to species interactions relies on having measured and correctly modelled the major environmental variables, fertility and rainfall in our case, that control species abundances (Hui, Taskinen, Pledger, Foster, & Warton, 2015). Our approach of crossing a natural fertility gradient with manipulation of biomass removal no doubt helped to disentangle competitive from environmental effects in this system, as it meant differences between the biomass treatments at each site were not confounded with environmental variation. Nevertheless, the model appeared successful in identifying species having impact in the unmanipulated treatment alone (grazed, unslashed; Figure 3.5), suggesting JSJMs can detect interactions in systems without experimental manipulation where the environmental drivers are well understood.

3.6 Conclusion

Quantifying the importance of competitive interactions is difficult when species abundance is confounded with environmental variation (Adler, Kleinhesselink, et al., 2018). We approached the problem by using a JSJM to model changes in the cover of Australian temperate grassland species in response to gradients of fertility and rainfall, biomass removal treatments, and variation in community composition. This identified the dominant non-native species driving compositional change through competitive displacement in this community, highlighting the utility of JSJMs in studies of plant invasion where it is often unclear which non-native species, if any, are directly impacting invaded communities (HilleRisLambers et al., 2010; Lai et al., 2015; MacDougall &

Turkington, 2005). By experimentally altering grazing we were able to show that the competitive impact of the dominant non-native species increased in the absence of grazing and that species responses were mediated by trait-differences in height, consistent with the outcome we would expect due to competition for light (Borer et al., 2014). Hence, the modelling approach provided insights into the mechanisms underlying impact, paving the way for general tests of the drivers of community structure in other communities (Mortensen et al., 2018). We have provided the data and code in an R package (<https://github.com/aornugent/impact2>) to reproduce our analyses and encourage further application of the approach.

4 INFERRING THE STRENGTH OF PLANT COMPETITION FROM FIELD DATA: RECONCILING FIELD AND EXPERIMENTAL RESULTS

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Keywords

4.1 Abstract

Competition is considered a key factor structuring plant communities, however estimating the relative importance of intra- and interspecific competition from field data is prone to bias. This can arise due to a failure to measure competition at sites where species are absent because they have been competitively excluded (the ghost of competition present). Joint species distribution models (JSDMs) may be less susceptible to this bias because they infer interactions such as competition based on residual covariation among species, which includes information on species absences. Glasshouse studies provide an alternative approach to estimating competitive effects but it often unclear whether the results from field and glasshouse studies are comparable.

We conducted a glasshouse competition experiment to validate a JSDM fitted to Australian temperate grassland communities. Three non-native grasses (*Avena fatua*, *Bromus diandrus* and *Eragrostis curvula*) were grown in monoculture and in mixture with a representative grassland community (*Bromus hordeaceus*, *Poa labillardierei*, *Rytidosperma caespitosum*) using a response surface study design that was replicated at three levels of nutrient addition. We fitted yield density curves at each fertility level to estimate the effects of intra- and interspecific competition, then compared our results with residual covariation between species abundances detected by the JSDM.

Although our experiment identified the same competitive associations that we detected in the field, our JSDM underestimated the effect of interspecific competition because it incorrectly predicted that high fertility sites were unsuitable for some species. We show through simulation that JSDMs are less biased when the patterns of observed abundance contain enough process noise to decouple species abundance from environmental factors.

There is significant potential to use JSDMs to identify when competitive interactions are strongly affecting community assembly but, like other phenomenological models, we suggest their limitations are carefully considered before drawing general conclusions. While JSDMs partially circumvent the limitation of field studies that only observe species in their realised niches, they should be validated against ecological knowledge and experimental tests.

4.2 Introduction

The relative strength of inter and intraspecific competition, and how this varies with environmental conditions, is central to understanding species coexistence and the forces structuring plant communities (Chesson, 2000, 2018). However, measuring competition in the field is difficult and there is concern that the ‘ghost of competition present’ may bias outcomes in field settings (Detto, Visser, Wright, & Pacala, 2019; Tuck, Porter, Rees, & Turnbull, 2018). This ghost arises when strong interspecific competition excludes a focal species from sites it would otherwise occupy (i.e. realised vs. potential niches; Jiménez-Valverde, Lobo, & Hortal, 2008; Kearney, 2006; Soberon & Nakamura, 2009). Field studies that measure interspecific interactions where the focal species is present may underestimate the strength of competition if these studies do not include sites where the focal species is absent due to particularly strong competition that resulted in exclusion (Figure 4.1; Adler, Kleinhesselink, et al., 2018; but see: Carmel et al., 2017; Tuck et al., 2018). This presents a fundamental limitation to what can be inferred from observational field studies of plant communities (Cale, Henebry, & Yeakley, 1989; Ovaskainen, Rybicki, & Abrego, 2019), with consequences for our understanding of coexistence across terrestrial plant communities (Adler, Smull, et al., 2018).

Joint species distribution models (JSDMs) estimate relationships between environmental factors and species presence or abundance in field data and interpret residual covariation as being potentially due to interactions among species (Ovaskainen et al., 2017; Pollock et al., 2014; Warton et al., 2015). Negative covariation, sometimes indicative of competition, can arise if the presence of one species causes the abundance of a second species to be lower than expected from environmental effects alone (J. S. Clark et al., 2017; Niku, Warton, Hui, & Taskinen, 2017). However, negative covariance could also arise due to unmeasured environmental variation or dispersal limitation (Barner, Coblentz, Hacker, & Menge, 2018; Cazelles, Araújo, Mouquet, & Gravel, 2016; Freilich, Wieters, Broitman, Marquet, & Navarrete, 2018). This means that although JSDMs can leverage information from species absences to detect where interspecific competition is strong, patterns of negative covariance could be confounded with other factors. Inferring competition from distributional patterns of species abundance instead requires *a priori* ecological knowledge about the scale, traits and mechanisms related to species interactions (Dormann, Bobrowski, et al., 2018; Dormann et al., 2012).

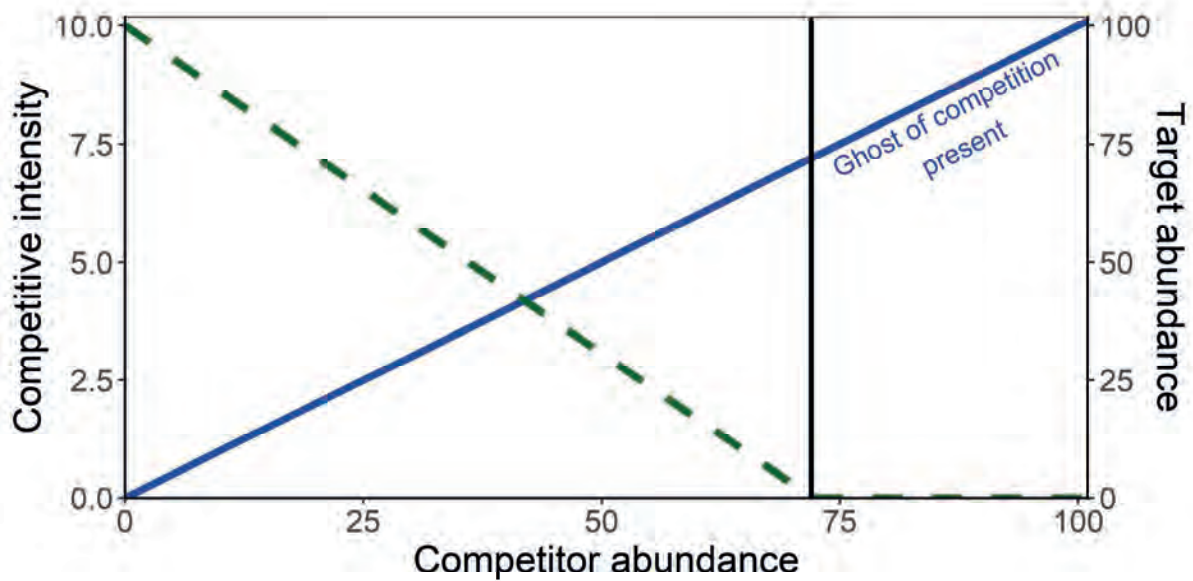


Figure 4.1. The ‘ghost of competition present’ can bias estimates of competition derived from patterns of observed abundance that do not include sites where species are excluded. Competitive intensity (blue line) continues to increase with competitor abundance beyond the point where a target species (dashed green line) has been completely excluded.

A growing number of studies confirm that JSDMs can be useful for identifying species interactions under select conditions (Norberg et al., 2019; Ovaskainen et al., 2019; Zurell et al., 2018), however JSDMs face two additional hurdles when inferring whether competition is important driver in plant communities. First, covariances are mathematically symmetric, meaning that they represent the average strength of interactions between two species, and do not imply a direction. Competition among plants, however, can be asymmetric, with larger individuals having disproportionate effects on their smaller competitors (DeMalach, Zaady, Weiner, & Kadmon, 2016; Schwinning & Weiner, 1998). The strength of competitive interactions may be underestimated by covariances if asymmetric effects are not accounted for. Secondly, JSDMs must specify an underlying environmental relationship for each species, which may have significant impacts on species interactions (Bar-Massada & Belmaker, 2017; Bimler, Stouffer, Lai, & Mayfield, 2018; Pellissier et al., 2018), such as size dependent competition along fertility gradients (Cameron, Coulson, & Marshall, 2019; Goldberg,

Martina, Elgersma, & Currie, 2017; Rees, 2013). While it is accepted that models will only ever provide an approximation of true ecological dynamics (Chu & Adler, 2015), there is a risk of misunderstanding the factors that shape species distributions if models are insufficiently flexible to capture the underlying environmental relationships (Merow et al., 2014).

Therefore, while JSDBMs may circumvent the ghost of competition present, the application of JSDBMs should build on established ecological knowledge to support inferences about species interactions. We conducted an experiment to validate a JSDBM previously fitted to observational data from an Australian temperate grassland (O'Reilly-Nugent et al., 2019) and test whether our JSDBM was also biased by the ghost of competition present (Adler, Kleinhesselink, et al., 2018; Tuck et al., 2018). The JSDBM analysis identified two dominant non-native grasses, *Avena fatua* and *Bromus diandrus*, that showed strong positive responses to soil fertility and negatively covaried with other native and non-native grassland species, indicative of competitive impact. However, our JSDBM predicted that many native species should decrease in abundance with increasing soil fertility, even in the absence of dominant competitors. This result was unexpected and indicated a potential misfit of our model. Our experiment sought to verify this finding by measuring the growth of individuals grown at different densities along a gradient of fertility, and by comparing species growth in isolation against growth in community mixtures (Harper, 1977; Hart, Freckleton, & Levine, 2018).

We used these experimental measurements to test whether the inferences derived from our JSDBM were correct in terms of whether: 1) the relationships with fertility derived using the JSDBM were accurate, 2) the competitive hierarchy derived from the JSDBM matched that obtained in the glasshouse experiment, and 3) the approximation of competitive interactions using a symmetric covariance in the JSDBM was appropriate. In a second analysis, we demonstrate through simulation how our experimental patterns of species interactions could indeed reflect the same underlying demographic and competitive processes occurring in the field. This simulation also allowed us to test for potential causes of bias in the JSDBM. More generally, this experiment enabled us to answer an important question: do associations in field data, when used to infer the strength of species interactions, match the outcomes of competition that we observe experimentally? (Cadotte & Tucker, 2017; D'Amen, Mod, Gotelli, & Guisan, 2018;

Dormann, Bobrowski, et al., 2018) Together, our JSDM, experiment and simulation demonstrate a general mismatch between observation and experimental studies of plant competition and suggest how they should be considered in conjunction with one another.

4.3 Methods

4.3.1 JSDM analysis of an Australian grassland community:

The results of our JSDM analysis have been published in a separate journal article (O'Reilly-Nugent et al., 2019), therefore our discussion of these methods will be brief. We used a novel JSDM to compare the competitive impacts of introduced species on grassland communities in the Australian Capital Territory (ACT). We used data from 3 years of vegetative community surveys in 400 x 1 m² quadrats. Species abundances were estimated as the percent areal cover within each quadrat. The model was fitted to abundance data to jointly estimate species environmental responses and residual covariation between 30 species.

Environmental responses were modelled as linear functions of fertility and spring rainfall, which are known to strongly influence species abundances in these grasslands (Leishman & Thomson, 2005; Morgan et al., 2016; Prober et al., 2016). There was no constraint on direction of these responses meaning that species could increase or decrease with increasing fertility or rainfall. Covariances estimated by our JSDM describe how residual variation in the cover of one species is related to residual variation in the cover of a second species. If, having accounted for environmental effects, the cover of one species declined in quadrats when the cover of a second species increased, the residuals of the two species would covary negatively. We took a conservative approach by specifying *a priori* that most variation in species abundances was independent of co-occurring species, meaning we required adequate data to support strong residual covariances, increasing our confidence of identifying potential interactions between species. Two species were identified as being especially dominant: *Avena fatua* and *Bromus diandrus* (O'Reilly-Nugent et al., 2019). Both species had strong positive relationships between abundance and fertility and were observed to negatively covary with other species in the community, meaning that as these species increased in abundance, resident species declined.

The impact of these dominant non-native grasses was consistent with *a priori* understanding of competition in grasslands. *Avena fatua* and *Bromus diandrus* had strong impacts where herbivores were excluded. Given that both dominant non-native species also increased in abundance with increasing fertility, they likely excluded resident species through competition for light (Lind et al., 2013; Seabloom et al., 2015). This was confirmed by a significant relationship between height differences between species and the magnitude of negative covariation in abundance (O'Reilly-Nugent et al., 2019). Impacts increased with increasing differences in height, but this was approximated in our JSDM using a symmetric covariance structure, meaning that a pair of species had equal impacts, which is unlikely during light competition. This limitation of a symmetric covariance approximation coupled with the unexpected negative relationships between abundance and fertility prompted us to conduct a glasshouse experiment to validate our findings.

4.3.2 Experimental measurement of competition between species:

For each of six species, we experimentally quantified the strength of per-capita competition by growing individuals of each species in a response-surface design (Damgaard 1998; Inouye 2001). Response surface designs estimate intra- and interspecific competition by measuring changes in species growth along gradients of intra- and inter-specific density (3, 6, 9 & 12 individuals per pot). Because our JSDM analysis was primarily focused on measuring the impact of non-native species, we measured the competitive effects of three non-native species on a resident grassland community at three fertility levels. Our three focal non-native species included the two grasses, *Avena fatua* and *Bromus diandrus*, that were identified as having significant negative associations in our JSDM analysis, and *Eragrostis curvula*, which was not abundant or dominant in our JSDM study but is a weed of national significance in Australia (Csurhes, Leigh, & Walton., 2016). Because *Eragrostis curvula* is an opportunistic coloniser that becomes dominant in marginal and disturbed habitats (such as along roadsides), it provides a good contrast to *Avena fatua* and *Bromus diandrus* which we identified as having impact through interspecific competition. We expected that *Eragrostis curvula* would have little interspecific competitive impact on the resident community.

Our resident community consisted of the native grasses *Rytidosperma caespitosum*, *Poa labillardierei* and the non-native *Bromus hordeaceus*, which is small statured and commonly coexists with native grassland species. We grew the resident community in fixed densities (1, 2, 3, & 4 individuals per species) such that the total pot densities were the same as the non-native monocultures described above (3-12 individuals per pot). We sourced seed from local distributors (Greening Australia ACT, Plant Science Consulting, Australian Grasses & Wildflowers), except for *Eragrostis curvula* which was collected from an existing population at the University of Canberra. We germinated seedlings of each species in monoculture on trays of peat coir in August 2016, in an environmental chamber with a heating mat set to 18 °C and a high intensity overhead lamp providing a 12 hr photoperiod. We transplanted seedlings approximately one week after emergence of the second leaf into 13 cm diameter pots with 2 cm deep saucers that contained 2 L of a 1:1 mixture of sterilised river sand and vermiculite, creating a nutrient poor substrate that required regular supply of nutrients and water.

We grew non-native and resident species in monoculture and in mixture with relative frequencies that ranged from 0.25 to 0.75 (that is mixtures of 3/9, 3/6, 3/3, 6/6, 6/3, and 9/3 non-native/resident individuals). We repeated this design at three levels of nutrient supply (Low, Medium, and High) resulting in 102 pot-level experimental treatments (4 x 4 x 3 = 48 non-native or resident monocultures, 6 x 3 x 3 = 54 non-native/resident mixtures). We added 10 ml of liquid nutrient solution (1/8, 1/2 and 1 x strength nitrogen and phosphorous, Appendix B1; Table B2-S1) uniformly to each pot twice per week. Pots were watered twice daily (dawn and dusk) by an automated sprinkler system at a rate of approximately 2 ml.day⁻¹, representative of average conditions in the area during the growing period although with much less variability (Bureau of Meteorology, Australian Government). We replicated this design in four blocks, each arrayed on a 0.9 m x 3 m bench, and randomised the layout of pots within each block each week to minimise the effect of neighbouring pots.

In total, we planted 3,601 seedlings into 408 pots and harvested them after 12 weeks growth (84 days). 11 seedlings that died during an initial two-week establishment period were replaced. Daily temperatures during the experiment ranged from 12/7 °C (max/min) to 42/20 °C. An automated cooling system was active at temperatures above 30 °C to limit the effects of very hot days. Similarly, we erected a permeable shade-cloth

in the final 6 weeks to control extreme temperatures but added high intensity discharge lighting to maintain a 12 hr photoperiod. A further 66 seedlings died after the establishment period, leaving 3,535 plants at the end of the experiment. The aboveground biomass of each individual plant was harvested, dried, and weighed.

4.3.3 Fitting yield density curves:

Our primary aim was to reconcile negative residual covariation estimated from abundance data recorded in the field with experimentally derived measurements of competition. We estimated how the aboveground biomass of one species changed with increasing abundance of a competitor by fitting yield density curves to the biomass of all individuals in a single pot. Although this approach examines the effect of competition on a different scale to our JSMD, the interactions estimated from species abundance observed in the field are driven by the outcomes of growth, survival, and reproduction of individual plants. Because biomass and plant cover are typically correlated (Axmanová et al., 2012; MacDonald, Burke, Chen, & Prepas, 2012), we make the simplifying assumption that reductions in growth and biomass due measured in our experiment will also result in reduced abundance and cover in the field.

Asymptotic yield density curves assume that biomass (either in a pot or in the field) is eventually limited by available resources and, as total biomass approaches this limit, the average biomass per individual will get progressively smaller (Spitters, 1983). For a single species, total biomass was described by

Equation 4.1

$$\lim_{N \rightarrow \infty} \hat{Y} = w \cdot N$$

where \hat{Y} was the maximum (asymptotic) biomass supported by the available resources, w was the average individual biomass (g) and N was the number of competing individuals. As N increased and \hat{Y} remained fixed, there were fewer resources for each individual, and therefore w decreased, otherwise known as the law of constant yield. We modelled the relationship between average biomass and density for small numbers of individuals by including an intercept:

Equation 4.2

$$\lim_{N \rightarrow \infty} w = \frac{\hat{Y}}{N} = \frac{1}{\alpha_0 + \alpha \cdot n}$$

where α_0 represented the inverse biomass of a single individual in isolation. α described how the biomass per plant decreased with each additional individual, and $n = N - 1$ described the density of competitors, not including the focal individual. α therefore measures the average intra-specific competitive effect, assuming that interactions between individuals are additive under fixed environmental conditions.

We extended this model to measure interspecific competition across our three fertility levels specifying separate intercepts and interaction terms for each species in each treatment:

Equation 4.3

$$w_{[jk]} = \left(\alpha_{0[jk]} + \sum_{l=1}^S \alpha_{[jkl]} \cdot n_{[l]} \right)^{-1}$$

where j corresponds to the focal species, k indexes fertility treatment, and l was one of S competing species. Comparing α_0 for each species described how they responded to increasing fertility, independently of competition. $\alpha_{[jkl]}$ represented the average effect of species l on individuals of species j in fertility treatment k . Intra-specific competition occurred when $l = j$, but again $n_{[l]}$ did not include the focal individual (that is, $\sum n = N - 1$). Because we expected significant variation in individual growth, as well as the potential for systematic bias due to the position of the pots in the glasshouse, we used the estimated average individual biomass as the expectation of a probabilistic observation model that described our experimental data:

Equation 4.4

$$\mu_{[i]} = \ln(w_{[jk]} \cdot \beta_{[b]}) - 0.5 \cdot \sigma_{[jk]}^2$$

$$y_{[i]} \sim \text{Lognormal}(\mu_{[i]}, \sigma_{[jk]}^2)$$

where y is the observed biomass of individual i , which is drawn from a lognormal distribution with mean μ and a variance term σ^2 on the log scale. μ includes a multiplicative offset β for all individuals in block b , relative to the first block ($\beta_1 = 1$), and

a small offset so that our fitted expectation of \mathbf{w} represents the mean biomass on the standardised scale (i.e. not log transformed).

In total, we fitted this model to 30,808 interactions between 3,535 individuals to parameterise 90 interaction coefficients ($\alpha_{[jkl]}$). All parameters were constrained to be positive and given weakly informative priors: gamma distributions for α_0 and α parameters, and half-normal distributions for β and σ^2 . We fitted this model to the data in a Bayesian framework using adaptive Hamiltonian Monte Carlo with the probabilistic programming language Stan (Carpenter et al., 2017) and the rstan interface (Guo et al., 2016) in R, version 3.5.1 (R Core Team, 2018). Both the model and data be found online at <https://github.com/aornugent/competition>.

4.3.4 Comparing observation and experimental results:

Plant communities are structured by both intra- and inter-specific effects, but observational studies, including JSDMs, typically focus on detecting when the impacts of interspecific competition is greater than intraspecific competition (Adler, Kleinhesselink, et al., 2018; Tuck et al., 2018). We derived a measure of relative competitive effect from our glasshouse experiment by predicting species mean biomass in two competitive scenarios: under increasing intra-specific competition and under increasing inter-specific competition. Using our posterior estimates of α_0 and α , we predicted the total biomass of three resident individuals, one from each species, then increased the number of intra- or interspecific competitors from 0 – 9. Similarly, we predicted the biomass of one individual of each non-native species, then increased competitor number from 0 – 11, such that total pot density was the same for non-native and resident comparisons. We limited the number of comparisons by pooling the competitive effects of resident species on the three focal species equally ($\alpha_{[jk[\text{residents}]]} = \sum(\alpha_{[jkl]}) / 3$, where $\mathbf{l} \in$ resident community species).

We then calculated the ratio of predicted mean biomass per plant under interspecific and intraspecific competition at each density, in each fertility treatment. Species strongly impacted by inter-specific competition had ratios below one (i.e. performed better in monoculture than in mixture) whereas species that are not strongly impacted by interspecific competition had ratios above one (i.e. were more limited in monoculture than in mixture). We ranked these ratios to identify which species had the greatest

interspecific competitive effect, which we predicted should match the degree of negative residual covariation observed in our JSJM. Additionally, we calculated this ratio for each posterior sample to generate 95% credible intervals and examined whether these overlapped between fertility treatments to test whether competitive interactions changed with nutrient supply.

4.3.5 Reconciling experiment and observation through simulation:

An inherent limitation of short-term experiments is that they can only focus on a subset of possible mechanisms that operate in the field over the longer term (Stachowicz, Fried, Osman, & Whitlatch, 2002). Competition is known to affect multiple population processes, with differing impacts on abundance patterns (Martorell & Freckleton, 2014). Although we assumed that competition measured in our experiment will also result in reduced abundance and cover in the field, our glasshouse experiment was of insufficient length to capture population-level responses. We therefore conducted a secondary analysis of our JSJM, using a simulation of population dynamics informed by our glasshouse experiment. This allowed us to model the same competitive processes we expected our JSJM to detect and examine any potential cause of bias.

Much like our glasshouse experiment, we simulated the equilibrium abundance of two species in isolation and in competition at 1,000 sites along a gradient of fertility using a Lotka-Volterra model. Based on our experimental results, we assumed that each species had positive intrinsic growth rates positive responses to fertility, and negative intra- and interspecific interaction coefficients (Table B2-S2). We assumed that each species follows logistic population growth and that equilibrium abundance was the number of individuals N when the population reached the carrying capacity of site i . For a single species, this was given by:

Equation 4.5

$$N_{[i]} = \frac{r + \beta \cdot x_{[i]}}{\alpha}$$

where r was the intrinsic per-capita growth rate, β was the increase in growth rate with respect to x fertility, and α was an intra-specific interaction coefficient. We extended this to two interacting species as follows:

Equation 4.6

$$N_{[ij]} = \frac{\alpha_{[kk]} \cdot (r_{[j]} + \beta_{[j]} \cdot x_{[i]}) - \alpha_{[jk]} \cdot (r_{[k]} + \beta_{[k]} \cdot x_{[i]})}{\alpha_{[jj]} \cdot \alpha_{[kk]} - \alpha_{[kj]} \cdot \alpha_{[jk]}}$$

where the number of individuals of species **j** was reduced proportionally to average effect of interspecific competition $\alpha_{[jk]}$ of the expected number of individuals of species **k**, which was also impacted by interspecific competition $\alpha_{[kj]}$ from individuals of species **j**. The terms $\alpha_{[jj]}$ and $\alpha_{[kk]}$ represented intraspecific competition for each species. We calculated the ratio of equilibrium abundance in mixture to abundance in monoculture to examine how the intensity of competition changed along an environmental gradient in a population-based model.

This simulation approximated a pattern of abundance that we would expect to see if populations in the field followed the same competitive processes observed in the glasshouse. However, populations in the field are also subject to demographic stochasticity, or process noise, that induces variation in abundance that is independent of environmental conditions. JSDMs make use of this residual variation to quantify the strength of covariation from patterns of abundance that are decoupled from environmental conditions. Any remaining variation that is not correlated with covariation in species abundances is assigned as observation noise. We introduced two parameters to simulate this effect in the two species model:

Equation 4.7

$$N_{[ij]} = \frac{\alpha_{[kk]} \cdot (r_{[j]} + \beta_{[j]} \cdot x_{[i]} + \gamma_{[ij]}) - \alpha_{[jk]} \cdot (r_{[k]} + \beta_{[k]} \cdot x_{[i]} + \gamma_{[ik]})}{\alpha_{[jj]} \cdot \alpha_{[kk]} - \alpha_{[kj]} \cdot \alpha_{[jk]}} + \sigma_{[ij]}$$

where $\boldsymbol{\gamma}$ is process noise and $\boldsymbol{\sigma}$ is observation noise for each species at each site. In our simulations, these parameters were drawn from normal distributions, centred on zero with hyper-parameters $\boldsymbol{\gamma}_{SD}$ and $\boldsymbol{\sigma}_{SD}$, meaning that they can take a range of positive or negative values. **N** was truncated at zero if process or observation noise led to predictions of negative abundance. Because abundances are truncated, competitors had no impact if they were predicted to have an abundance less than zero.

Introducing parameters to control process noise enabled us to test how well a JSDM was able to recover the underlying environmental and competitive interactions specified in

our simulation. Increasing the level of process noise (Figure B3-S1), decouples the relationship between the relationship between abundance and fertility, thereby increasing the potential for the model to detect strong residual covariation. We repeated our simulation 2,000 times, progressively increasing γ_{SD} from 0 to 1, and fitted a bivariate JSDM to the pattern of competing species abundances in each simulation, using the same general model structure as O'Reilly-Nugent et al., (2019). Repeatedly fitting this model in a Bayesian framework was computationally prohibitive, therefore we attempted to recover the model parameters in each simulation with maximum likelihood estimation using the optimr (Nash, 2016) and furr packages (Vaughan & Dancho, 2018) in R version 3.5.1 (R Core Team, 2018). We calculated the bias in estimated environmental response as the square error between the JSDM parameter estimates from the true values and examined the ability of the JSDM to detect competitive interactions as negatively correlated, non-zero covariance between both species.

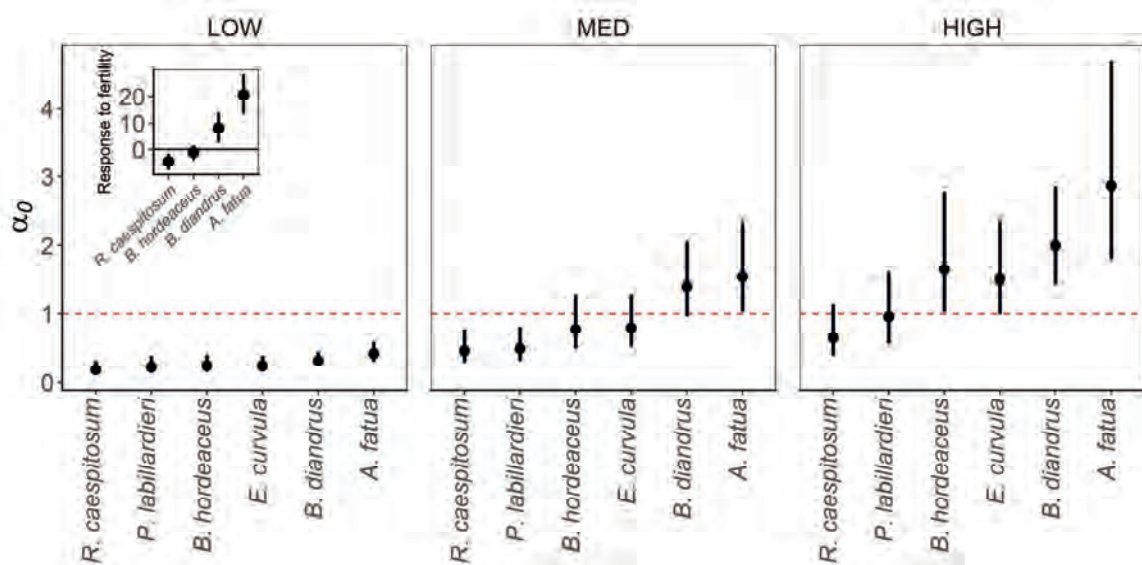


Figure 4.2. Species' responses to fertility estimated in the glasshouse and field. The estimated biomass (in grams) of a single individual (α_0) increases for all species with increasing fertility. This differs from the relationship between abundance fertility (inset), estimated from field data using a JSDM, which is positive for non-native species *A. fatua* and *B. diandrus*, but negative for resident species *B. hordeaceus* and *R. caespitosum*. Points indicate the posterior means, while error-bars describe the 95% credible intervals.

4.4 Results

4.4.1 Contrasting JSMD and experiment results:

Yield density curves fitted our experimental data well (Figure B4-S2). For all six species, the estimated intercept terms α_0 showed increasing biomass in response to increasing fertility (Figure 4.2). *Avena fatua* was consistently larger than all other species. Average aboveground biomass of *Avena fatua* ranged from 0.4 g per individual at low fertility to 2.9 g per individual at high fertility, followed by *Bromus diandrus* at 0.3 g to 2.0 g. In comparison, *Eragrostis curvula* and individuals of the resident species performed much more similarly, with an average biomass per individual of all species of approximately 0.2 g at low fertility. *Eragrostis curvula* and *Bromus hordeaceus* performed better at high fertility, with average biomass at 1.5 g and 1.7 g, respectively, which was significantly larger than *Poa labillardierei* and *Rytidosperma caespitosum* at 1.0 g and 0.7 g. There was significant variation in growth for all species, but even so, these results differed from the JSMD where *Bromus hordeaceus* and *Rytidosperma caespitosum* decreased in cover with increasing fertility (Figure 4.2, inset panel).

The competitive ranking of interspecific impacts was consistent between analyses, with *Avena fatua* and *Bromus diandrus* having the largest interspecific impacts in the field and in the glasshouse (Table 4-A). *A. fatua* was identified as strongly negatively covarying with *Bromus hordeaceus* and *Rytidosperma caespitosum* in the field. *Bromus diandrus* negatively covaried with *Rytidosperma caespitosum* but had positive covariation with *Bromus hordeaceus*. *Eragrostis curvula* and *Poa labillardierei* were not observed in our field study. The experimentally derived interaction coefficients were negative for all species pairs (Figure B2-S3). The interspecific impacts of *Avena fatua* and *Bromus diandrus* were highly asymmetric, having greater competitive impacts on resident species than imposed by resident species (Table 4-A). *Eragrostis curvula* had far smaller impacts than the other non-native species. Our experiment was not able to distinguish between the interspecific effects of each resident species (Figure B2-S3). We therefore focus on the overall impact of the community from here on.

Table 4-A. Interspecific competitive impact estimated from our JSMD (σ) and glasshouse experiment (α) at low, medium and high fertility. While not directly comparable between treatments, the scale of interaction coefficients within each column gives an indication of the degree to which increasing abundance of the competitor decreases the abundance of other species. Importantly, σ is forced to be symmetric, with the direction of competitive impact inferred from *a priori* ecological knowledge, whereas interspecific dominance is clear when α takes different values for pairs of non-native / resident competitors.

Non-native	Resident	σ [JSMD]	α [Low]	α [Medium]	α [High]
	<i>B. hordeaceus</i>	-43.2	4.60 / 0.67	1.76 / 0.30	1.15 / 0.18
<i>A. fatua</i>	<i>R. caespitosum</i>	-102	7.55 / 0.65	1.75 / 0.30	1.76 / 0.17
	<i>P. labillardierei</i>	--	7.65 / 0.66	2.77 / 0.29	2.15 / 0.18
	<i>B. hordeaceus</i>	+27.9	4.01 / 0.74	2.17 / 0.26	1.31 / 0.16
<i>B. diandrus</i>	<i>R. caespitosum</i>	-89.7	5.00 / 0.78	1.62 / 0.26	1.57 / 0.15
	<i>P. labillardierei</i>	--	5.99 / 0.78	3.69 / 0.27	2.30 / 0.16
	<i>B. hordeaceus</i>	--	1.64 / 5.63	0.48 / 1.76	0.24 / 1.03
<i>E. curvula</i>	<i>R. caespitosum</i>	--	2.13 / 5.43	0.68 / 1.69	0.37 / 1.06
	<i>P. labillardierei</i>	--	2.21 / 6.33	0.95 / 1.71	0.46 / 0.68

Avena fatua was uniformly dominant, having the greatest competitive effect on the resident community across all three fertility levels. Competitive intensity increased with fertility for *Bromus diandrus* (Figure 4.3), which had less impact at low fertility. *Eragrostis curvula* experienced greater impact at high fertility. The competitive impact of our resident species was broadly uniform across all three treatments, except for slightly reduced impact on *Bromus diandrus* at low fertility. Large uncertainties in the estimates of inter- and intra-specific competition coefficients meant there were no significant differences between treatments. This uncertainty may come from individual variation in

species interactions (Figure B2-S3), even though the overall observation noise in our experiment was low (Figure B2-S4).

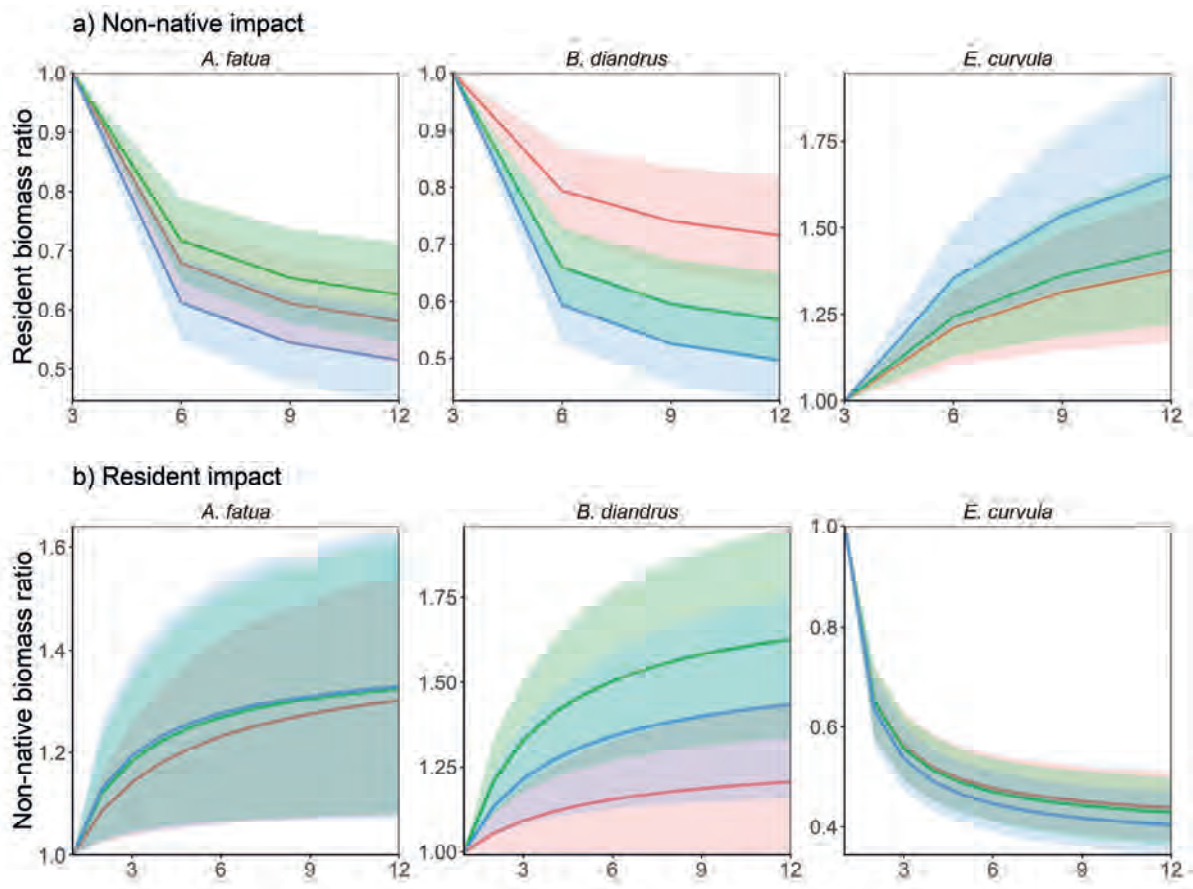


Figure 4.3. The ratio of predicted mean biomass per plant under interspecific and intraspecific competition in each fertility treatment. **a)** Ratio of resident biomass under increasing intra- and interspecific competition. **b)** Ratio of non-native species biomass under increasing intra- and interspecific competition. A ratio less than one indicates that resident biomass is reduced by interspecific competition more than intraspecific competition, while ratios greater than one indicate the opposite. (red = Low, blue = Medium, green = High fertility).

4.4.2 Simulating the effect competition on abundance

In our simulation, the equilibrium abundance of both species increased linearly with fertility (Figure 4.4a). However, when grown in competition, the abundance of the less competitive species (blue) declined with increasing fertility (Figure 4.4b). The relationship between abundance and fertility was largely unchanged for the dominant species when grown in competition. Competitive intensity experienced by each species

changed along the fertility gradient, notably for the subordinate species which experienced a large degree of suppression at high fertility, even though per-capita impact remains the same (Figure 4.4c)

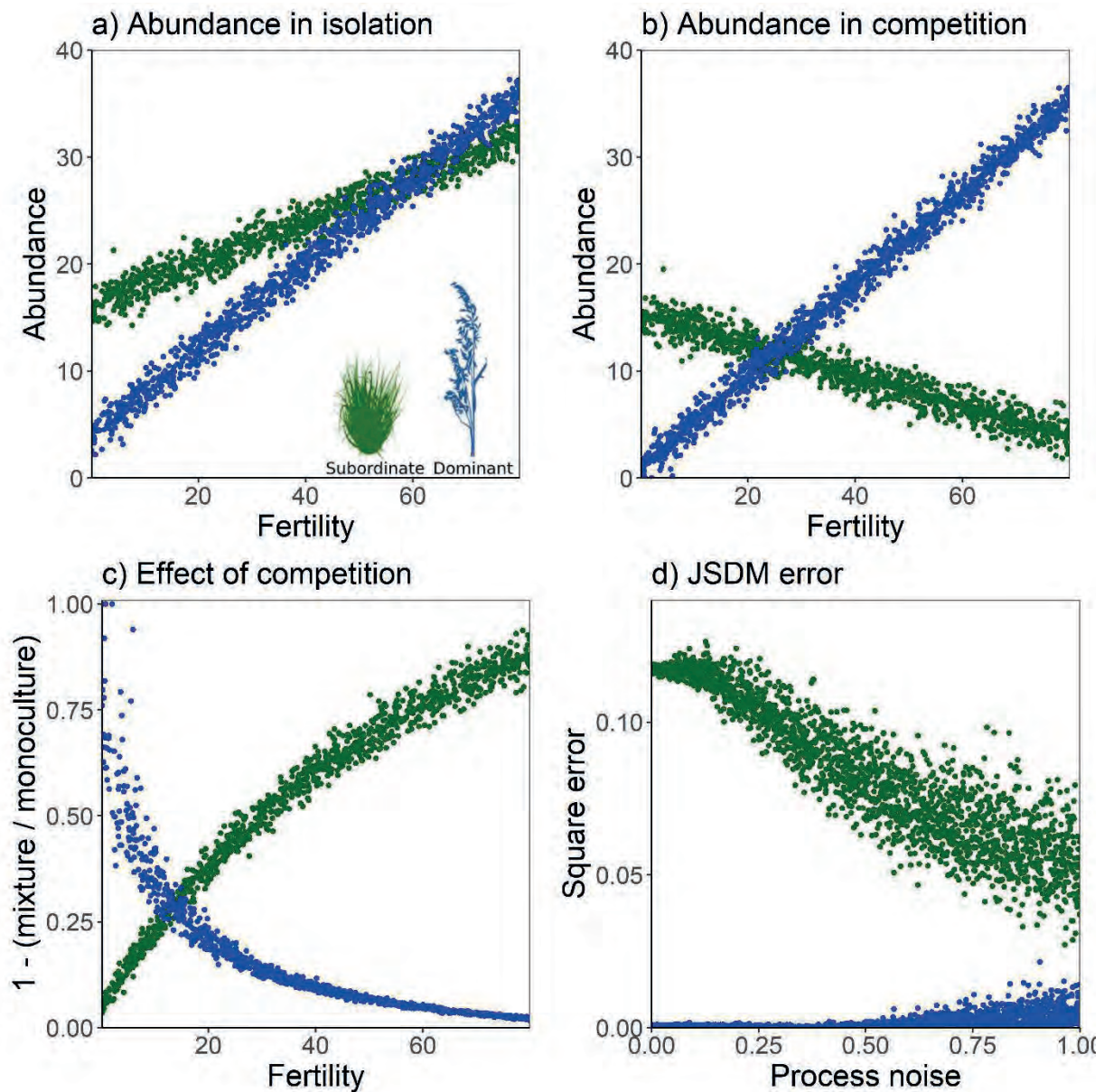


Figure 4.4. Reconciling JSDM and experimental results with simulation. **A)** The simulated abundance of the subordinate species (green) is initially higher than that of the dominant species (blue) at low fertility, when grown in isolation. The dominant species achieves higher abundance at high fertility sites. **B)** The subordinate species has higher abundance at low fertility, when grown in competition together, however the abundance of the subordinate species declines with increasing fertility as the dominant species increases in abundance at moderate levels of fertility. **C)** Competitive impact is shown to change

with fertility for both species, with the degree of suppression, measured as the ratio of abundance when grown in mixture to monoculture, increasing rapidly for the subordinate species and decreasing rapidly for the dominant species. Values less than one indicate that the focal species performs worse under competition than in isolation. **D)** Repeating this simulation with increasing process noise, independent of environmental or competitive conditions, decreases the degree of non-identifiability in a JSDM model and reduces bias in the estimates of response to fertility.

A JSDM did not detect any negative associations in species abundance when there was no variation independent of environment conditions (Figure B2-S5). Because environmental and competitive drivers were confounded, the JSDM did not properly recover the relationship between abundance and fertility for the subordinate species when process noise was low (Figure 4.4d). This bias was negligible for the competitively dominant species. However, the competitive relationship was detected as process noise increased. As process noise increased, species abundance became decoupled from environmental factors, allowing for greater separation of competitive effects. Negative correlation in species residual error stabilised at moderate levels of process noise, while the error captured as covariance between two species continued to decrease with increasing amounts of variation (Figure B2-S5). Increasing process noise reduced bias in the estimates of environmental relationship for the subordinate species, but the JSDM was unable to recover the true response to fertility even with a large degree of process noise in the simulated patterns of abundance (Figure 4.4d).

4.5 Discussion

Together our JSDM, experiment and simulation demonstrate the difficulty of inferring species interactions from observational data. Our experiment confirmed the competitive dominance of two non-native species *Avena fatua* and *Bromus diandrus* that were identified as strongly impacting community structure in the field (O'Reilly-Nugent et al., 2019). However, our experiment also showed that our JSDM underestimated the underlying relationships between abundance and fertility for two subordinate species *Rytidosperma caespitosum* and *Bromus hordeaceus* (Figure 4.2). Reconciling these results through simulation suggested that environmental and competitive drivers remained confounded in our JSDM, causing competitive interactions in the field to be

underestimated. While underestimating competitive impacts is a documented problem of observational studies that do not account for species exclusions – the ‘ghost of competition present’ (Figure 4.1; Adler, Kleinhesselink, et al., 2018; Tuck et al., 2018) – our model failed because it falsely predicted high fertility sites to be outside the potential niches of many species, when their absence was instead most likely due to competitive exclusion. We therefore suggest that JSDMs can be useful for identifying strong competitive interactions, but that the impact of dominant species may be underestimated if competitive interactions are confounded with environmental variation (Godsoe, Franklin, et al., 2017).

It was reassuring to see that, overall, our inferences of competitive interactions in the field were aligned with our experimental results, despite measuring different responses in terms of abundance and biomass, respectively. The assumptions of our JSDM provided valid approximations, even using a single, symmetric covariance matrix to approximate competitive interactions that were likely asymmetric (Table 4-A). Even though the intensity of competition is expected to increase with fertility (Figure 4.4c; Rees, 2013), there was little difference in relative impact across fertility treatments (Figure 4.3), meaning that assuming a constant per-capita effect may be suitable to capture general trends. Large, annual species like *Avena fatua* and *Bromus diandrus* may have been particularly dominant at high fertility if rapid growth improved the chances of reaching reproductive maturity before the available resources were depleted (Aarssen, 2015). However, these same species can be excluded at resource poor sites where competition for resources may prevent recruitment (Martorell & Freckleton, 2014). If the recruitment of large species is limited at resource poor sites, then there are opportunities for more diverse communities of less competitive species (Dostál, Tasevová, & Klinerová, 2019). While our single covariance matrix over-simplified this complexity, it otherwise provided an appropriate approximation of average competitive outcomes in the field.

One reason our JSDM may have worked well for dominant species is because their large competitive impacts meant that they were prevalent across many sites, providing enough information to make robust inferences about the relationship between abundance and fertility (Segurado & Araújo, 2004). Some studies have demonstrated improved predictive power by including the presence of dominant species as covariates that determine the abundance of subordinate species (Kissling et al., 2012; Le Roux, Pellissier,

Wisz, & Luoto, 2014). This approach can, however, lead to over-fitting if correlated residual variation between species is not accounted for (J. S. Clark, Gelfand, Woodall, & Zhu, 2014; Maguire et al., 2016). Hierarchical modelling, as in our JSJM, instead attempts to 'borrow strength' from common species to improve predictions for rarer species (Gelfand et al., 2005; Ovaskainen & Soininen, 2011). However, we found that partial pooling between species was not strong enough to identify a common environmental relationship that was observed in our experiment. Our model fitting procedure instead minimised negatively correlated residual variation among species by predicting negative relationships between abundance and fertility. Although our sample of field data did not contain enough information to accurately estimate the interactions of less common species (Popovic, Warton, Thomson, Hui, & Moles, 2019), validating our inferences with an experiment provided evidence to introduce additional constraints (Kearney & Porter, 2009; Kearney, Wintle, & Porter, 2010). In future analyses, all species could be assumed to have positive relationships with fertility.

In fact, building experimental evidence into phenomenological models, such as JSJMs, is fundamentally necessary to test theories of how the world works (Alexander, Diez, Hart, & Levine, 2016; Evans, Merow, Record, McMahon, & Enquist, 2016). Studying complex systems in ecology requires a trade-off between precision, generalism and realism (Mark van Kleunen, Dawson, Bossdorf, & Fischer, 2014) and while experiments allow us to conduct robust tests that isolate confounded processes, they are inevitably limited in scope (Letten et al., 2017; Maynard, Miller, & Allesina, 2020). Incorporating physiological and mechanistic drivers into models of competition that can be applied in the field allows us to test our theories at scale by providing support to processes that are not directly observable (e.g. Hooper et al., 2008) and confirming where and when competition is actively structuring communities (Dostál et al., 2019; Hart & Marshall, 2013). This is particularly important for making predictions where species performance under field conditions has not yet been observed (T. E. Miller, TerHorst, & Burns, 2009; Mark van Kleunen et al., 2014). *Eragrostis curvula* and *Poa labillardierei* were not included in our JSJM analysis, but their slow growth (Figure 4.2) and limited competitive impact (Figure 4.3) measured in our experiment suggests that they may be excluded from invaded communities in the field, which could in turn be tested by seed addition (Wandrag et al., 2019) or direct invasion experiments (Grainger, Letten, et al., 2019).

Frameworks that integrate experiment, observation and theory are improving rapidly (Grainger, Levine, et al., 2019; Maynard, Wootton, Serván, & Allesina, 2019), leading to ever more realistic simulations of plausible community assembly processes (Carmel et al., 2017; Ellner, Snyder, & Adler, 2016). These simulations are extremely valuable for testing the sensitivity and specificity of models that rely on observational data (Norberg et al., 2019; Ovaskainen et al., 2019; Zurell et al., 2019). Our simulation demonstrated the importance of process noise for JSDMs to isolate confounded processes driving patterns of species abundance. The requirement of process noise may also suggest that there is a limit to the precision with which JSDMs can recover the environmental relationships of multiple species at once (Figure 4.4d). Practitioners applying these models must be aware that species may appear to interact weakly because they are often confined to their realised niches by competition (Tuck et al., 2018) and should attempt to include observations from sites where species are absent whenever possible. Ultimately, inferences drawn from observational data must consider that patterns in the field could be generated by multiple processes and should be validated with experiments (Barner et al., 2018).

4.6 Conclusion

There is justifiable concern that non-random associations detected by JSDMs might not reflect species interactions. We show that although JSDM analysis correctly identified competitively dominant, non-native species impacting native grassland communities, the magnitude of these impacts was likely underestimated. JSDMs, like other models that infer competitive interactions from observational data, require enough information to decouple patterns of species abundance from environmental drivers. Where this condition is met, JSDMs are powerful tools for investigating competitive dynamics in diverse plant communities. Future extensions of JSDMs should look to incorporate process-based models that improve predictions of abundance under field conditions. Even then, inferences should be tested using complementary datasets, such as traits, ecological theory, and ultimately experimentation.

5 CAN REHABILITATION ALTER LONG-TERM TRAJECTORIES OF VEGETATION CHANGE IN DEGRADED GRASSLANDS?

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Keywords

5.1 Abstract

1) The short-term effects of interventions such as seed addition may be overwhelmed by natural successional change in the long run. This calls into question the value of rehabilitation efforts. Identifying appropriate controls to assess long-term rehabilitation outcomes can be challenging when control plots within rehabilitated areas are themselves affected by rehabilitation actions (e.g. through the local spread of native species). However matching external reference sites can be rare, and trajectories of community development vary significantly across the landscape.

2) We compared vegetative changes in a rehabilitated old field against three sets of non-intervention controls: non-intervention plots in the rehabilitated field; plots from two matched reference fields of the same successional age; and plots in 21 nearby old fields that varied in time of abandonment. We examined the cover of five functional groups over 27 years to assess whether vegetative change in the rehabilitated field differed from natural successional trajectories of abandoned grasslands in this area.

3) Rehabilitation, involving seed addition of native grassland species coupled with herbicide application, burning and rototilling, led to lower abundance of non-native species and higher abundance of native grasses and forbs 27 years after intervention, relative to natural successional trajectories of control plots in 21 unrehabilitated fields.

4) Nevertheless, conclusions about the long-term outcome of rehabilitation varied depending on the choice of non-intervention controls. Local control plots demonstrated the short-term (1-2 years) effects of rehabilitation on the establishment of native species, but little long-term difference between rehabilitated and non-intervention plots after 27 years. Rehabilitation appeared effective in restoring native vegetation relative to the two reference fields. But examination of a larger number of abandoned old fields showed that many equivalent communities' transition to native dominance without intervention.

5) *Synthesis and applications.* Rehabilitation of degraded communities is only necessary where natural succession to native dominance has either slowed, stalled, or diverged. Accounting for natural succession by forecasting possible scenarios of community change will enable rehabilitation practitioners to target sites that maximise the certainty of rehabilitation outcomes.

5.2 Introduction

“If we seek to recreate the temperate forests, tall grass savannas or desert communities of centuries past, it is not to turn back [time] but to set it ticking again.”

(Falk, 1990)

Successful rehabilitation of degraded grasslands means altering the trajectory of vegetative change toward enhanced indigenous habitat (Gann et al., 2019; SERA, 2017), often involving interventions that encourage the reestablishment of native species, and create the conditions necessary for their long-term persistence (Buisson et al., 2019; Johnson, Catford, Driscoll, & Gibbons, 2018). These interventions are especially important where the non-native species are expected to remain dominant, long after cultivation has ceased (Cramer, Hobbs, & Standish, 2008; MacDougall et al., 2014). Many studies have shown that rehabilitation interventions can have positive outcomes in the short-term (e.g. Kiehl, Kirmer, Donath, Rasran, & Hölzel, 2010; Kiehl & Pfadenhauer, 2007; Pywell et al., 2002, 2007), but sustaining native populations requires the creation of persistent feedbacks that support recovery after disturbance and limit the potential for re-invasion (Buckley et al., 2007; Nimmo, Mac Nally, Cunningham, Haslem, & Bennett, 2015). Meta-analyses of ecosystem recovery show little long-term difference between rehabilitated sites and sites left to recover naturally (Jones et al., 2018; Meli et al., 2017), suggesting that natural successional processes can often overwhelm rehabilitation efforts in the long run (decades to centuries; Walker & del Moral, 2009).

Succession describes the sequential development of plant communities following disturbance, which can occur predictably, due to the primary effects of environmental conditions on community assembly, or exhibit significant variation depending on initial conditions or the timing of species establishment (Fukami, Bezemer, Mortimer, & Van Der Putten, 2005). Where environmental conditions are the primary driver of vegetative change, communities of the same age and stage are expected to share similar compositions of native and non-native species. However, large-scale drivers, such as changing climatic patterns (Walther et al., 2009), pollution (MacDougall et al., 2014) and species dispersal (Matthews et al., 2009), can act as key forcing factors that overwhelm the effects of local restoration interventions. Long-term changes in environmental conditions could preclude the pathways that lead to native dominated communities

(Macdougall, Beckwith, & Maslovat, 2004; J. W. Williams & Jackson, 2007). Alternatively, if the trajectories of vegetative change are contingent on differences between communities, then variation in community development can lead to significantly different compositions, including alternative stable states dominated by non-native species that are difficult to escape (Shriver et al., 2019; Suding, Gross, & Houseman, 2004). Understanding where succession will lead to native dominated communities, or where interventions result in short-term changes but little long-term effect, is essential for rehabilitation planning (Matthews & Spyreas, 2010; Prach & Hobbs, 2008).

Separating the effects of rehabilitation from succession is complicated because it is difficult to predict what would have happened had intervention not occurred. Most rehabilitation assessments compare the trajectory of vegetative change against a reference community that shared similar starting conditions (Montoya, Rogers, & Memmott, 2012). An ideal reference would be an exact replica where community development proceeded without intervention, leading many studies to use unrehabilitated control plots within the same site (Christie et al., 2019). However, because many rehabilitation interventions are often carried out at small spatial and temporal scales, local control plots may not be independent from intervention effects (Underwood, 1990). For example, seed addition is often used to establish persistent populations of extirpated native species, or supplement existing native populations (Cox & Anderson, 2004; Kardol et al., 2008; Prober et al., 2005), but local control plots that did not receive seed addition could resemble seed addition plots due to local dispersal, or if community development is overridden by external drivers, with seed addition having little effect on the long-term outcome of community development (Brudvig, 2011; Grman, Bassett, & Brudvig, 2013).

Where local control plots are inadequate, many studies compare the effect of rehabilitation intervention against the passive development of unrehabilitated communities at external reference sites (P. S. Lake, 2001). However, it can be difficult to find reference sites that share similar legacies of land use, were not rehabilitated and otherwise match the degraded community in all relevant dimensions of ecological development (White & Walker, 1997). One option is to use abandoned communities of the same successional age, which assumes a common pattern of vegetative change. But true replicas can be rare when there is significant variation in the patterns of natural

succession can across the landscape (Woods, 2007). Chronosequences of similar abandoned communities could be used to examine regional-scale trends of community development by comparing patterns of vegetative change across sites of different ages (Bakker, Olf, Willems, & Zobel, 1996; Michener, 1997). This space-for-time substitution would identify how trajectories of succession vary between developing communities (Foster & Tilman, 2000). With a good understanding of successional variation across a landscape, it should be possible to set an appropriate reference for rehabilitation.

We present a case-study that compares post-rehabilitation changes in a recovering old field plant community against un-rehabilitated controls at three scales: 1) 5 plots in the focal field that had no intervention; 2) 100 plots in two nearby fields, which had similar previous land-use and were abandoned at similar times; and 3) 1,100 plots in 21 nearby old fields that varied in time of abandonment. The rehabilitation experiment trialled six rehabilitation interventions to establish native grassland species in an abandoned old field dominated by non-native grasses at Cedar Creek Ecosystem Science Reserve. In 1993, 30 plots in the focal field received one-off interventions of native seed addition in combination with burning, herbicide, and tilling. The plots were revisited five times over a 25-year period to track changes in plant community composition to assess whether the community shifted from non-native to native grass dominance. Revisiting these fields, we sought to test whether our conclusions about the long-term effect of rehabilitation intervention was dependent on the choice of non-intervention control for comparison. We expected that if all fields followed consistent natural successional processes, then then the effect of rehabilitation and restoration would be clear, but if fields followed very different trajectories, then the outcomes of restoration would depend on the choice of reference ecosystem.

5.3 Methods

5.3.1 Site details:

Cedar Creek Ecosystem Science Reserve (CCESR) in Bethel, Minnesota (45.4086° N, 93.2008° W) is a ~2,200 ha area that includes a mosaic of ex-agricultural, prairie and oak savanna communities, as well as woodlands and wetlands. Cedar Creek was declared a National Natural Landmark in 1945 and has been a Long-Term Ecological Research site since 1982. CCESR has hot, humid summers (~27 °C June-August) and cold winters (-14

°C December – February; A. T. Clark, Knops, & Tilman, 2019). Mean annual precipitation is roughly 775 mm (± 16 mm), ~60% falling between April and August. Soils come from a sandy glacial outwash and are low in organic matter, nitrogen and water-holding capacity (Grigal, Chamberlain, Finney, Wroblewski, & Gross, 1974). Abandoned fields are typically dominated by cool-season C3 grasses, shifting slowly to dominance by native perennial C4 grasses with increasing time since abandonment (Inouye et al., 1987). Old fields at Cedar Creek had a mean richness of 43 species during initial surveys in 1983, with more biennial species than either annual or perennial species. The most abundant species included the non-native C3 grasses *Poa pratensis*, followed by *Elymus repens* (formerly *Agropyron repens*), then native C4 grasses *Schizachyrium scoparium* and *Andropogon gerardii* (Foster & Tilman, 2000). Common forbs included the non-native *Crepis tectorum* and native *Erigeron canadensis* and *Ambrosia artemisiifolia*.

5.3.2 Rehabilitation experiment details:

We studied the effect of rehabilitation interventions in 35 plots in a single field (F0) that was abandoned in 1965 (Svenson, 1995). Each plot was 6 m x 6 m and arrayed in a 36 m x 48 m grid with a 1 m buffer between plots. Six rehabilitation interventions and a non-intervention control were randomly assigned to plots, with five replicates each. The interventions were carried out in May 1993. All six interventions involved adding seeds of 18 native grassland species (5 grasses and 13 forbs; Table C3-S1) to each plot. Seed of each species added at a density of 100 seeds/m² except *Bouteloua curtipendula*, *Elymus canadensis*, *Helianthus pauciflorus*, and *Asclepias tuberosa* which were seeded at 50 seeds/m² due to limited seed availability. Prior to seeding, one of the following interventions was applied to each plot: (1) no manipulation other than seed addition; (2) burning; (3) herbicide application; (4) tilling; (5) seed addition of a nurse crop species; and (6) both herbicide and tilling (details given in Table 5-A). These interventions were intended to increase the success of native seed addition by removing the resident non-native species and/or remediating local nutrient cycles.

Community composition was first measured in September 1993, and again in August 1994, by visually estimating the percent cover of all plant species, litter and bare ground in a single 1 x 0.5 m quadrats located in each plot (Svenson, 1995). Cover was standardised to sum to 100% providing a relative measure of species abundance in each plot. In 1995 all plots in the field were burned. In 1999 and 2000, community composition

was remeasured in 15 plots (corresponding to interventions 0, 1 and 6; Table 5-A) using four 1 x 1 m quadrats in each plot (Blumenthal, Jordan, & Svenson, 2005). Three quadrats were perturbed by burning and/or the addition of nitrogen fertilizer and plant biomass was harvested by clipping within 1 cm of the soil surface. Biomass was summed across quadrats in each plot but left unstandardized. All 35 plots were then remeasured in June 2017 using the same four 1 m x 1 m quadrats as the second set of surveys. The total cover of all plant species, bare ground and litter was visually estimating in each quadrat, then summed across quadrats within each plot. Cover was unstandardized and could therefore sum to > 100% where there was vertical overlap between species. Standardisation of measurement types is described in section 5.3.5. *Data compilation*. The effects of quadrat perturbation were not evident in a final survey in 2017 and we thus ignore them for the remainder of our analyses (details of this sub-experiment can be found in Appendix C1).

Table 5-A. Summary of 1-6 seed addition interventions applied to field F0 in 1993, and two un-rehabilitated conditions found in plots across all 22 old fields. Seed addition aimed to establish persistent populations of native species, additional interventions were intended to increase the success of native seed addition. Herbicide treated plots were sprayed with glyphosate (Roundup®; 110 ml/m²) on the 15th May 1993. Burning occurred on the 15th June 1993. Tilled plots were rototilled to ~8 cm, raked and packed on the 17th-18th June 1993. Native species seed composition is described in Table C3-S1.

#	Code	Interventions	Native seed addition
0	C-	None (un-rehabilitated)	✗
0b	B-	Burned (un-rehabilitated)	✗
1	C+	Native seed only	✓
2	B+	Burned	✓
3	HB+	Burned & herbicide	✓
4	BR+	Burned & tilled	✓
5	BRN+	Burned & nurse crop	✓
6	HBR+	Burned & herbicide & tilled	✓

5.3.3 Matched reference sites:

As a second set of non-intervention controls, we examined changes in plant community composition over time in permanently marked plots in two nearby fields (F1 and F2; ~2,200 m and ~2,000 m from F0, respectively). Community composition was repeatedly surveyed in 100 1 m x 0.5 m plots arrayed along four 40 m transects in each field (1 m between plots; 25 m between transects). Within each field, two transects (0b) are regularly burned, while the remaining half (0) are unmanaged and are primarily only disturbed by herbivores (e.g. insects, deer, gophers; Table 5-A). Cover of all species, litter and bare ground was visually estimated in each quadrat and normalised so that the total cover in a single plot was equal to 100 (i.e. relative abundance). Surveys were conducted in 1983, 1989, 1994, 1997, 2002, 2006, 2011 and 2016, spanning the same timeframe as our rehabilitation experiment (A. T. Clark et al., 2019). These fields had similar land use, and were of similar successional age, both abandoned in 1961. We therefore assumed to share similar community development trajectories as our focal field (F0) at the time of rehabilitation intervention, providing $2 \times 50 = 100$ control plots (intervention 0) that were spatially independent from our focal field (F0).

5.3.4 Landscape chronosequence:

For a final set of non-intervention controls, we examined changes in 21 old fields, including F1 and F2, that had been abandoned at various times in the past. These fields ranged in size from 2 ha to 14 ha and form a 70-year successional chronosequence with the earliest year of field abandonment in 1927 and the most recent in 1997 (Inouye et al., 1987). The fields previously produced corn, oats, potato, rye, and soybeans but otherwise shared similar post-abandonment histories. All fields were distributed within a ~3,500 m radius, often separated by roads, waterways, or forest fragments, with the nearest field ~570 m from F0. 100 permanent plots were established in each field, half of which were regularly burned, and community composition was measured in the same way as the matched reference sites (above), except that data from the 2016 survey was only available for F1 and F2. One field was not burned and had 100 non-intervention control plots only (C-). In total, we had 1,100 non-intervention control plots from fields of different ages.

5.3.5 Data compilation:

Species name, functional group and origin were resolved using the USDA PLANTS database (Natural Resources Conservation Service, 2018). 169 distinct taxa were recorded in plots, 137 of which were resolved to species level and 29 to genus level. Taxa unable to be assigned to genera were aggregated by functional group, leaving entries for miscellaneous forbs, legumes, grasses, mosses & lichens, woody plants, and fungi. 0.3% of records had no distinguishing features and were treated as miscellaneous species. Records of disturbance (e.g. anthills and gopher mounds) and debris were treated as bare ground and litter, respectively. We grouped species into functional groups of native grasses (primarily C4 species; 67%), non-native grasses (primarily C3 species; 67%), native forbs (6% legumes) and non-native forbs (20% legumes). Woody plants, ferns, and species of unknown origin were grouped as “other”. We summed the cover or biomass for species in each group in each quadrat at each measurement. We had 14,431 repeat measurements of five functional groups in 2,135 plots in 22 fields (F0 – F21), with each field surveyed at least three times from the 12 occasions surveys were conducted between 1983 to 2017. This totalled 72,155 observations, which included 18,215 functional group absences (25%) which were recorded as zero abundance.

We scaled our data by discarding records for bare-ground and litter and dividing observations of functional group abundance within a plot by the standard deviation (SD) of functional group abundance across all plots in each survey. Standardising by SD gives a comparable scale between surveys by normalising for differences in plot sizes, observers, and survey methods. Because all observations for a given year were of the same type, this scaling maintains relative differences in functional group abundances among plots in each survey. Discarding bare ground and litter was important to compare percent cover that had been standardised to relative abundance. Relative abundance can be difficult to model because the abundance of one functional group is dependent on the abundance of other functional groups in the plot, and two plots can have the same relative abundance but very different total cover. Bare ground and litter therefore provide common reference across plots, within a survey. Where functional group abundance is low, there is little vegetative cover and lots of bare ground and litter. This contrasts with plots that have high functional group abundance and have lots of vegetative cover, meaning that bare ground and litter make up a relatively small proportion of percent cover. Dividing by the SD of the remaining observations then puts percent cover on a

standardised abundance scale. Although biomass measurements may have different distributions than cover, these are highly correlated (MacDonald et al., 2012) and make up only a small proportion of our total dataset (<1%).

5.3.6 Assessment of rehabilitation:

We attempted to identify the effect of rehabilitation intervention on community development by fitting a model to records of standardised abundances in rehabilitated plots and comparing the trajectory of vegetative change with that of three sets of non-intervention controls. We described this pattern of vegetation change as a function of time, with each functional group increasing or decreasing monotonically. We modelled the relationship between functional group abundance λ and time since abandonment t in each plot using a type IIa parameterisation of the Gompertz curve (Eq. 14; Tjørve & Tjørve, 2017), with three parameters:

Equation 5.1

$$\lambda(t)_{[ijk]} = \alpha_{K[ijkl]} \cdot \left(\frac{\alpha_{0[ijk]}}{\alpha_{K[ijkl]}} \right)^{\exp(-r_{[ij]}\cdot t)}$$

where α_0 is the initial functional group abundance at the time of abandonment ($t = 0$), α_K is the equilibrium abundance at the end of succession, and r is the intrinsic rate of change in abundance of functional group i in plot j in field k given rehabilitation intervention l . All parameters were constrained to be positive. In this parameterisation, α_0 and α_K are independent and the greater the difference between abundances at the start and end, the longer succession would take for a fixed r . α_0 and α_K also determine the direction of change, increasing or decreasing monotonically from start to end. Rehabilitation interventions affected the trajectory of vegetative change by increasing or decreasing α_K , the expected final abundance within a given plot. We did not observe α_0 and α_K directly but modelled them as latent parameters. Parameter estimates were drawn from hierarchical normal distributions, with functional group-level means and plot-level random effects. Distributions for α_0 and α_K shared a common standard deviation parameter for each functional group to constrain the initial and final abundances to the same scale.

We fitted this model to two subsets of our data: 1) our focal field and matched reference sites (F0-2) and 2) the full Cedar Creek chronosequence (F0-21). Appendix C2 describes

our model structure, which includes an auto-correlation component to capture short- and medium-term variation in plot level abundance and a lognormal observation component to describe the probabilistic distribution of our data.

5.3.7 Comparing intervention effects:

Rather than examine the effect of intervention by comparing the final outcome of succession, which could be expected to vary between fields, we calculated response ratios using posterior predictions of expected functional group abundance in each plot at a fixed point in time, $t = 52$ which was the age of abandonment of F0 in 2017. Response ratios can be used to measure the effect size of multiple interventions against a common set of non-intervention controls (Lajeunesse, 2011). We tested for differences between treatment and control plots calculating response ratios using: 1) data from 5 non-intervention control plots nested in F0, 2) posterior predictions of 105 control plots from a model fitted to fields F0-F2 and 3) posterior predictions 1,105 control plots from a model fitted to fields F0-F21. Posterior predictions were generated by taking 1,200 samples of the expected abundance of each functional group in control plots. In addition, we drew 1,200 samples of the expected abundance of each functional group in five plots under each intervention ($T = 1-6$) in field F0. These samples represented our uncertainty in the underlying trajectory of community development in each field but ignored plot effects and auto-correlation between observations. Unrehabilitated burned plots (B-) were not included in this analysis.

For each function group, we calculated response ratios for each intervention in field F0 as $RR = \log(\bar{y}_{T+} / \bar{y}_{C-})$, which is the log transformed proportion of expected functional group abundance in plots rehabilitated with intervention $T+$ relative to non-intervention control plots $C-$ in 2017 (see Table 5-A for interventions). We assessed whether the treatment plots clearly differed from the control plots by calculating the uncertainty associated with each RR. We calculated the standard deviation σ_{RR} of the aggregate response ratio, pooling the RR from all six rehabilitation interventions, which accounts for potential bias in using a single set of controls for repeated comparisons of multiple treatments within a single study (Lajeunesse, 2011). Response ratios significantly greater than zero mean that functional group abundance is greater in rehabilitated plots 24 years after intervention, while values less than zero indicate that functional abundance is greater in non-intervention control plots. Significant effects were determined by

examining whether the confidence interval of each response ratio ($CI_{RR} = RR \pm 1.96 \cdot \sigma_{RR}$) included zero. Calculating response ratios using an increasing number of fields allowed us to explore whether our reference controls were suitable for separating the effect of rehabilitation from variation in natural succession.

5.4 Results

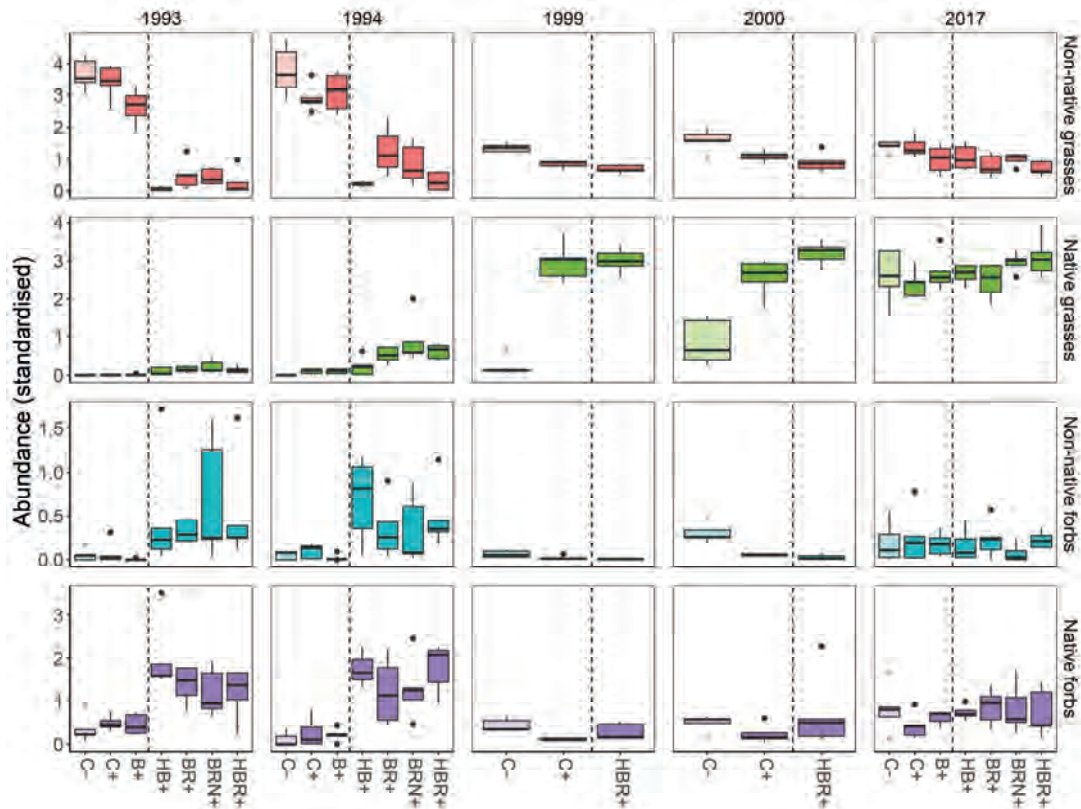


Figure 5.1. **Change in functional group abundance following rehabilitation** in 35 plots. Negative control plots (C-) received no intervention, all other interventions were seeded with native grassland species. Interventions included seed addition only (C+), burning (B), herbicide and burning (HB), burning and tilling (BR), burning, tilling and a nurse crop (BRN), and herbicide, burning and tilling (HBR). Dashed lines separate plots that followed typical management practices from more intensively restored plots.

5.4.1 Comparison with local control plots:

Native grass and forb species increased in abundance following seed addition interventions (Figure 5.1; see Table C3-S1 for extant and added species). Although native

forb abundance decreased between 1994 and 1999, native grasses became persistently dominant in plots where seed was added, including plots with no removal of existing vegetation (C+, B+). In 2017, interventions that combined burning and seed addition appeared to have reduced the abundance of non-native grasses relative to non-intervention controls (e.g. $RR_{HBR+} = -0.69$; $CI_{HBR+} = [-0.84, -0.54]$), whereas seed addition alone had not ($RR_{C+} = -0.02$; $CI_{C+} = [-0.17, +0.13]$).

Control plots that did not receive seed addition (C-) converged on a similar native dominated community as treatment plots after 27 years, with both having similar abundances of native grasses and forbs (Figure 5.1). There was no clear difference between treatment and control plots in response ratios for native grass abundance (e.g. $RR_{HBR+} = 0.18$; $CI_{HBR+} = [-0.07, +0.43]$) or native forbs (e.g. $RR_{BR+} = 0.06$; $CI_{BR+} = [-0.55, +0.67]$).

5.4.2 Comparison with matched reference fields:

During the same period, external reference fields F1 & F2 were not rehabilitated and showed markedly little change in the abundance of native grasses and forbs, 56 years after abandonment (Figure 5.2). Functional group abundances were similar across fields F0, F1 and F2 at the time rehabilitation interventions were applied, but native grasses only increased in the rehabilitated field.

Control plots in all three fields shared very similar, stationary trends for non-native grass abundance. Strong fluctuations around the successional mean are observed in all functional groups and estimates of $\delta > 0.5$ imply strong autocorrelation between observations (Figure 5.2). One such fluctuation may explain the observed decline in non-native abundance in F0 following rehabilitation. After controlling for auto-correlated stochastic variation, some intervention specific effects are detectable (Table 5-B). The application of herbicide combined with burning and rototilling (HB+, HBR+) was most effective at reducing the abundance of non-native grasses (e.g. $RR_{HB+} = -1.52$; $CI_{HB+} = [-1.74, -1.29]$), however, the strongest result was the uniform increase in native grass (RR between 3.98 and 4.35) and forb abundance (RR between 1.96 and 2.91) in all seed addition plots, compared to unrehabilitated controls from fields F0-F2.

Table 5-B. Response ratios (RR) and associated uncertainties of restoration intervention using the expected abundance of each functional group at $t = 52$ (equivalent to the age of

the restored field in 2017) compared with unrestored plots (C-) at three scales. N_C is the number of control plots used at each scale. σ_{RR} is the aggregate standard deviation across the response ratios of all six interventions. **RR** are the response ratios of each restoration intervention. Positive values indicate greater abundance after intervention compared to controls. **RR** where the 95% confidence interval does not span zero are italicised and underlined.

Single field (F0; $N_C = 5$)	σ_{RR}	RR_{C+}	RR_{B+}	RR_{HB+}	RR_{BR+}	RR_{BRN+}	RR_{HBR+}
Non-native grasses	0.076	-0.02	<u>-0.35</u>	<u>-0.28</u>	<u>-0.57</u>	<u>-0.35</u>	<u>-0.69</u>
Native grasses	0.127	-0.08	0.03	0.02	-0.05	0.13	0.18
Non-native forbs	0.541	0.23	-0.11	-0.22	0.17	-0.99	0.12
Native forbs	0.313	<u>-0.65</u>	-0.28	-0.11	0.06	0.02	-0.11
Other	0.873	-0.01	0.68	-1.20	0.62	-0.48	0.20
Matched reference sites (F0-F2; $N_C = 105$)							
Non-native grasses	0.115	-0.03	0.18	<u>-1.52</u>	<u>-0.51</u>	<u>-0.51</u>	<u>-1.09</u>
Native grasses	0.518	<u>3.98</u>	<u>3.90</u>	<u>3.85</u>	<u>4.21</u>	<u>4.28</u>	<u>4.35</u>
Non-native forbs	0.167	<u>-0.86</u>	<u>-1.50</u>	-0.02	-0.04	<u>-0.35</u>	<u>-0.53</u>
Native forbs	0.346	<u>1.96</u>	<u>2.42</u>	<u>2.91</u>	<u>2.83</u>	<u>2.80</u>	<u>2.68</u>
Other	0.557	<u>1.45</u>	<u>1.68</u>	<u>1.65</u>	0.85	<u>1.35</u>	0.66
Landscape chronosequence (F0-F21; $N_C = 1,055$)							
Non-native grasses	0.047	<u>0.16</u>	<u>0.22</u>	<u>-0.61</u>	<u>-0.17</u>	<u>-0.09</u>	<u>-0.36</u>
Native grasses	0.058	<u>0.41</u>	<u>0.35</u>	<u>0.42</u>	<u>0.45</u>	<u>0.51</u>	<u>0.58</u>
Non-native forbs	0.051	-0.01	<u>-0.24</u>	<u>0.26</u>	<u>0.32</u>	<u>0.10</u>	0.09
Native forbs	0.041	<u>0.49</u>	<u>0.63</u>	<u>0.94</u>	<u>0.90</u>	<u>0.89</u>	<u>0.75</u>
Other	0.062	<u>-1.55</u>	<u>-1.49</u>	<u>-1.49</u>	<u>-1.79</u>	<u>-1.57</u>	<u>-1.66</u>

5.4.3 Comparison with landscape chronosequence:

The effect of rehabilitation was less evident when compared at the landscape scale (Figure 5.3). Averaging across all 22 fields showed that, on average, native grasses should eventually dominate abandoned old fields (α_K [Native grasses] = 4.09, CI = [3.53, 4.65]). There was, however, substantial variation between fields in the eventual outcomes (Figure C4-S2). Assuming our posterior samples of α_K capture the likely variation in community development, non-native grasses were predicted to have greater final abundance (α_K) than native grasses 23% of the time. Similarly, non-native forbs had greater abundance than native forbs in 43% of posterior samples across all fields.

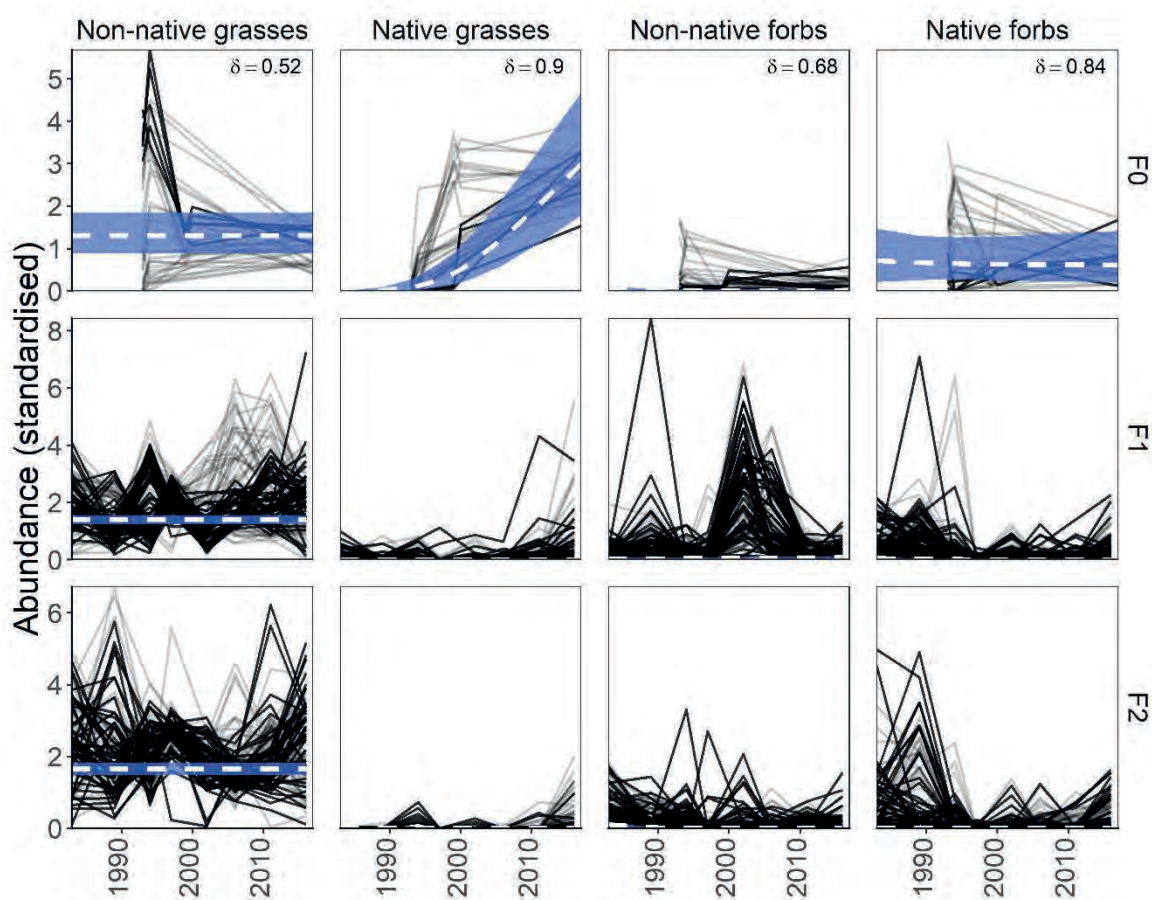


Figure 5.2. Repeated measurements of functional group abundances measured in non-intervention control plots (solid lines) and burned or rehabilitated plots (faded lines) in three old fields abandoned between 1961 and 1965. The estimated modal trajectory (dashed white lines) of native grasses and forbs indicate a transition to native dominance in non-intervention control plots (C-) of the rehabilitated field (F0), but not in

unrehabilitated fields (F1-F2). Blue shading indicates 95% credible intervals. Estimates of $\delta > 0.5$ suggest functional group abundance is highly correlated between measurements.

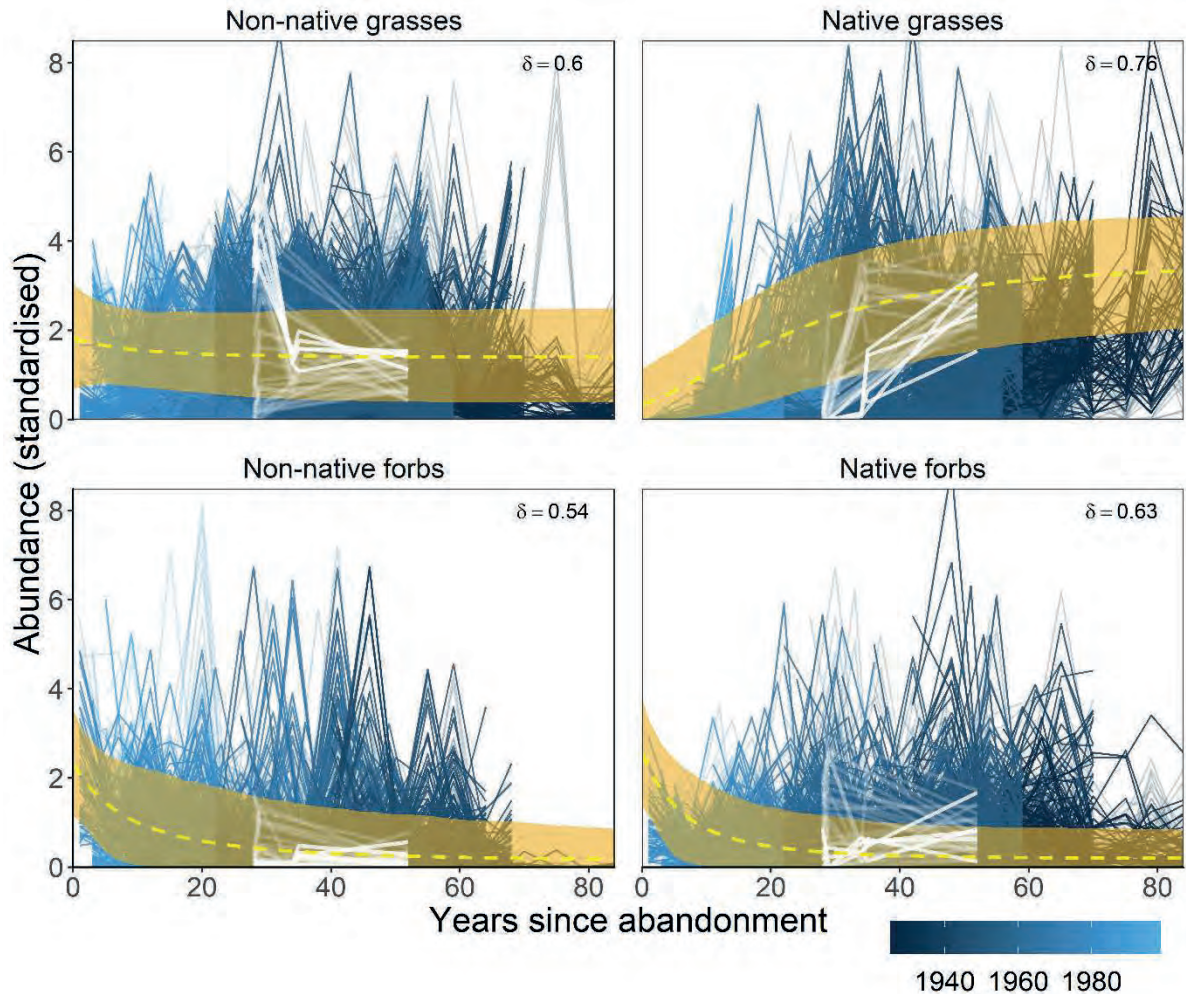


Figure 5.3. Community composition measured from 1983 to 2017 in non-intervention control plots (solid lines) and burned or rehabilitated plots (faded lines) that span more than 80 years of successional change. Repeated measurements of functional group abundances following rehabilitation (white) closely followed the average predicted trajectories of community development (yellow), estimated from non-intervention control plots in 22 abandoned fields (blue). Yellow shading indicates 95% credible intervals. Colour indicates the year a field was abandoned ranging from 1927 in dark blue to 1997 in light blue.

Fitting our model to 2,135 plots dramatically increased the statistical power of our study to detect the effect of rehabilitation intervention (Table 5-B). We observed small but clear positive effects of seed addition on the abundance of native grasses (**RR** between 0.41 and 0.58) compared with 1,105 unrehabilitated control plots across all 22 fields. Non-native grasses decreased in plots that received herbicide (e.g. **RR_{HB+}** = -0.61; **CI_{HB+}** = [-0.70, -0.52]) but there was no clear pattern of effects on non-native forb abundance in rehabilitated plots. The most convincing effect of rehabilitation was the greater abundance of native forbs after 27 years across all interventions (**RR** between 0.49 and 0.94).

5.5 Discussion

Comparing vegetative change against non-intervention controls at three scales showed that conclusions about the long-term outcome of rehabilitation intervention can vary significantly depending on the choice of non-intervention reference (Table 5-B). At the plot level within our study field (F0), the convergent trajectories of intervention and control plots (C-) meant that it was unclear whether the native grass populations present in rehabilitated plots were the result of local dispersal following seed addition or because the effects of intervention had been overwhelmed by external factors driving community development (Brudvig, 2011; Grman et al., 2013). Comparing our study field with two matched reference fields (F1-F2; Figure 5.2) suggested that seed addition increased native species abundance in F0 compared to non-intervention controls. However, old fields at Cedar Creek, on average, started with low abundance of native species and increased in native dominance without intervention (Figure 5.3). Considering our experiment in the context of a larger sample of 22 fields showed that seed addition did have a positive, long-term effect on native species abundance, but the effect was stronger for native forbs than for native grasses. This discrepancy demonstrates that the recommendation of two matched references sites (Ruiz-Jaen & Mitchell Aide, 2005) may be inadequate when there is large variation in successional outcomes across the landscape (White & Walker, 1997).

Considering rehabilitation within a successional framework is not a new idea (Suding, 2011; Walker, Walker, & Hobbs, 2007) but it remains difficult to distinguish where intervention is necessary. Non-intervention is a viable option where native species are

available to colonise degraded communities and successional dynamics are predicted to lead to native species recovery (Fensham et al., 2016; Prach & Hobbs, 2008). At Cedar Creek, native grasses are known to increase in dominance with enough time since abandonment which were already predicted to become dominant in this landscape (A. T. Clark et al., 2019). Native perennial grasses like *Andropogon gerardii*, *Schizachyrium scoparium* and *Sorghastrum nutans* are considered superior nitrogen competitors and are known to displace dominant non-native grasses *Elymus repens* and *Poa pratensis* (Craine et al., 2002; Tilman & Wedin, 1991). Seed addition may have accelerated this displacement if community development was primarily dispersal limited (Li et al., 2015), but may have had little effect if competitive interactions were only important in late succession (A. T. Clark et al., 2019; Purschke et al., 2013) or if abiotic constraints limited establishment (Bakker & Berendse, 1999). Native forbs, on the other hand, may have benefited from early seed addition if they were able to establish before local competitive interactions prevented subsequent colonisation (Fukami, 2015; Young, Stuble, Balachowski, & Werner, 2017).

If successional dynamics are well understood, then rehabilitation should attempt to target communities where local development is predicted to stall or diverge (Li et al., 2016; Walker & del Moral, 2009). Fields where non-native species were predicted to remain dominant, (e.g. fields F1-F2; Figure C3-S3) may benefit from interventions that remove dominant non-native species and establish persistent populations of native grasses and forbs (e.g. HB+, HBR+). Divergences in successional trajectory can occur when priority effects, environmental feedbacks or demographic stochasticity lead community development to an alternative stable state (Fukami et al., 2005; Shriver et al., 2019; Suding et al., 2004). Invasion of *Elymus repens* following nutrient enrichment is known to shift old fields communities in Cedar Creek into a low-diversity state (Isbell, Tilman, Polasky, Binder, & Hawthorne, 2013), which persists due to altered nutrient cycling, litter accumulation and fire regimes that disproportionately favour annual non-native species (Knapp & Seastedt, 1986). Interrupting these feedbacks with tilling or herbicide may have been an effective component of rehabilitation, enabling native species to establish better than seeding alone. We note that non-intervention control plots in F0 had significantly lower abundance of native grasses at the time of rehabilitation intervention, compared to other abandoned old-fields in this study (Figure 5.3). While we cannot assess whether F0 would have persisted in a non-native dominated

state, rehabilitation appears to have enhanced the recovery of a field that was otherwise lagging behind natural succession.

Long-term datasets are necessary to understand how community dynamics change across large temporal scales but analysing historical data can be complicated by differences in data type and quality (Woods 2007). Quantitative and theoretical models that predict rehabilitation outcomes over long time-scales and across broad successional contexts can be useful to integrate studies designed to monitor different outcomes (Brudvig et al., 2017). Using a predictive modelling framework, we combined a chronosequence study and restoration experiment to demonstrate that the choice of reference sites can significantly alter conclusions about the effectiveness of seed addition. Although more complex than a typical case-control analysis, where rehabilitation is matched with a non-intervention control, we obtained a broader picture of potential non-intervention outcomes and avoided overstating the effect of our interventions (Ioannidis, 2005; Lawlor, Smith, & Ebrahim, 2004). Identifying the effect of rehabilitation requires detailed domain knowledge about the recovery processes of each study system, which may not be adequately captured in meta-analyses (e.g. Jones et al., 2018). Integrative, predictive approaches can also improve the precision of interventions needed to alter landscape level feedbacks (Bowman, Perry, & Marston, 2015) and improve habitat configuration (Fahrig et al., 2011) by prioritising where intervention should target. Incorporating additional drivers of vegetative change into our model may have improved predictions of community development in non-intervention plots, however forecasting successional trajectories prior to intervention would truly test our understanding of ecosystem recovery (Dietze et al., 2018).

5.6 Conclusion

It is unclear whether rehabilitation interventions such as seed addition have persistent, long term effects on ecosystem recovery. Our results show that removing non-native species and establishing populations of native grasses and forbs can improve community development in abandoned old fields, also that the choice of reference is important. If there is significant variation in natural successional trajectories then, rehabilitation should only target sites that are predicted to remain in a degraded state, lest the effect of intervention be overwhelmed by natural succession. The large number of control sites

required to accurately quantify the outcomes of rehabilitation demonstrates the complexity of processes occurring during ecosystem development and suggests that we should remain humble in our expectations of ecosystem control. Interventions rehabilitating degraded communities must be pursued in tandem with the conservation of remnant ecosystems. Once gone, these systems are very hard to bring back.

6 SUMMARY

Author

Andrew O'Reilly-Nugent.

(2019).

6.1 Overall findings

This thesis has a simple aim: to identify dominant non-native species that have significant negative impacts on grassland communities. Understanding how and where impacts occurred would mean that impactful invaders could be prevented or targeted for management. I therefore sought to contribute to the ecology and management of invaded grassland communities by answering three main questions:

1. What determines the spread of potentially invasive plants?
2. How can the impacts of non-native plants be quantified?
3. How can these impacts be managed?

It is clear, however, that no single factor is likely to determine invasion success (Catford et al., 2009; Jeschke, 2014). Although my findings are not enough to understand the context for all invasions, I believe the methods presented here can be useful for identifying dominant non-native species, and that successful management can limit or remove their impacts. In the process of answering specific questions on spread, impact and persistence, I took the view that invaders must be considered in a broader context, be it the landscape through which they moved or the community in which they established. This hopefully means that these findings can be applied beyond the handful of non-native species that I examined. In this summary I will demonstrate how I answered the questions above 'by briefly reporting major findings of each chapter and then discussing their implication.

6.1.1 What determines the spread of potentially invasive plants?

In **Chapter 2**, we showed how landscape heterogeneity affects invasive species spread by inducing variation in dispersal, settlement, and population growth. Because the joint effects of these processes are not additive, interactions between these processes can result in a diverse range of outcomes, from stalled invasions where species ranges do not expand beyond their original point of introduction, to invasions that move great distances by relying on infrequent but long-distance dispersal events.

Much less is understood about how dispersal behaviour varies across the landscape, and how this affects spread dynamics, compared to how variation in population processes affect the spread of non-native species. This is likely because dispersal is hard to examine directly, particularly when important dispersal events are long-distance and rare (Ellner

& Schreiber, 2012). Biosecurity detection programs are aware of this problem, in that non-detection at potential introduction sites is not considered the same as non-introduction (Caley, Ingram, & De Barro, 2015). However much of invasive species management focuses on where species have already established (Coutts et al., 2011), which gives little insight into future dispersal events. This is a thorny issue, because once invaders are moderately widespread, there usually aren't enough resources to monitor far away from the immediate range front (Epanchin-Niell & Hastings, 2010; Magarey, Colunga-Garcia, & Fieselmann, 2009).

That said, we know that dispersal dynamics influence spread inasmuch as they are correlated with variation in population processes across the landscape. Finding patches well suited to reproduction results in the production of greater numbers of propagules, leading to positive feedbacks that disproportionately drives spread (Dewhurst & Lutscher, 2009). Successful management could therefore focus on rehabilitating the communities found in habitat patches that are suitable for both settlement and reproduction, before an invader has arrived (Pachepsky & Levine, 2011). If the primary feedbacks that support the native community, such as fire regime, grazing and nutrient cycling, are well established then arriving propagules may have little opportunity to establish (Buckley et al., 2007).

6.1.2 How can the impacts of non-native plants be quantified?

Negative associations in patterns of species abundance

Once species have established within a community, we showed how the competitive impacts of non-native species can be quantified using a joint-species distribution model (JSDM). Existing JSDMs had been used to model co-occurrence data, but non-native impacts can be more nuanced than just causing local exclusion. In **Chapter 3**, we developed a method to detect covariation in patterns of species abundance and applied it to data from a field experiment that manipulated two major axes of environmental variation that determine community structure. This allowed us to infer the impact of two dominant, non-native species, *Avena fatua* and *Bromus diandrus*, that were driving compositional change through competitive displacement in a temperate grassland, and allowed us to identify where, across a landscape, competitive impacts were greatest. While we identified two non-native species having disproportional impacts on

community composition, many widespread, abundant non-native species appeared to have little or no impact on the community, suggesting they invaded native communities without competitively displacing any other species.

Variation in the importance of environmental and competitive drivers, across a landscape, is closely linked to the impacts of non-native species. Non-native species can have direct impacts by reducing the population growth of community residents, however this requires that they maintain an advantage when competing for limited resources (I. T. Carroll et al., 2011). Plant functional traits provide an excellent indication of the differences and similarities between competing species (Adler et al., 2013; Kraft et al., 2015). Traits are particularly important where differences between species represent easily understood trade-offs between alternative ecological strategies (Aerts, 1999; Westoby & Wright, 2006). In this thesis, we found that traits indicative of species' ability to compete for light were particularly useful for explaining the dominance of fast growing, non-native annual species in simplified environments of high fertility and low disturbance.

However, the benefits of trait differences are context dependent, and may confer a disadvantage where environmental conditions are a more important driver of community composition than competitive interactions (Catford et al., 2019). At infertile sites or under sustained grazing pressure, many grassland species favour slow growth and investments in defences against herbivory (Lind et al., 2013). In our study, communities at infertile and grazed sites were often diverse mixtures of native and non-native species, suggesting that non-native species may be less impactful where there is limited scope for larger, functionally different species to establish. The changing importance of trait trade-offs between communities may explain the limited success to identify general traits of invasiveness (Mark Van Kleunen, Weber, & Fischer, 2010).

Validation with controlled glasshouse experiments

In **Chapter 4** we conducted a glasshouse experiment that showed our JSDM was biased toward the detection of strong species interactions, while also demonstrating the inherent difficulty of inferring processes from patterns. JSDMs require variation in patterns of species abundance to separate environmental and competitive drivers. Our experiment showed that we had underestimated how well many species would perform

along a gradient of increasing fertility, and subsequently underestimated the competitive interactions of between species of our grassland community. This bias did not affect dominant species, and our JSDM predicted the same competitive hierarchy that we measured in the glasshouse, suggesting there is still merit in using JSDMs for identifying the impact of dominant invaders in diverse communities, but that non-native species' impacts may be greater than we would infer from field data alone.

Identifying when plant populations are limited by environmental drivers or by competitive interactions is challenging, because these drivers are often confounded in observed patterns of species abundance in grassland communities. Estimating species interactions from field data remains difficult because their impacts cannot be observed outside the restricted realised niches that species occupy (Tuck et al., 2018). Most studies of plant invasion focus on either the native or introduced ranges of non-native species, meaning that there is often little evidence to suggest how non-native species will perform, or what impacts they will have when interacting with new communities in novel environments (Godsoe, Jankowski, Holt, & Gravel, 2017).

Although similarities and differences in species' functional traits can provide strong indications of the processes underlying community assembly, experimental validation is vital to truly break the confounding of environmental and competitive drivers (Adler, Kleinhesselink, et al., 2018; Detto et al., 2019). Coupling experimental and correlative methods has long been advocated in the study of species distributions, where species are spread across spatial scales that far exceed the resources available for direct measurement (Kearney & Porter, 2009; Kearney et al., 2010). This need is especially acute when considering species interactions, as the number of pairwise species combinations scales quadratically (Maynard et al., 2020). Constraining our JSDM model with evidence of how species perform beyond their current realised niche could significantly improve estimates of competitive interactions and potentially allow us to predict species impacts beyond communities that are already colonised.

6.1.3 How can these impacts be managed?

Chapter 5 showed that the effects of dominant non-native grassland species can persist over long timespans. Interventions that both remove non-native species and establish native populations can help to rehabilitate recovering ecosystems, however we also found that some abandoned old fields of Minnesota, USA recovered passively, over

decades to centuries, meaning that the effect of rehabilitation interventions could be overwhelmed by natural successional processes. This finding highlights the need to consider rehabilitation in a landscape context and take careful stock of possible outcomes before embarking on expensive rehabilitation interventions.

The management of non-native species is a relentless task and predictions of non-native impact could be used to prioritise the protection of vulnerable communities or target dominant species that have particularly outsized effects. Prioritisation is needed because propagule supply continues unabated and the risks of successful establishment are highly asymmetrical (Epanchin-Niell, Haight, Berc, Kean, & Liebhold, 2012; Yemshanov et al., 2019): for all the countless invasions that are prevented, only one dominant non-native species is needed to significantly disrupt native communities (Richardson & Pyšek, 2006). One source of hope is the growing body of evidence that suggests that many non-native species appear to integrate into grassland communities with little fanfare (Lai et al., 2015). It may be acceptable to consider these species as an established part of the community, increasing overall diversity and productivity (S. P. Carroll, 2011; Vellend et al., 2017).

While identifying current impacts is valuable, it is also necessary to understand how communities grow and change to determine what the outcomes of these impacts will be in the future (Kueffer et al., 2013). Some grassland communities appear to transition back to native dominance without intervention, if given enough time to recover from disturbance (A. T. Clark et al., 2019; Fensham et al., 2016). But there are still many significantly degraded communities that can be improved (Kettenring & Adams, 2011). Rehabilitation and restoration interventions should target communities where the recovery of native dominance is stalled or disrupted (e.g. Chisholm, Menge, Fung, Williams, & Levin, 2015). This appears to be the case of many invaded communities in Australia, suggesting that significant rehabilitation effort is still needed (Cuneo et al., 2018; Driscoll, 2017; Johnson et al., 2018).

6.2 Implications

The methods presented here have the capacity to meaningfully improve our response to plant invasion, by increasing our ability to predict where impacts will be greatest and increasing management efficiency. Our framework for understanding the spread of non-

native species across a landscape can be used to direct where effort should focus – long-distance dispersal means we must look well beyond just the primary invasion front. Identifying which species have major impacts, and where, means that dominant species can be targeted directly with interventions that are related to the competitive advantages determining community composition. By understanding where competitive interactions are important, we can identify when the removal of non-native species will be successful, and when management can be expected to lead to native communities that persist long term.

That said, the management of non-native species might be futile if the large-scale drivers of climate and human activity overwhelm any chances of native community recovery. Forecasting successional change before undertaking management can help to make decisions about where to intervene with the information we currently have. When doing so, we must be critical of obvious assumptions, particularly in modelling, but even in experiments where the observed outcomes may be the result of confounded processes. These studies have shown when models can fail and highlighted the need for experiments that are both general and robust, especially in ecology where we have little control over the conditions of natural settings.

6.3 Future research

6.3.1 Improved detection and risk assessment:

Because of the variety of processes that are important to plant invasions, attempts to find general rules relating to invasion success and non-native impacts remain largely unsuccessful. We could likely study any number of invasions and still find novelty in how species spread, establish, and persist. As with the bias of our models to detect strong competitive interactions, here too there is bias in the selection of species to study: we tend not to study the non-native species we do not notice (Guerin, Martín-Forés, Sparrow, & Lowe, 2018), or that have established at inaccessible sites (Tomasetto, Duncan, & Hulme, 2019).

Technologically, we may make progress with the introduction of high-throughput detection networks that can detect incursions of non-native plants at large spatial scales (Cavender-Bares et al., 2017; Lehmann et al., 2017). Early detection is particularly effective when coupled with strong biosecurity practices to enable cost effective

interventions while establishing non-native populations are small (Kompas, Chu, Van Ha, & Spring, 2019; Pluess et al., 2012). Pessimistically though, species introductions will continue apace, both deliberately and accidentally (Seebens et al., 2017). Many species in degraded grasslands were originally introduced for pasture improvement and were only considered invaders after marginally productive communities were abandoned, or newer pasture crops became available (Meffin et al., 2015). Better predictions of the impacts that un-introduced non-native species will have on existing communities may allow for informed decisions about deliberate species introductions (Genovesi, Carboneras, Vilà, & Walton, 2015; Roy et al., 2018).

6.3.2 Physiology as unifying process:

Community ecology is an active field but understanding the drivers of community assembly remains a foremost challenge of ecology. Even so, there has been significant progress toward experimental and analytical designs that test key theoretical aspects of modern community ecology (Ellner et al., 2016; Grainger, Levine, et al., 2019; Kraft et al., 2015). Research that brings together commonalities across communities tempts hope that general rules may yet be uncovered. Coupling experimental measurement with physiological, ecological and even evolutionary processes is a natural path to continue expanding our knowledge on the major controls of vegetative ecosystems (Camac et al., 2018; Falster, Brännström, Westoby, & Dieckmann, 2017). Physiological rules, sometimes referred to as ‘hard traits’, are a sensible foundation to build on as they provide a direct link between abiotic conditions and species distributions (Belluau & Shipley, 2018; Farrior et al., 2013). This moniker refers to the fixed nature of physiological limitations rather than more plastic morphological traits. However, hard traits are also difficult to measure, and their relative importance will need to be mapped against a wide range of possible conditions.

One avenue of research will be to develop a common suite of automatic “unit tests” to identify signals of mechanistic processes. Unit testing comes from software engineering practices, where individual units of code are tested independently to ensure the overall system functions as intended. Standardised tests that can be quickly and reproducibly applied to common data types may uncover general patterns that are common (or differ) between communities. Examples of these tests exist for the study of biodiversity (e.g. MoB; McGlenn et al., 2019) and population dynamics (e.g. COMPADRE; Salguero-Gómez

et al., 2015). Because standardised tests ensure that the functioning of each unit is well understood, more time can be spent understanding higher order patterns that occur from combinations of smaller processes. This suite of tests would require constant experimentation and critical questioning to validate the underlying processes represented in these patterns, however by repeating the same analysis across communities around the world we can seek to understand how relevant different mechanisms are at any given point in time.

6.3.3 Steps toward predictive ecology:

Hierarchical modelling, used throughout this thesis, is a powerful tool for integrating many independent processes. Hierarchical modelling provides a coherent framework to account for variation within individual plots and between datasets that can frustrate direct comparisons of spatial and temporal trends at large scales. However, this approach faces two types of problem: choosing the level at which inferences are pooled (i.e. splitting vs. lumping) and rapidly increasing computational complexity.

The first problem arises from generalising processes by assuming that similar species, and communities, behave similarly (Taylor-Rodríguez, Kaufeld, Schliep, Clark, & Gelfand, 2017). Although this is immensely helpful to identify common factors promoting or preventing invasion, aggregating at too coarse a scale can mask variation that is just as important (Smith, Godsoe, Rodríguez-Sánchez, Wang, & Warren, 2019). Understanding variation between non-native species is important because the impacts of dominant non-native species may be infrequent but very damaging. Future research should consider the consequences of rare events as well as general trends (Bailey & van de Pol, 2016; Breiner, Guisan, Bergamini, & Nobis, 2015), especially when optimizing the limited available resources for surveillance and control (Epanchin-Niell et al., 2012).

Secondly, computational burden increases as we attempt to extend our analyses across ever larger scales, datasets and model compilations (Al-Jarrah, Yoo, Muhaidat, Karagiannidis, & Taha, 2015; Dormann, Calabrese, et al., 2018). While hardware and software improvements will continue to help, significant inroads may be made by considering 'online learning' where models are continuously updated with data and knowledge (Lima, Cannon, & Hsieh, 2016; MacKay, 2005). This is common in weather forecasting systems that integrate daily data, as well as update parameters based on predictions that are incorrect (Bauer, Thorpe, & Brunet, 2015). Like the weather, iterative

forecasting holds great potential to infer processes from patterns that are well beyond our control (Dietze et al., 2018).

6.4 Conclusions

Although the existence of general drivers of invasion success remains uncertain, this does not mean that we should not act at all. Waiting to examine every possibility, until we understand all potential outcomes, likely means missing opportunities to significantly improve the quality of our natural world. Acting with uncertainty means diligently recording, exploring, and declaring the limitations of our understanding so that we can reflect and adapt when our environmental management does not proceed as intended. Making careful choices and documenting management activities, collating, and disseminating the data we collect and openly sharing the tools to contribute new research will see greater impact of our work as ecologists. General inferences about the processes underlying invasion are important, but patterns must be cautiously interpreted and stringently validated using both experimental and field studies. Approaches that combine observational and experimental data have great potential to contribute to our understanding of invasion and community ecology. I hope that the methods presented in this thesis can be used to identify dominant non-native species and improve our response to their impacts across all stages of the invasion life cycle.

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Article 2 - *Measuring competitive impact: joint-species modelling of invaded plant communities.*

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Article 3 - *Inferring the strength of plant competition from field data: reconciling field and experimental results.*

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Article 4 - *Separating rehabilitation from succession: cross-scale evaluation of grassland rehabilitation in abandoned old fields.*

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A. APPENDICES FOR CHAPTER 3

A.1 Data collection

The data in this study are from an experiment designed to test if different management interventions could increase species richness of native grasses and forbs (Driscoll, 2017). Ten sites were established in 2010 in relatively uniform areas of unshaded grassy vegetation that encompassed the range of grassland communities in the reserve, from relatively uninvaded communities to communities dominated by non-native species. Sites were 20 m x 25 m in size and situated 200 m – 600 m apart. At each site, 10 permanently marked 5 m x 5 m plots were laid out, with each plot separated by at least 1 m. In late spring (October) 2010, the vegetation in each 5 m x 5 m plot was surveyed by placing four 1 m x 1 m quadrats in the corners of each plot and recording all vascular plant species present in each quadrat along with their cover, estimated visually as the proportion of each quadrat covered by the canopy of each species. Total cover of all species in a quadrat could sum to greater than one if plant canopies overlapped. Plants were identified to species, and any plants that could not be reliably identified in the field were collected and pressed, with identifications subsequently determined by referring to collections at the Australian National Herbarium. Three genera in which species were difficult to distinguish were grouped and treated as species complexes: *Vulpia* (3 species; non-native), *Rytidosperma* (4 species; native) and *Aira* (2 species; non-native).

In 2011 experimental treatments were applied to each plot. First, five of the 10 plots at each site were chosen and a fence constructed around these to exclude large mammalian herbivores (predominantly kangaroos but also rabbits). Second, an experimental treatment was assigned to each of the five plots inside and outside each fence: unslashed, vegetation removal by slashing, vegetation removal by burning, nutrient reduction by sugar addition, and biomass suppression by planting a barley crop (see Driscoll, 2017). For this study, we restricted our analysis to the unslashed and slashed plots, because we were primarily interested in how biomass removal by herbivores might alter competitive interactions and the impact of non-native species across the landscape. The unslashed plots inside and outside the fence allowed us to compare vegetation responses in the

presence and absence of herbivores. Slashing provided an additional biomass removal treatment that we could contrast with herbivory to assess whether it was biomass removal *per se* that moderated non-native impact.

We therefore analysed data from four plots at each site: the fenced and grazed unslashed plots, and the fenced and grazed slashed plots. Slashing was carried out annually at the beginning of the growing season using a brush cutter to remove all vegetation above a height of about 2 cm. The slashing treatment was applied each year from 2011-2016, except for 2014. Vegetation surveys were repeated in all plots from 2011-2016, except for 2014. Our dataset thus comprised six years of vegetation cover data from 160 quadrats in 40 plots (four quadrats per plot, four plots per site, and 10 sites), although due to time constraints only three quadrats per plot were surveyed in 2013. This meant we had a total of 920 quadrat level vegetation measurements, comprising 10,780 individual cover estimates for 142 species (70 native and 72 non-natives; Figure A4-S2).

We measured traits associated with growth rate and light capture in 2015 and 2016 following standard protocols (Pérez-Harguindeguy et al., 2013). Canopy height (m) was measured as the distance from the base of a plant to the highest leaf, and maximum height (m) was measured as the distance from the base to the highest point of the plant. Canopy width (m) was measured as the horizontal distance between the two furthest points. Whole adult leaves were collected, scanned to obtain their surface area, dried and weighed to measure leaf dry matter content (mg; LDMC) and to calculate specific leaf area ($\text{mm}^2 \text{mg}^{-1}$; SLA). Traits were measured on at least five adult individuals of the species that comprised at least 80% of the total cover in all 20 unslashed plots in the fenced and grazed treatments. Species level trait data was aggregated across plots and years, and traits for less abundant species that were not sampled in the field were taken from the TRY database (TRY-db.org). We used 90th quantile values as a species maximum potential for each trait to avoid the outcome being overly influenced by outliers.

In autumn 2011 and 2015, five 75 mm x 100 mm soil cores were taken from each plot, the soil from each plot was bulked, and then analysed for total carbon, nitrogen and phosphorus, and available phosphorus, nitrate, and ammonium. Available phosphorus and nitrate were measured with Colwell and KCl extractions, respectively, and organic carbon was measured with wet oxidation and colorimetric determination (Driscoll & Strong, 2017). Nitrogen, phosphorus and carbon levels were strongly correlated in these

soils (Spearman rho: 0.53-0.62) and previous studies have shown that covariation in these two nutrients comprises the dominant fertility gradient (Driscoll & Strong, 2017). No treatment specific effects were detected between 2011 and 2015, thus we opted to use total extractable nitrogen (ppm) measured in 2011 as an overall measure soil fertility.

Water availability can also strongly influence non-native species abundances in Australian grasslands (Morgan et al., 2016). To account for inter-annual variation in species cover due to rainfall variation, we obtained rainfall data from the two weather stations closest to the reserve (3-6 km distance) that had records for the period 2010-2016 (Ainslie #70242 and Melba #70277; Australian Government Bureau of Meteorology, 2017). Vegetation surveys were undertaken in late October and completed in November. We used the cumulative rainfall total in the four months prior to each survey (August - November) as an explanatory variable representative of water availability that might explain inter-annual variation in cover, with rainfall averaged between the two stations in each year. This ranged from 185 - 414 mm during the study period.

A.2 Model fitting

Regression of non-native dominance:

Our response variable was the logit-transformed proportion of introduced species cover within a plot, constrained to be greater than 0 and less than 1 following the protocol of (Smithson, 2006). Covariates of fertility and rainfall were centred and scaled.

Equation A2-S1

$$\begin{aligned} \text{logit}(y_{[ijk]}) &\sim \text{Normal}(\mu_{[ijk]}, \sigma^2) \\ \mu_{[ijk]} &= \beta_{\text{intercept}_{[ij]}} + \beta_{\text{slope}_{[ij]}} \cdot \text{fertility}_{[jk]} + \beta_{\text{rain}} \cdot \text{rainfall}_i + \beta_{\text{plot}_{[jk]}} \\ \beta_{\text{plot}_{[jk]}} &\sim \text{Normal}(\beta_{\text{site}_{[k]}}, \sigma_{\text{plot}}^2) \\ \beta_{\text{site}_{[k]}} &\sim \text{Normal}(0, \sigma_{\text{site}}^2) \end{aligned}$$

where $y_{[ijk]}$ is the proportion of non-native cover (240 observations) in year i (1–6), under treatment j (1–4), at site k (1 – 10). The intercept and slope coefficients were modelled hierarchically, with each value drawn from a Student's t-distribution in each treatment with four degrees of freedom and a mean and variance estimated from the data. This provided some degree of pooling between species, but still allowed for outliers with strong positive or negative responses to environmental conditions. We included random effect parameters for each plot to account for the repeated measurements across years, modelling these parameters as drawn from a hierarchical normal distribution with a different mean for each site to allow for the nested structure of plots within sites. Additionally, we included a random effect for each plot to account for repeated measurements, which were drawn from a hierarchical normal distribution at each site to incorporate the nested nature of plots within sites.

JSDM specification:

For both JSDMs, we specified an LKJ prior on the correlation component of the covariance matrices (Lewandowski, Kurowicka, & Joe, 2009) which maintains the positive semi-definite nature of correlation matrices. An LKJ prior of 1 is close to uniform with equal likelihood of strong positive and strong negative correlations, which we believed to be unlikely (Adler, Smull, et al., 2018). We therefore tested LKJ priors of 10, 25 and 50, with

25 providing the best fit to the data. This is a very conservative prior, meaning that strong correlations required substantial support from the data. We specified weakly informative priors for all other parameters, with unit normal distributions for hyper-parameters such as hierarchical means, and half unit Cauchy distributions (i.e. bounded above zero) for any variance terms. All analyses in this paper were run using Hamiltonian Monte Carlo implemented in the probabilistic programming language Stan (Carpenter et al., 2017). Models were run with an adaptation delta of 0.8 and a maximum tree-depth of 15. For each model, we ran four Markov chains to generate 1,000 posterior samples after discarding 1,000 warmup samples. We looked for adequate sampling depth using the number of effective samples, and checked for model convergence using the Rubin-Gelman statistic, which was less than 1.01 for all models indicating adequate convergence (Gelman, Rubin, Gelman, & Rubin, 1992).

Comparison of model fit

We first compared the fit of both JSDMs to the data to examine how separate covariance matrices affected parameter estimation. Model fit was evaluated by generating posterior predictions of cover for each quadrat and comparing predicted values to the observed data. We used five posterior predictive metrics to identify the best fitting model: the root square mean error (RMSE), 2) the mean Euclidean distance between predictions and data (both censored below zero), 3 & 4) the probabilities that estimates of latent suitability from environmental conditions correctly predicted species presence or absence (true positive, true negative respectively), and 5) the coefficient of determination (R^2) as the ratio of the sums of squares (SS) of predicted latent suitability and posterior predictions of cover, omitting species absences (Gelman, Goodrich, Gabry, & Vehtari, 2018). We considered a better fitting model to be one that minimised RMSE and Euclidean distance, but maximised the accuracy of predicted presences, absences, and cover. We also compared the number of parameters in each model to demonstrate the added complexity of including separate multiple covariance matrices.

We then compared how negative between-species covariances changed between models with a single covariance matrix (constant across treatments) and with multiple covariance matrices (varying across treatments). Covariance matrices are the combination of separate correlation (ρ) and variance (σ^2) components, with correlations describing how tightly residual variation in one species was associated with residual

variation in another, and variances describing the scale of residual variation for each species. This means that changes in the cover of one species will be associated with large changes in the cover of a second species (i.e. dominance effects) when the variances are large and strongly correlated. Less common species, with low overall cover, and species with cover that is well explained by environment variables will have smaller covariances because there is little variation that could be attributed to co-occurring species. However, covariance matrices are positive-semidefinite, with an upper limit on the proportion of negative to positive correlations. If species driving change in the community negatively covary with multiple neighbouring species, these neighbours will positively covary with one another. We therefore selectively focus on negative covariances as indicative of dominance effects arising from competition. We calculated the average, 2.5% and 97.5% quantiles of all negative posterior samples of each covariance matrix and, for the second model, calculated the mean difference between covariance parameters of the grazed, unslashed treatment (which may be positive) and the negative covariances of the remaining treatments.

Allowing both species' environmental responses and potential interactions to vary in JSMD2 did not significantly improve model fit (Table A3-S1). The low proportion of variance explained in both models is indicative of the fact JSMDs are analysis of residual variation. However, specifying additional covariance matrices highlighted the ability of JSMDs to detect variation in species interactions (Table A3-S2). The magnitude of negative covariances was greatest in the fenced, unslashed treatment and were typically more negative than the corresponding covariance in the grazed, unslashed treatment. Slashing reduced the range and magnitude of negative covariances but appeared to be less effective (on average) in the grazed treatment.

A.3 Supplementary tables

Table A3-S1. Posterior predictive checks of JSDBMs fit to 30 species with constant (JSDBM1) and treatment specific (JSDBM2) covariance matrices. Mean and standard deviation of five summary statistics show similar goodness-of-fit between models. Root square mean error (RSME) and Euclidean distance are calculated after censoring the posterior predictions, in order to match the observed data. R^2 is fit with observed abundance only (does not include zeros). The accuracy of the JSDBMs to predict presence or absence are summarised as a probabilities.

	Number parameters	RSME	Euclidean dist.	R²	P(Pres)	P(Abs)
JSDBM1	884	10.02 (±0.07)	1219 (±7.88)	0.26 (±0.02)	0.76 (±0.01)	0.77 (±0.00)
JSDBM2	2,279	10.23 (±0.07)	1227 (±8.05)	0.25 (±0.02)	0.72 (±0.01)	0.78 (±0.00)

Table A3-S2. Summary statistics of negative between-species covariances from constant (JSDBM1) and treatment specific (JSDBM2) covariance matrices.

Treatment	Mean negative covariance	Mean change from reference*	2.5 % least negative quantile	97.5% most negative quantile
<i>JSDBM1</i>				
All treatments	-31.79	--	-0.48	-173.76
<i>JSDBM2</i>				
Grazed + unslashed	-21.23	0	-0.26	-125.43
Grazed + slashed	-10.60	-2.19	-0.17	-56.08
Fenced + unslashed	-36.55	-27.99	-0.34	-239.56
Fenced + slashed	-18.53	-12.10	-0.33	-81.25

*Covariance from grazed/unslashed treatment used as reference class in M2.

A.4 Supplementary figures

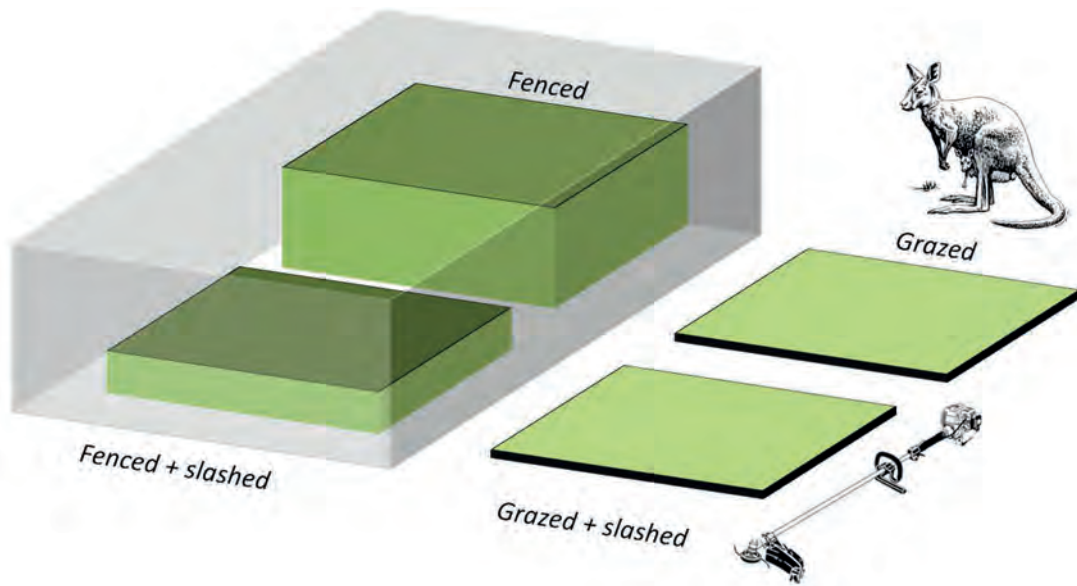
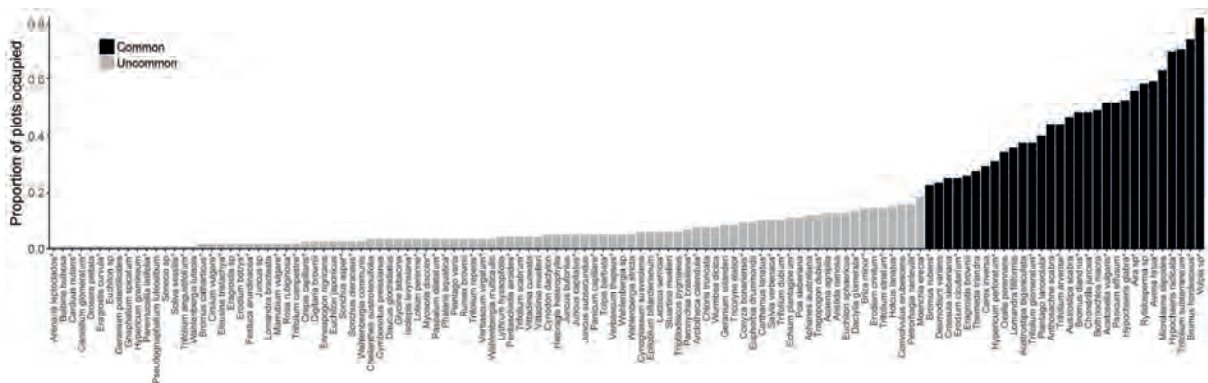


Figure A4-S1. Experimental design of paired fenced, unfenced, slashed and unslashed 5m x 5m plots., replicated at 10 sites.



**non-native species indicated with an asterisk*

Figure A4-S2. Species abundance distribution from 2013-2016. 30 common species (black) were observed 20% of plots in all years. The remaining species in this dataset have the potential to be dispersal limited or be rare or transient species which are only observed in one or two years.

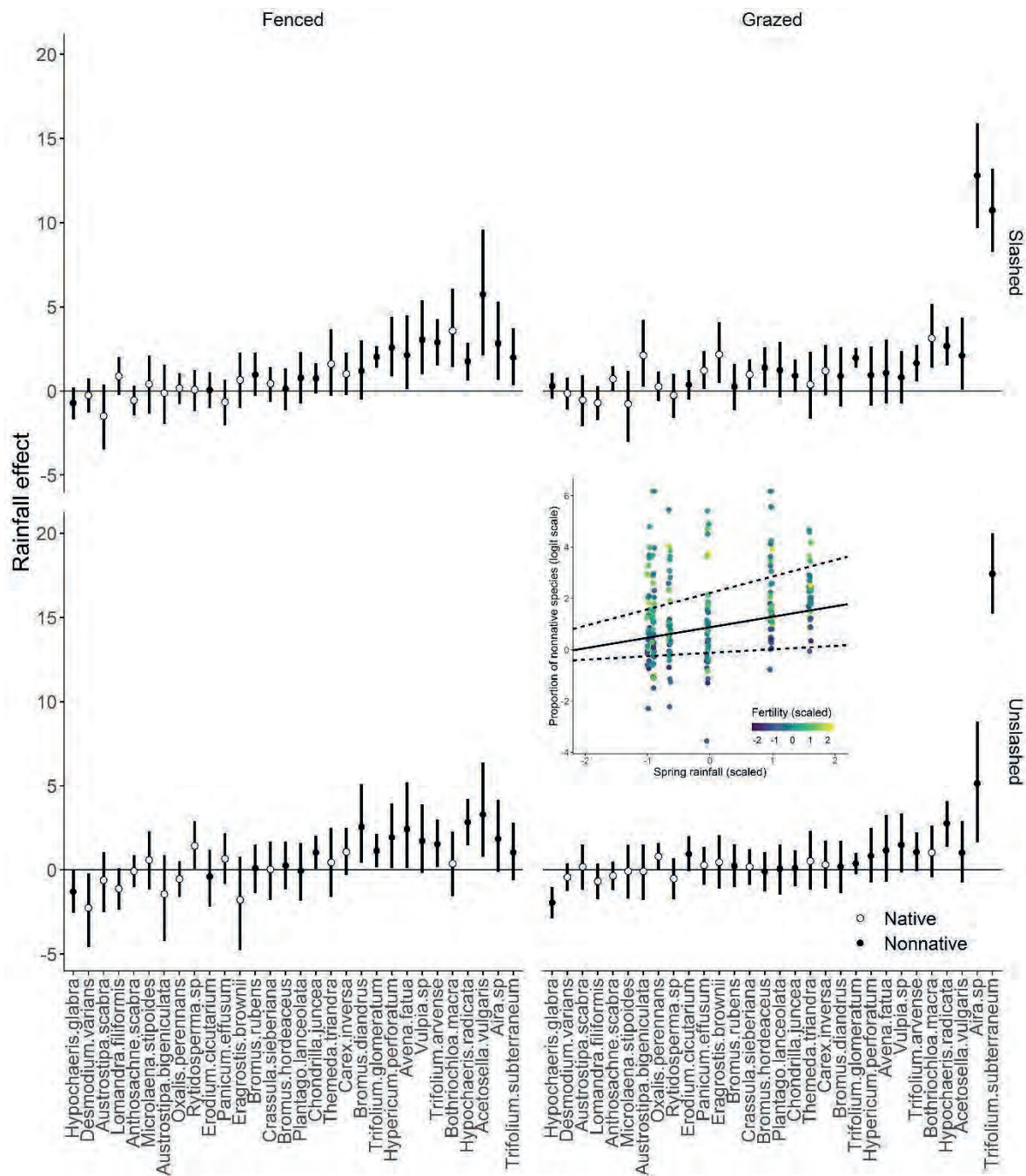


Figure A4-S3. Effect of rainfall on inter-annual site suitability. Estimated latent suitability for 30 species in relation to spring rainfall under treatments of fencing and slashing fitted using tobit regression. Most species have small positive responses, however a few nonnative species (solid lines) show stronger relationships. Lines are coloured from dark blue to light yellow corresponding to a shift from negative to positive slopes. **(inset)** Plot-level relative abundance (logit-transformed) of non-native species shows a slight positive trend in response to spring rainfall. The effect of fertility (coloured from low in blue to high in yellow) is described in Figure 3.2.

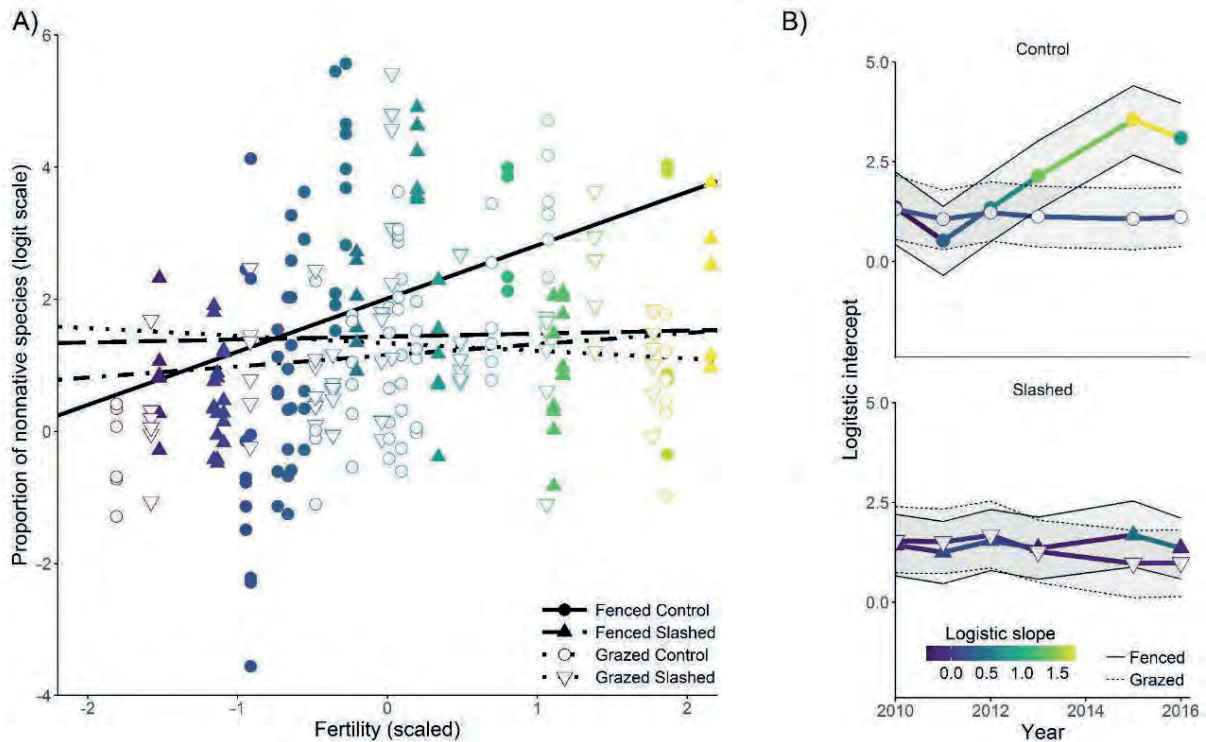


Figure A4-S4. Relationship between soil fertility and non-native dominance. **a)** Overall relationship between the proportion of non-native species (logit transformed) and an environmental gradient of fertility between 2010 and 2016, under treatments of fencing and grazing. Filled points indicate fenced plots, while open points indicate grazed plots. Circles correspond to unslashed plots and triangles correspond to grazed plots. Treatments are also indicated by line type. Points are coloured from dark blue to light yellow with increasing fertility **b)** Annual changes in the relationship between the proportion of non-native species and fertility. The posterior mean of a logistic regression intercept is shown for each year, with the 95% credible interval shown by the shaded areas. Points are coloured from dark to light with increasing posterior means of a logistic regression slope, indicating greater dominance at high fertility. Filled points again correspond to fenced plots, while open points correspond to grazed plots

B. APPENDICES FOR CHAPTER 4

B.1 Hoaglands nutrient solution

Hoaglands solution is a useful nutrient supplement to grow plants on sand substrate. Because nutrients are in liquid form, they can be added in precise amounts. The procedure calls for the creation of four stock solutions (A, B, C, D; Table B2-S3). These solutions are then combined into a single nutrient supplement before application.

In our experiment we varied the concentration of nitrogen, phosphorus, and potassium by varying the amount of stock A and B that were applied to pots. Our High fertility treatment had 8 ml (1x strength), Medium had 4 ml (0.5 x strength) and Low had 1ml (1/8 x strength) of each stock added to each L of water. All treatments had 1 ml each of stocks C and D, meaning all treatments had the same level of micro-nutrients.

B.2 Supplementary tables

Table B2-S1. Recipes for four stock solutions, to be combined into Hoaglands nutrient solution.

Stock	Compound	Final Conc.	MW	Amount of compound per L	Stock conc. (mM)
A	KNO ₃	6.2 mM	101.11	82.15	812
	Ca(NO ₃) ₂ ·4H ₂ O	4.0 mM	236.16	118.08	500
B	NH ₄ H ₂ PO ₄	2.0 mM	115.03	28.80	250
	MgSO ₄ ·7H ₂ O	2.0 mM	246.47	61.62	250
C	H ₃ BO ₃	4.6 μM	61.83	0.248	4.60
	MnCl ₂ ·4H ₂ O	0.5 μM	197.9	0.099	0.50
	ZNSO ₄ ·7H ₂ O	0.2 μM	287.54	0.055	0.20
	(NH ₄) ₆ Mo ₇ O ₂₄ ·4H ₂ O	0.1 μM	1235.95	0.124	0.10
	CuSO ₄ ·5H ₂ O	0.1 μM	249.7	0.050	0.20
D	FeCl ₃	45 μM	162.2	24 ml of 60%	45.0

Table B2-S2. Lotka Volterra simulation parameters

Parameter	Symbol	Subordinate species	Dominant species
Intrinsic per-capita growth rate	r	0.80	0.20
Response to fertility	β	0.01	0.02
Intraspecific interaction (effect on conspecifics)	α _[jj]	0.05	0.05
Interspecific interaction (effect on competitors)	α _[kj]	0.01	0.04

B.3 Supplementary figures

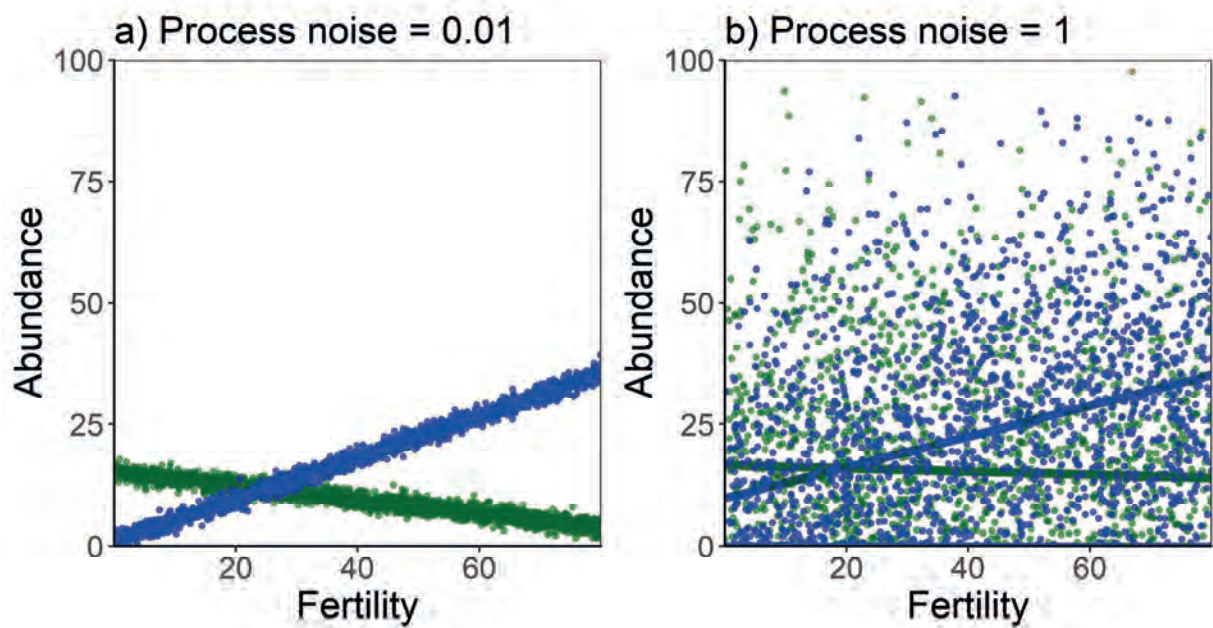


Figure B3-S1. Contrasting levels of process noise example . a) Abundances of two species with low levels of process noise and b) high levels of process noise due in a Lotka Volterra model. Coloured lines are linear regressions fit to each species individually, representing a naïve estimate of the relationship between abundance and fertility for each species.

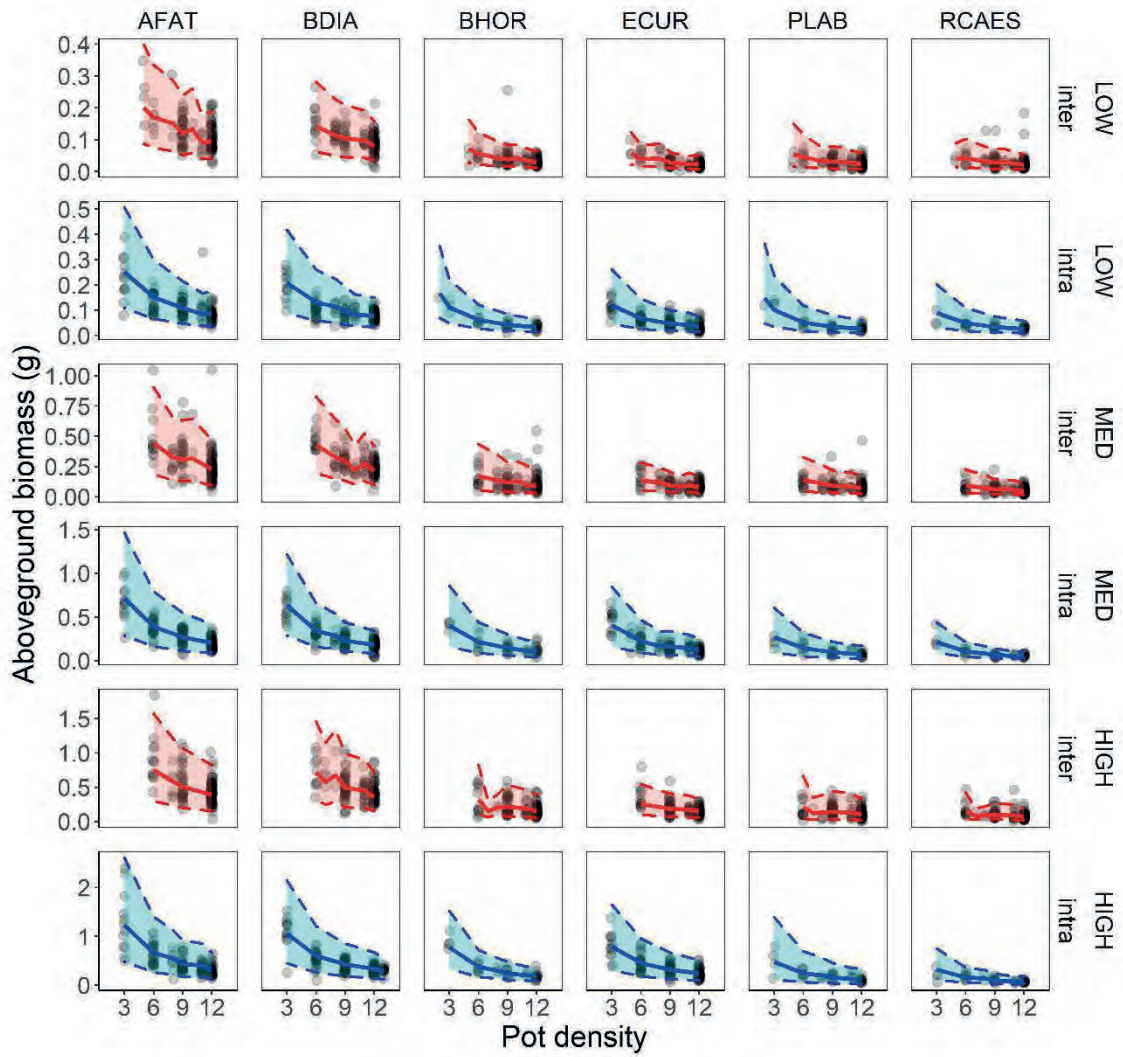


Figure B3-S2. Yield density relationship for six species (columns) in monoculture (blue) and mixture (red), at each of three fertility treatments (rows). Points are aboveground biomass harvested after 12 weeks, while lines are the mean and 95% credible intervals of the posterior predictions. Note: y-axis scale varies between fertility (low to high) and community treatments (mixture and monoculture competition).

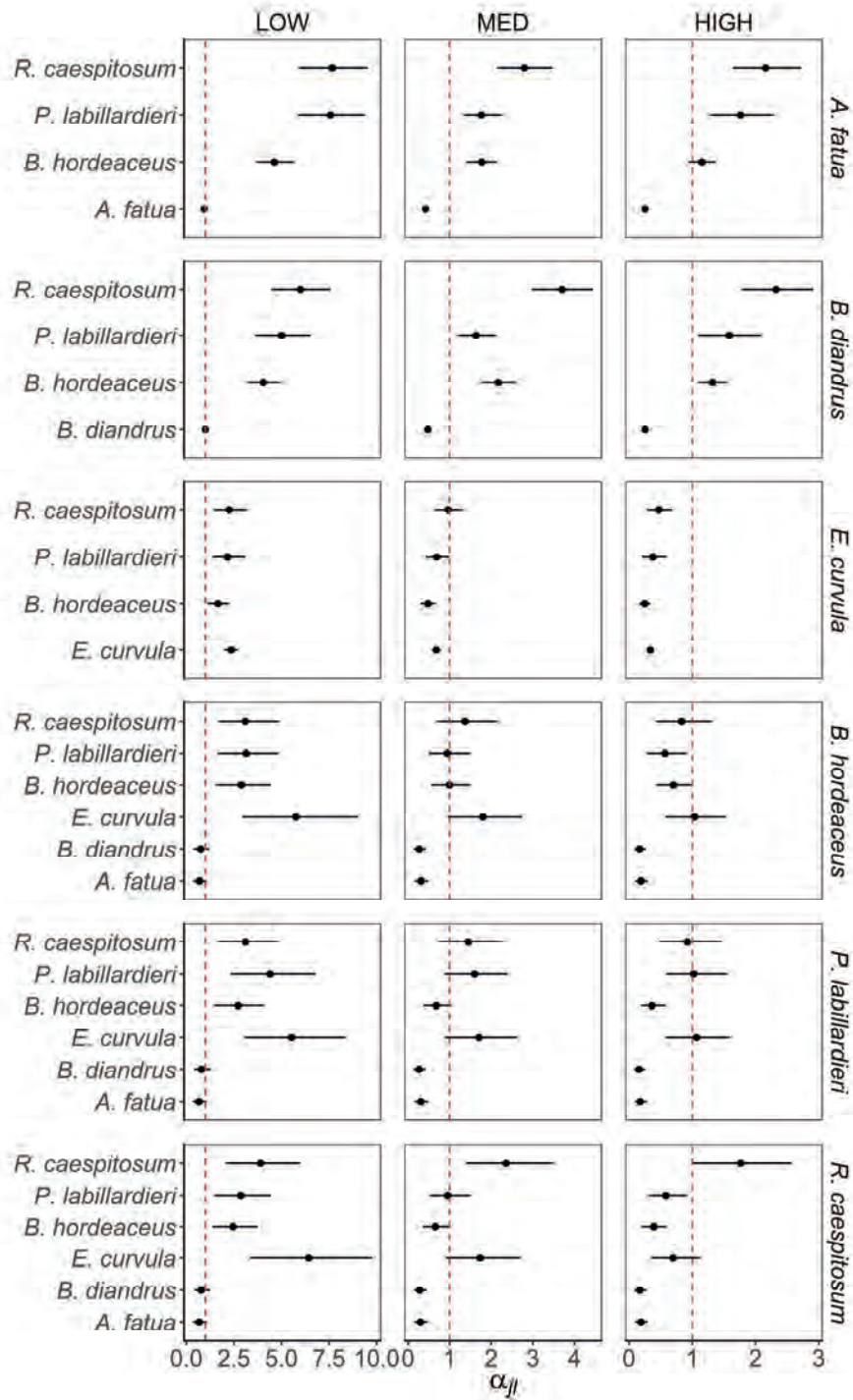


Figure B2-S3. Experimentally estimated interspecific competition coefficients (α_{ij}), describing the per-capita effect that a species (right) has on its competitors (left) at each fertility level. Yield density curves are fitted on the inverse scale, such that larger interaction coefficients lower the expected biomass of a focal individual more than smaller interaction coefficients.

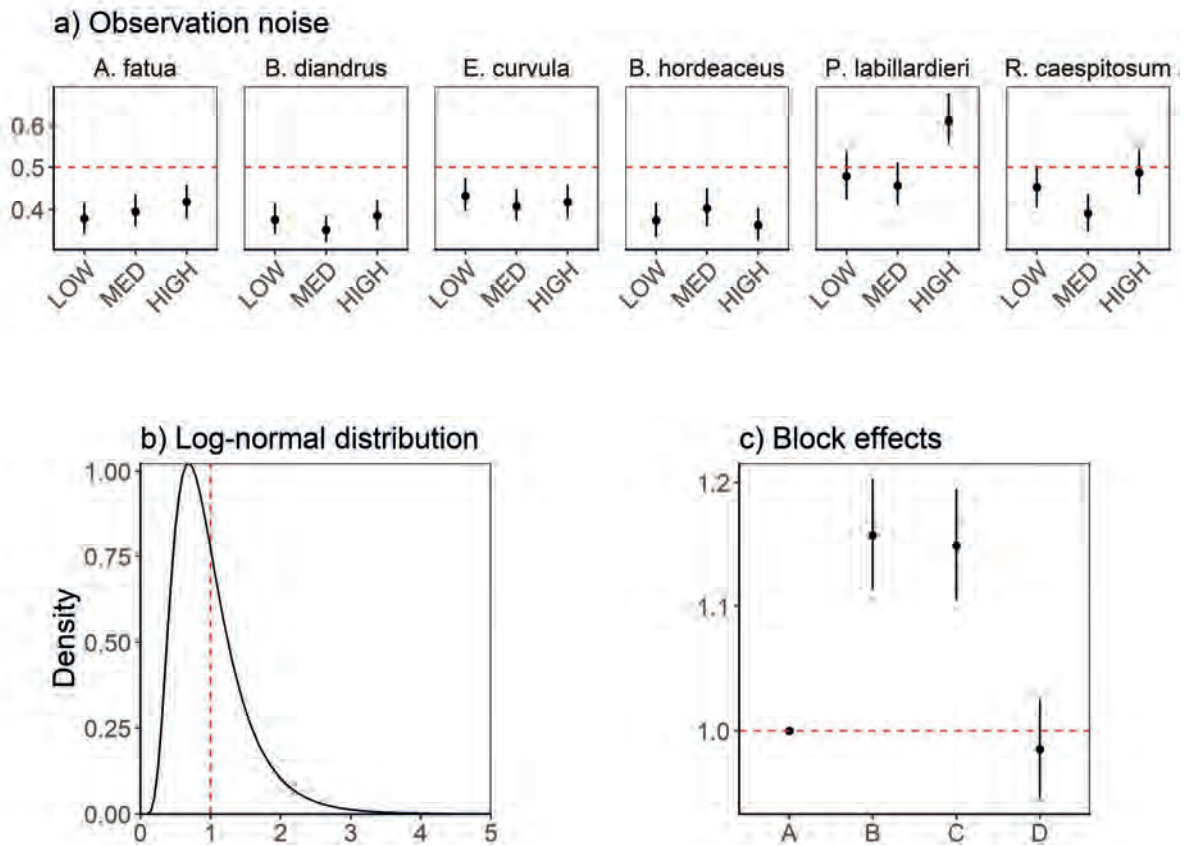


Figure B4-S4. Diagnostic plots showing **a)** the log-standard deviation σ of the log-normal observation model for each species in each fertility treatment, **b)** a demonstration of this lognormal distribution with the expected biomass $w = 1$, and log-standard deviation $\sigma = 0.5$ and **c)** the multiplicative offsets to account for systematic effects of glasshouse position for all individuals in each block, relative to block A.

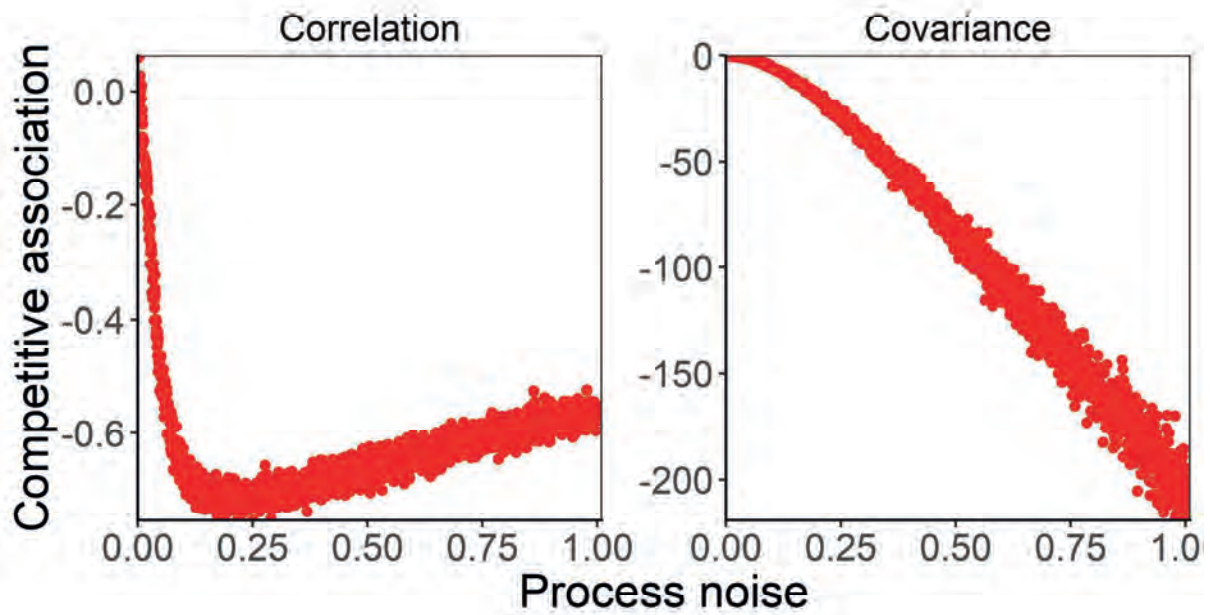


Figure B3-S5. Estimates of residual covariance between-species partitioned into correlation (left) and covariance (right) from JSDM models fitted to of equilibrium abundances of two species, simulated using a Lotka-Volterra model. When there is little to no variation, the JSDM is unable to detect any associations between species, but the correlation quickly becomes more negative with increasing process noise. However, this effect on negative correlation appears to saturate at moderate levels of process noise, whereas covariances continue to become more negative as the scale of variation in patterns of species abundance increases.

C. APPENDICES FOR CHAPTER 5

C.1 Disturbance and reinvasion sub-experiment

Blumenthal et. al (2005) visited the rehabilitation experiment in F0 in 1998 to assess the effect of rehabilitation on suppressing weed species invasion. Four 1 x 2 m quadrats were established in 15 plots (five plots in three treatments, corresponding to interventions 0, 1 and 6; Table 4-A). Quadrats were randomly assigned to one of four perturbation treatments: no perturbation (C), nitrogen addition (N), burning (B) or nitrogen and burning (N/B). Burning was conducted to remove litter and improve seedling establishment, while nitrogen was applied to reduced competition for soil nitrogen. If restoration suppressed invasion by reducing establishment, burning lead to an increase in non-native establishment. If restoration suppressed invasion through increased competition for soil nitrogen, N addition should lead to an increase in non-native establishment.

Burning was conducted in October 1998 and nitrogen addition carried out in May 1999, July 1999, May 2000, and August 2000. N plots received 10 g m⁻² nitrogen at each addition and non-N plots were all amended with phosphorus, potassium, and micronutrients to ensure that only nitrogen would be limiting. Non-native species (Table C3-S2) were seeded into each sub plot in November 1998 and the establishment of non-native species measured in terms of seedling biomass, harvested between July and September in 1999 and 2000. All resident vegetation was harvested in September of each year. Biomass was collected by clipping within 1 cm of the soil surface, separated by species and functional groups, then dried at 60 °C. Fallen (non-green) litter was also collected, dried, and weighed.

The initial results of this sub-experiment showed that rehabilitated quadrats were less likely to be invaded by non-native species than negative control plots or perturbed quadrats (Blumenthal et al., 2005). Both nitrogen addition and burning increased the establishment of seeded non-native species. We tested whether these quadrat level

differences persisted 17 years later during our final survey of F0 in 2017. We resurveyed the same quadrats and visually estimated the total cover of each species, which was summed by functional group in each quadrat (see *Data compilation* section of the methods). Because we only needed to test for difference community composition single survey, the relative abundance of each functional group was comparable between quadrats. Relative abundance was calculated by normalising the cover of each function group with the total cover of all groups recorded in a quadrat.

We tested for the effects of perturbation experiment within restoration interventions by calculating the calculated the adjusted R^2 for overall community composition using a multivariate analysis of variance (MANOVA). We included terms for restoration intervention (R), perturbation intervention (P) and the interaction between the two (R x P), with a plot level random effect in the analysis to account for the nested design of quadrats within plots. There appeared to be little effect of sub-plot perturbations remaining in 2017, 17 years after the fact (Wilks' statistic = 0.70, $p = 0.15$; Figure C4-S1). The abundance of non-native forbs (including those seeded in 1999) was very low in all plots, with marginally higher abundance in plots that received nitrogen addition. The variance explained by subplot perturbation was low (adjusted- $R^2 = 0.03$) and did not vary by restoration intervention (adjusted- $R^2 = 0.04$). We therefore concluded that there was no significant effect of this sub-experiment on plot level community composition in 2017 and ignored differences between quadrats for the remainder of our analyses.

C.2 Model fitting

Our model attempts to estimate long term trends within a field, however we expected there to be significant short- and medium-term variation in plot level abundance. [Here we describe the model structure used to separate this variation from successional trends]. Within a plot, we also expected functional group abundance at one time-point to be correlated with abundance at the next observation, due to inter-annual variation that was independent of successional change. We modelled this autocorrelation by including a lagged observation of functional group abundance $\mathbf{y}_{(t-1)}$ as a covariate for our expected functional group abundance $\bar{\mathbf{y}}_t$:

Equation C2-S1

$$\bar{y}_{t[i]} = \delta_{[i]} \cdot y_{(t-1)[i]} + (1 - \delta_{[i]}) \cdot \lambda(t)_{[i]}$$

**additional indices dropped for brevity*

where the auto-correlation term δ partitioned the degree to which we expected the current functional group abundance to be affected by the previously observed abundance in the same plot. δ was pooled across all fields for each group i and bounded between 0 and 1 (negative correlation is possible, but unintuitive and unlikely in our system). As δ approached one, the functional group abundances were strongly influenced by the previous state and may have followed divergent trajectories away from expected values $\lambda(\mathbf{t})$. As δ approached zero, there was little correlation between observations and any stochastic variation was randomly distributed around $\lambda(\mathbf{t})$.

However, our dataset rarely contained consecutive observations at \mathbf{t} and $(\mathbf{t} - \mathbf{1})$. We accounted for irregular time between observations by defining \mathbf{g} as the ‘gap’ between measurement \mathbf{m} and the preceding $(\mathbf{m} - \mathbf{1})$, then scaling the contribution of auto-correlation at each observation (Millimet & McDonough, 2017). That is:

Equation C2-S2

$$g_{[m]} = t_{[m]} - t_{[(m-1)]}$$

$$\bar{y}_{t[im]} = \delta_{[i]}^{g_{[m]}} \cdot y_{t[i(m-1)]} + (1 - \delta_{[i]}^{g_{[m]}}) \cdot \lambda(t)_{[im]}$$

When $\mathbf{g}_m = \mathbf{1}$, the model proceeded as normal, but as the time between observations increased the effect of δ_j decreased. Our approach to standardisation resulted in positive continuous abundance data \mathbf{y}_t with a range of 0 - 12 on the standard abundance scale, which was well described by a lognormal model, with mean $\boldsymbol{\mu}$ and variance $\boldsymbol{\sigma}^2$ parameters on the log scale. We also scaled the error term of our model $\boldsymbol{\varepsilon}$ to allow for increased chances of extreme values with strong autocorrelation and large gaps between observations:

Equation C2-S3

$$y_{t[im]} \sim \text{Lognormal}(\mu_{t[im]}, \sigma_{[im]}^2)$$

$$\mu_{t[im]} = \ln(\bar{y}_{t[im]}) - 0.5 \cdot \sigma_{[im]}^2$$

$$\sigma_{[im]}^2 = \ln \left(1 + \left(\frac{1 - \delta_{[i]}^{g_{[m]}}}{1 - \delta_{[i]}} \cdot \varepsilon_{[i]}^2 \right) \cdot \bar{y}_{[im]}^{-2} \right)$$

This parameterisation includes an offset so that our expected abundance $\bar{\mathbf{y}}_t$ represents the mean functional group abundance on the standardised scale (i.e. not log transformed). We assumed that zero observations were not true zeros (meaning a functional group was absent from a field) but reflected functional groups at sufficiently low abundance they were not recorded in the sample plots. We accounted for this by drawing latent abundance values from our lognormal distribution between zero and an upper limit set by the minimum standardised abundance recorded in each year $\mathbf{L} = \mathbf{min}(\mathbf{y} > \mathbf{0})$. This upper limit ranged from 0.00006 to 0.01 on the standardised abundance scale, with a mean of 0.005.

We fitted this model to two subsets of our data: 1) our focal field and matched reference sites (F0-2) and 2) the full Cedar Creek chronosequence (F0-21). We estimated our model parameters in a Bayesian framework using adaptive Hamiltonian Monte Carlo with the probabilistic programming language Stan (Carpenter et al., 2017) and the rstan interface (Guo et al., 2016) in R, version 3.5.1 (R Core Team, 2018). Details of model fitting and prior specification are online at <https://github.com/aornugent/cc>.

C.3 Supplementary tables

Table C3-S1. List of extant and added species in rehabilitated field (F0). Asterisks indicate non-native species

Extant community		
<i>Ambrosia artemisiifolia</i>	<i>Erigeron canadensis</i>	<i>Poa pratensis</i> *
<i>Ambrosia coronopifolia</i>	<i>Erigeron strigosus</i>	<i>Polygonum convolvulus</i> *
<i>Berteroa incana</i> *	<i>Euphorbia glyptosperma</i>	<i>Polygonum pennsylvanicum</i>
<i>Bromus inermis</i> *	<i>Gnaphalium obtusifolium</i>	<i>Potentilla argentea</i> *
<i>Chenopodium album</i> *	<i>Lepidium densiflorum</i>	<i>Potentilla simplex</i>
<i>Cyperus spp.</i>	<i>Mollugo verticillata</i> *	<i>Rumex acetosella</i> *
<i>Danthonia spicata</i>	<i>Oxalis stricta</i>	<i>Setaria lutescens</i> *
<i>Digitaria ischaemum</i> *	<i>Panicum capillare</i>	<i>Tragopogon dubius</i> *
<i>Elymus repens</i> *	<i>Panicum oligosanthos</i>	<i>Verbascum thapsus</i> *
<i>Equisetum spp.</i>	<i>Physalis heterophylla</i>	<i>Vicia villosa</i> *
Added species (1993)		
<i>Andropogon gerardii</i>	<i>Lespedeza capitata</i>	<i>Petalostemum purpureum</i>
<i>Asclepias tuberosa</i>	<i>Liatris aspera</i>	<i>Rudbeckia hirta</i>
<i>Aster oolentangiensis</i>	<i>Monarda fistulosa</i>	<i>Schizachyrium scoparium</i>
<i>Bouteloua curtipendula</i>	<i>Penstemon gracilis</i>	<i>Solidago speciosa</i>
<i>Elymus canadensis</i>	<i>Penstemon grandiflorus</i>	<i>Solidago rigida</i>
<i>Helianthus pauciflorus</i>	<i>Petalostemum candidum</i>	<i>Sorghastrum nutans</i>

Table C3-S2. Non-native species seeded in sub-experiment (see: Appendix C1; Blumenthal et al., 2005).

Species	Life cycle	Functional group	Amount of seed added (g m⁻²)
<i>Chenopodium album</i>	Annual	Non-native forb	3.0
<i>Digitaria ischaemum</i>	Annual	Non-native forb	2.5
<i>Polygonum convolvulus</i>	Annual	Non-native forb	2.0
<i>Setaria glauca</i>	Annual	Non-native forb	3.0
<i>Asclepias syriaca</i> *	Perennial	Non-native forb	3.0
<i>Berteroa incana</i>	Perennial	Non-native forb	3.0
<i>Cirsium arvense</i>	Perennial	Non-native forb	2.5
<i>Crepis tectorum</i>	Perennial	Non-native forb	1.0
<i>Silene latifolia</i>	Perennial	Non-native forb	3.0
<i>Sonchus arvensis</i>	Perennial	Non-native forb	2.0
<i>Tragopogon dubius</i>	Perennial	Non-native forb	2.0
<i>Verbascum thapsus</i>	Perennial	Non-native forb	2.0

**A. syriaca* is native to Northern America but a noxious weed in Minnesota

C.4 Supplementary figures

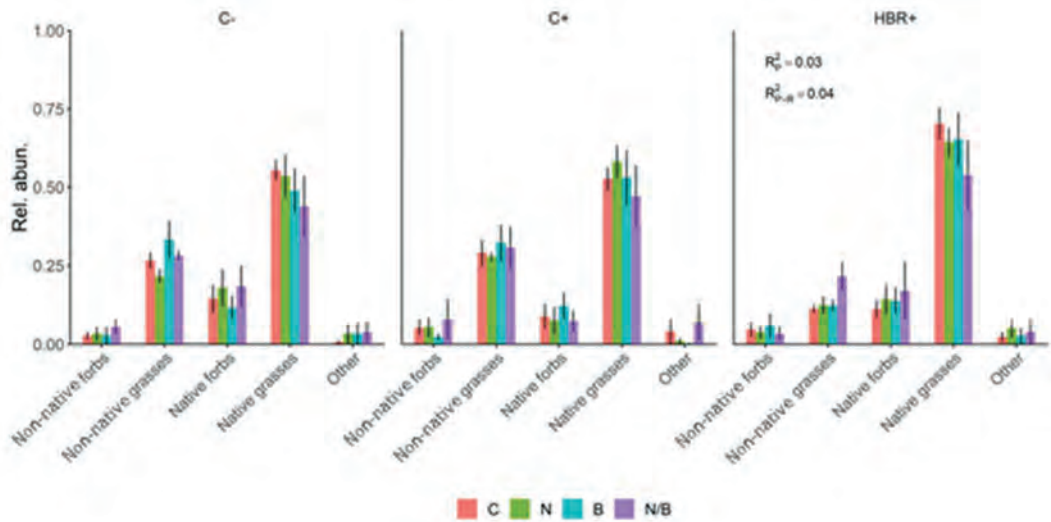


Figure C4-S1. The relative abundance of non-native and native species in sub-plot interventions, 17 years after perturbation (see *Appendix C1*). Adjusted- R^2 describe the proportion of variance explained by perturbation (P) or the interaction of restoration intervention and perturbation (P x R). Perturbations included nitrogen addition (N), burning (B) and burning with nitrogen addition (N / B). Control sub-plots (C) received no perturbation. Panels, from left to right, correspond with rehabilitation interventions of non-intervention (C-), seed addition only (C+) and seed addition with herbicide application, burning and rototilling (HBR+; Table 4-A).

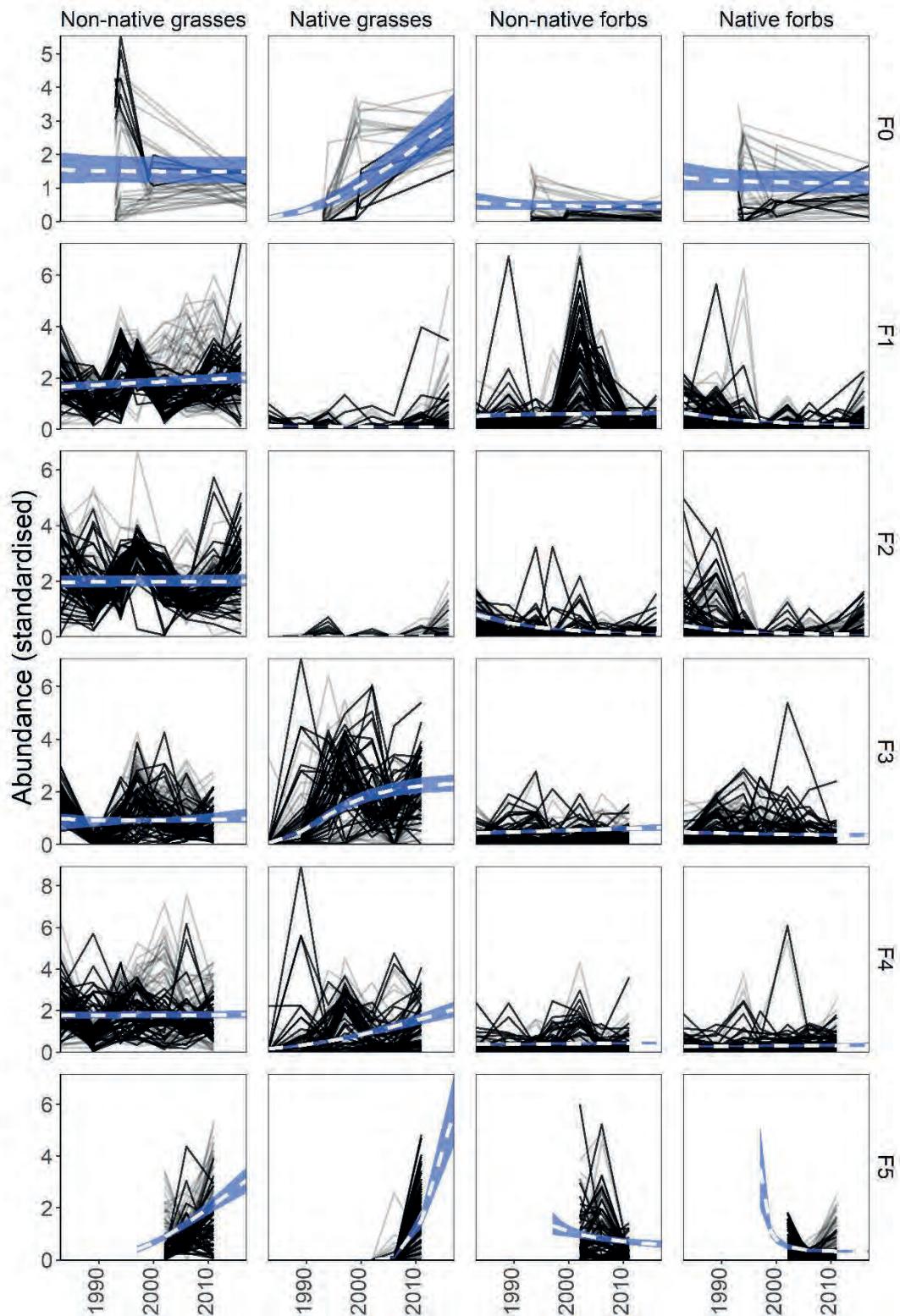


Figure C4-S2. Recovery trajectories of 22 abandoned fields over four decades (one field per row for the next five pages). Black lines are the trajectories of individual control plots (R-), while light grey lines are plots that were regularly burned (RB-) or received-

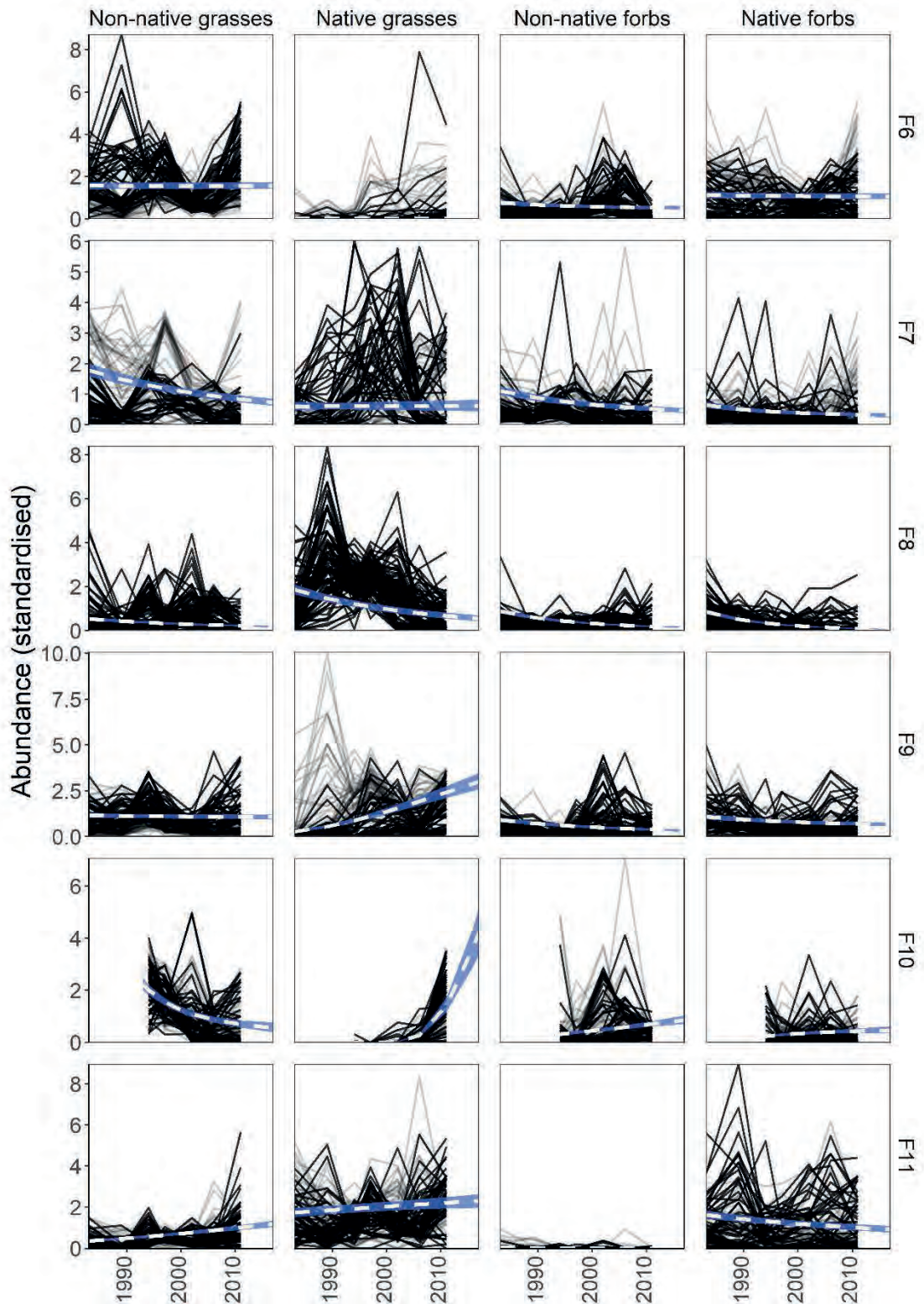


Figure C4-S2 cont. restoration intervention (Table 4-A). Fitted estimates of field level mean abundances in plots are shown by dashed white lines. Blue shading indicates 95% credible intervals.

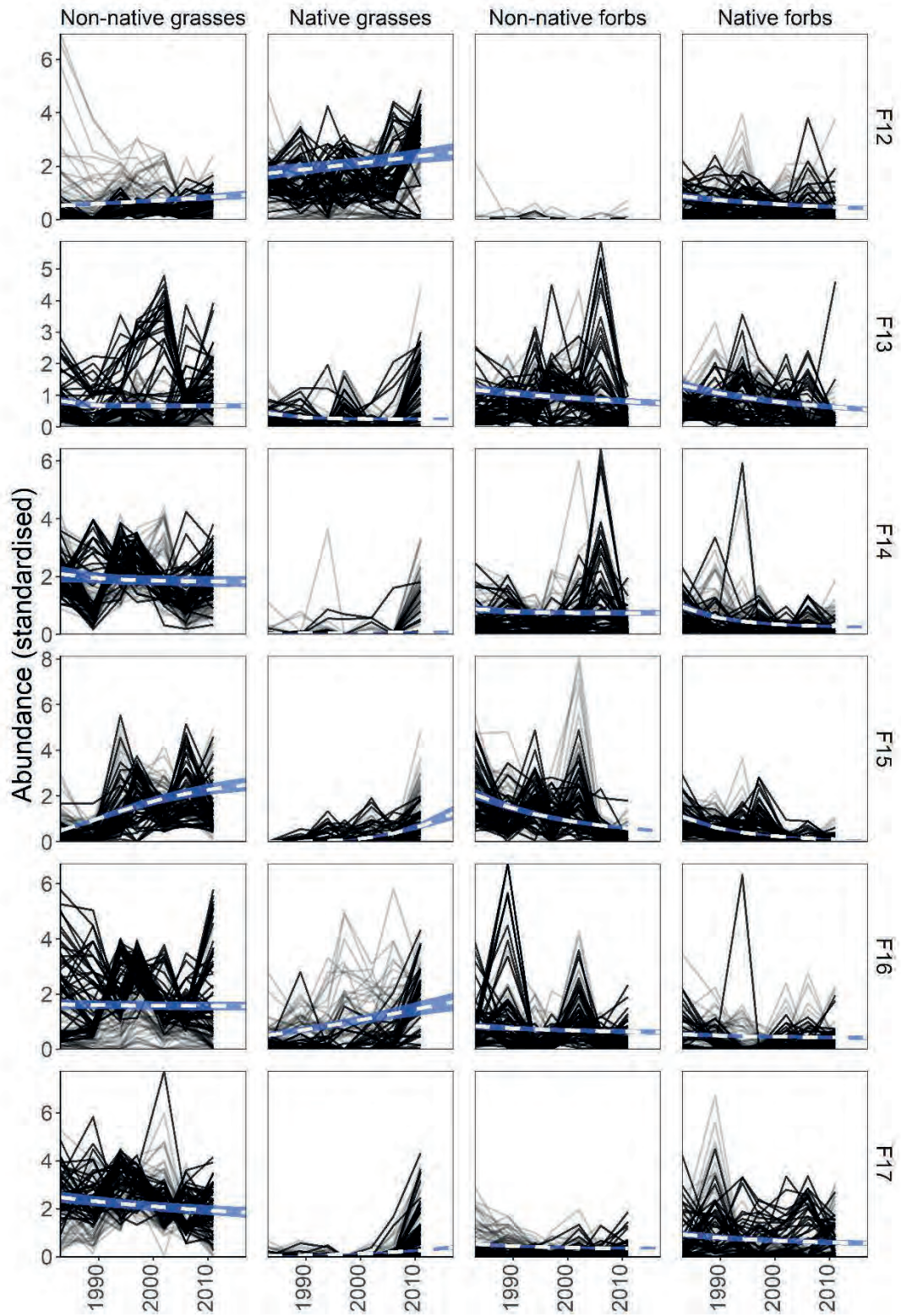


Figure C4-S2 cont.

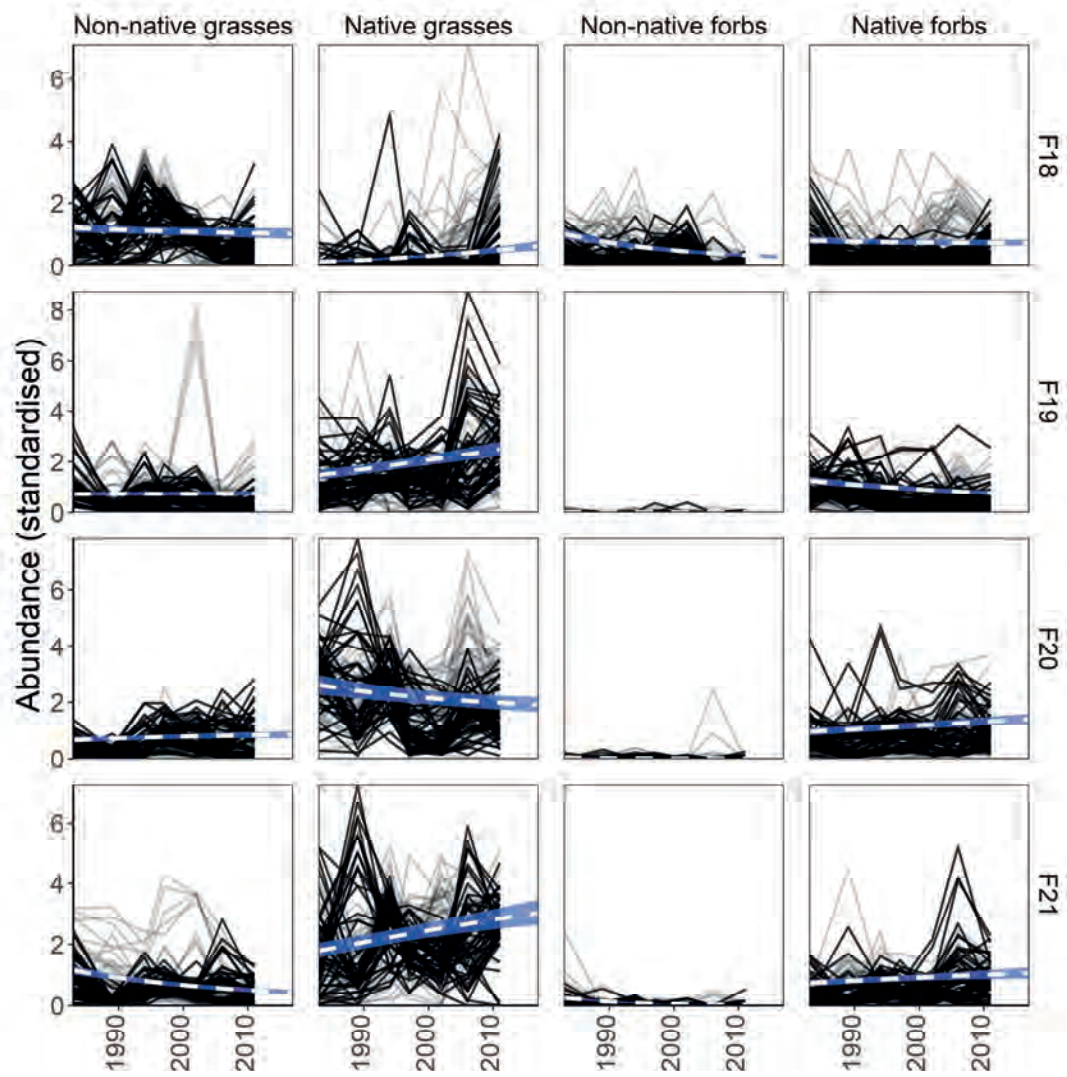


Figure C4-S2 cont.