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Species interactions and the formation of novel annual plant communities following rapid environmental change

Claire Elizabeth Wainwright
MSc

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Abstract

Recent environmental change associated with human activities has given rise to ecological communities that have no historical counterpart. In particular, introductions of non-native plant species have in many cases altered the structure and functioning of resident plant communities through changes in species composition and the surrounding environment within which species interact. As a result, new combinations of species are forming “novel” communities across an increasingly large portion of the earth’s land surface. Because novel plant communities differ in configuration from original native-dominated communities, they present unique challenges to management, restoration, and conservation efforts. Thus, there is a growing need to understand how novel communities function differently from the original communities they replace.

In this thesis, I investigate a variety of interactions in original and novel plant communities. Using a diverse annual plant system that persists within a fragmented agricultural landscape in Western Australia, I focus on the role of local-scale species interactions, an important biotic component of plant community assembly. I explore the complexities of local-scale interactions between native and non-native invasive species in light of coexistence theory, community assembly, and conservation of native floral diversity.

This thesis comprises seven chapters. The first chapter serves as a general introduction which places the thesis within the larger context of multispecies coexistence in novel plant communities. The second chapter serves as a description of the York gum (*Eucalyptus loxophleba* subsp. *loxophleba*) – jam (*Acacia acuminata*) woodland annual flora, the study system for the data chapters (3 – 6) which are based on laboratory and field experiments. Chapters 3 and 4 are experimental evaluations of frequency-dependent and density-dependent performance of native and invasive species that co-occur in York gum-jam annual plant communities. Chapter 5 reports on a field experiment, which investigates the performance of common native and non-native invasive annuals experiencing inter- and intraspecific competition in natural York gum-jam annual assemblages. Chapter 5 also assesses changes in community-level functioning due to compositional differences by evaluating diversity effects in novel and original annual communities. The final data chapter, Chapter 6, experimentally investigates how local-scale environmental gradients and a non-native invasive annual grass impacts annual plant community structure in the field. Finally, I conclude with a discussion of my results in Chapter 7, which unites the previous chapters, addresses limitations of the thesis, and presents suggestions for future research.

Overall, my results suggest that the local-scale impacts of non-native invasive species on native species may be more variable than those often reported in the literature on plant invasions (i.e. competitive exclusion). Consistent with previous studies, I did indeed observe negative interactions among invasive non-native and native annual plant species in field and laboratory settings. Specifically, I found that some species of invasive annual grass have the potential to negatively impact native populations over very short timescales through direct competition as well as interference from litter. These negative interactions, however, were not representative of interactions in novel communities as a whole. Notably, I found interactions between native annual forbs and an invasive non-native annual grass that ranged from neutral to positive. The direction and magnitude of invader impacts were highly dependent on species identity and the composition of the community, but were generally consistent across community densities and natural environmental gradients.

Species interactions play a potentially complex role in the assembly of annual plant communities post-invasion. My results lend empirical support to the notion that species in these novel communities should be considered according to their impacts rather than their origins. These studies serve as some of the first investigations into the processes that stabilize interactions among native and invasive non-native species and contribute to novel community formation and maintenance. When considered alongside large-scale patterns from observational studies, my findings demonstrate that interactions that occur over small spatial and temporal scales have the potential to influence large-scale plant community dynamics. In total, this thesis represents a valuable contribution to the community ecology and biological invasions literature, and has the potential to inform future restoration and conservation efforts in this threatened woodland ecosystem and beyond.

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Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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Publications during candidature

Conference abstracts:

Wainwright, C.E., Hobbs, R.J., Buckley, Y.M., Dwyer, J.M., Mayfield, M.M. “Positive interactions in a novel annual plant community”. Ecological Society of Australia/New Zealand Ecological Society Joint Annual Meeting, Auckland, New Zealand, 2013.

Wainwright, C.E., Hobbs, R.J., Buckley, Y.M., Dwyer, J.M., Mayfield, M.M. “Biotic interactions among annual plant species in a novel ecosystem” Ecological Society of Australia Annual Meeting, Melbourne, Australia, 2012

Peer-reviewed paper relevant to the thesis, but not forming part of it:

Dwyer, J.M., Hobbs, R.J., **Wainwright, C.E.**, Mayfield, M.M. Climate moderates release from nutrient limitation in natural annual plant communities. *Global Ecology and Biogeography* 24.5: 549-561.

Publications included in this thesis

No publications included.

Contributions by others to the thesis

All experiments (Chapters 3 – 6) were conceived of by the candidate and advisors Dr. Margaret Mayfield, Dr. Richard Hobbs, and Dr. John Dwyer unless otherwise stated below. Data collection and analysis was carried out by the candidate with input from advisors described below. All writing of the thesis was done by the candidate, and underwent revision by all advisors. The larger research project which this PhD contributed to was designed by Dr. Mayfield and Dr. Hobbs, and was funded by a grant from the Australian Research Council (DP1094413) awarded to Dr. Mayfield and Dr. Hobbs. All field soil samples were analysed by CSBP Limited.

Chapters 1, 2, and 7 were written by the candidate with improvements to drafts made by all advisors.

Chapter 3 was conceived of by the candidate and Dr. Mayfield. Data collection and analysis was carried out by the candidate with guidance from Dr. Dwyer. The manuscript was written by the candidate with editorial input by Dr. Mayfield, Dr. Hobbs, and Dr. Dwyer.

Chapter 4 was designed by the candidate with input from Dr. Mayfield and Dr. Dwyer. The candidate collected all field data and the majority of the data at UQ, the remainder of which was collected by volunteers (see Acknowledgments). Analysis was carried about by the candidate with advice from Dr. Dwyer. The manuscript was written by the candidate with editorial input from all advisors.

The community-level component of Chapter 5 was conceptualized by Dr. Mayfield and Dr. Hobbs in ARC grant DP1094413 and modified by the candidate in the field. Data was collected primarily by the candidate with help from field volunteers (see Acknowledgments), and analysed by the candidate with input from Dr. Dwyer. The neighbourhood-level component was conceptualized by Dr. Mayfield and Dr. Janneke HilleRisLambers and data was collected by the candidate, Hao Ran Lai, Dr. Mayfield, and Dr. HilleRisLambers. The manuscript was written by the candidate with input from all advisors.

Chapter 6 was conceptualized by the candidate and Dr. Mayfield, with input from Dr. Hobbs. The candidate collected data with help from volunteers in the field, and analysed the data with advice from Dr. Dwyer. The manuscript was written by the candidate with input from all advisors.

Statement of parts of the thesis submitted to qualify for the award of another degree

None.

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Keywords

Annual plants, biotic interactions, coexistence, community ecology, competition, facilitation, invasion, novel ecosystem, semi-arid ecosystem

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List of abbreviations used in the thesis

ANOVA - analysis of variance

df or DF - degrees of freedom

Fig - figure

N – nitrogen

K - potassium

P - phosphorus

SE - standard error

TDR - time domain reflectometry

Chapter 1: General introduction

This thesis is composed of seven chapters, four of which are based on data collected in experiments and are intended for publication (Chapters 3 – 6). This chapter serves as a general introduction which places the thesis within the broader context of multispecies coexistence in novel plant communities. The second chapter is dedicated to a description of the York gum-jam woodland annual flora of southwest Western Australia, the study system for the experiment-based chapters. Elements of the first two introductory chapters appear throughout the subsequent four chapters to provide context for the specific questions that directed each experiment. Finally, Chapter 7 of this thesis contains a general discussion of my findings, drawing on all previous chapters.

Emergence of novel ecological communities

Human-induced environmental change is now recognized as an inevitable component of most natural ecosystems (Millennium Ecosystem Assessment 2005). The spatial extent of anthropogenic modification to the global land surface is vast, affecting most of the terrestrial biosphere (Ellis & Ramankutty 2008). In addition, the rate at which natural ecosystems are experiencing change is unprecedentedly rapid (M.E.A. 2005). Land-use transformation is among the most severe drivers of environmental change (Foley et al. 2005), along with species introductions (Vitousek et al. 1997), invasions (Mack et al. 2000), and extinctions (Pimm & Raven 2000). Although these phenomena may modify ecosystems on different spatial and temporal scales, rarely do they occur in isolation. Rather, a suite of factors may synergistically incur greater total change to a system than change inflicted by individual component drivers (Brook et al. 2008). Determining the effects of these synergies on ecosystem function is challenging, as impacts of climate change are likely to modify or exacerbate their effects (Chapin et al. 2008).

As a result of synergistic environmental change associated with human activities, an increasing number of ecosystems are emerging that have no historical counterpart (Lindenmayer et al. 2008). These environmental changes alter abiotic and biotic ecosystem properties, in turn modifying determinants of ecological community structure. Global and regional-scale modifications include climate change-induced range or phenological shifts for certain species (Parmesan 2006; Cleland et al. 2007), or introductions of species into non-native ranges (Vitousek et al. 1997), resulting in ecosystems composed of both native and non-native members. Moreover, changes in land-use may result in species interacting under novel abiotic conditions, in addition to the effects of clearing, fragmentation, or abandonment of previously exploited lands (Foley et al. 2005). These wideranging factors affect diversity patterns at regional and site scales, as well as community composition on local and even microsite scales. In addition to changing the identities of constituent species and their surrounding environment, drivers of environmental change may further alter community composition by shifting the nature of interactions among trophic levels (Tylianakis et al. 2008). In sum, new combinations of species interacting within altered landscapes forming “no-analog”, “emerging”, or “novel” communities are developing across an increasingly large portion of the earth’s land surface (Milton 2003; Hobbs et al. 2006). Because these novel communities differ from the “original” communities they replace in terms of composition and functioning, they present unprecedented challenges to land management, ecosystem restoration, and conservation efforts (Lindenmayer et al. 2008; Hobbs et al. 2009).

The main focus of this thesis is the biotic component of novel plant community formation and maintenance. Using an annual plant system found in fragmented and degraded landscapes in southwest Western Australia, I study the dynamics within novel communities that differ in composition to original communities because of invasion by non-native species and modifications to the soil environment. While invasion is often associated with reduced native species richness and diversity, there are several other potential outcomes of interactions between native and non-native species. I explore the complexities of these interaction outcomes in light of modern coexistence theory, ecosystem function, and conservation of floral diversity.

Community assembly: the role of species interactions

In its most basic sense, a community can be viewed simply as a collection of species that co-occur within a given environment (Morin 2011). Observations that properties of communities (e.g. species richness, diversity) often vary in predictable ways have served as the basis for studying community formation and maintenance within trophic levels. However, determining the most relevant processes has been a long-standing challenge for ecologists (Elton 1927; Hutchinson 1959; Diamond 1975). Many theories have been generated about mechanisms responsible for coexistence within communities of similar individuals, the resolution of which has often inspired intensive debate (Lewin 1983; Grace 1991; Hubbell 2001).

From these debates, it has become clear that the relative contribution of any process to community structure depends on the spatial and temporal scale of the entity in question. Historical processes drive large-scale patterns of diversity through macroevolutionary dynamics, and global geographic and environmental variability provide barriers to range expansions, determining the composition of regional species pools (Wiens & Donoghue 2004). Environmental filtering then restricts groups of species to particular habitats within landscapes based on dispersal and physiological constraints to survival and reproduction (Keddy 1992; Myers & Harms 2011). Within neighbourhoods, biotic interactions impose further limits on which species can coexist locally (Chesson 2000). Environmental and biotic filtering represent deterministic assembly processes. Conversely, historically contingent processes may dominate, such that the order of species' arrivals in a habitat will determine the colonization abilities of subsequent species (i.e. priority effects; Belyea & Lancaster 1999). In addition, "neutral" models of community assembly posit that species effects on one another are equivalent, with coexistence driven by random demographic variance (Hubbell 2001). Ultimately, ecologists recognize that there are multiple models that can explain observed patterns among a variety of communities. These models interact and form feedbacks within a complex hierarchy of spatio-temporal scales (Whittaker et al. 2001). The most realistic goal is thus to quantify the relative contributions of these processes to observed patterns of species coexistence across systems.

Although community composition is bounded by the regional species pool, interactions among individuals undoubtedly play a role in determining which species coexist in a given locality. Patterns of plant community diversity may be attributable in some part to net results of interactions among individuals (Brooker & Callaghan 1998). Negative interactions, particularly competition, are the most well-studied class of interaction among plants (Goldberg & Barton 1992), although the importance of positive interactions has been recently recognized and incorporated into models of coexistence (Bruno et al. 2003).

The current paradigm concerning the role of species interactions in structuring communities is one based on the concept of the ecological niche. Niche theory was developed from the observation that species fundamentally differ both in their requirements (Grinnell 1917) and effects on their surroundings (Elton 1927). Chase and Leibold (2003) define a species' ecological niche as the set of environmental conditions that allow a species to maintain zero net local population growth, and the per capita impact of that species on those environmental conditions. A species' niche may be determined by several factors, including minimum resource requirements, regeneration strategy, and temporal partitioning of activity (Grubb 1977; Tilman 1981; Levine & Rees 2004). The theoretical implications of niches on community structure have been explored for some time, beginning with the basic (yet oversimplified) proposition that species with similar niches will fail to stably coexist due to competitive exclusion (Hardin 1960). This was followed by the notion that competition would lead to ecological divergence within communities due to limiting similarity among species (MacArthur & Levins 1967).

In modern coexistence theory outlined by Chesson (2000), niche differences generally serve to “stabilize” communities by causing increased negative intraspecific effects relative to negative interspecific effects, i.e., causing species to limit themselves more than they limit others (Adler et al. 2007). The hallmark of stabilizing niche differences is negative frequency-dependent population growth, such that species experience higher relative growth rates when rare than when common (Chesson 2000). Some niche differences can stabilize communities independently of environmental fluctuations, such as resource partitioning or differences in density-dependent predation among species (Chesson 2000). Other stabilizing niche differences require environmental fluctuations to operate. The two main fluctuation-dependent mechanisms that stabilize communities as outlined by Chesson (2000) include relative nonlinearity of competition, and the spatial and temporal storage effect. The former implies that species’ different nonlinear responses to variation in resources may themselves drive resource fluctuation cycles that permit multispecies coexistence. The storage effect model, by contrast, posits that when species require different conditions for growth and reproduction, they will differentially partition their activities in time and space. This can promote coexistence provided the impact of competition is limited when environmental conditions are unfavourable and provided species differ in the strength of covariance between environment and intensity of competition (Chesson 2000b).

Observed patterns of species interactions, however, highlight that some differences among species will lead to competitive exclusion rather than stable coexistence. When species differ sufficiently in their fitness, these “relative fitness differences” will confer a competitive advantage to the species possessing the greatest fitness relative to all co-occurring species, and other species will be eventually excluded (Chesson 2000). Overall, coexistence in diverse communities may thus be viewed as the result of stabilizing niche differences offset by relative fitness differences among species, where stronger stabilizing mechanisms will require larger differences in relative fitness among species in order for competitive exclusion to occur (Adler et al. 2007).

Quantifying relevance of small-scale interactions to community structure

Over the past 15 years, new techniques for measuring patterns within and among communities have fuelled renewed interest in community assembly. Comparisons of observed distributions of species occurrences, functional traits, and community-level phylogenies to distributions predicted by null models of community assembly have yielded support for non-random processes such as environmental and biotic filtering (Webb et al. 2002; Cavender-Bares et al. 2009; Cornwell & Ackerly 2009). These methods have been especially useful in systems or across scales that are intractable to direct manipulation.

Experimentation is also a valuable tool for teasing apart the complex set of processes involved in community assembly (HilleRisLambers et al. 2012). Experiments can isolate the mechanisms thought to promote or prevent coexistence, and can also examine the context-dependence of interactions, both increasingly important goals of community ecology (Agrawal et al. 2007). With regards to modern coexistence theory, examples of empirical evaluations are still relatively rare despite the widespread citation of this theoretical framework (Siepielski & McPeek 2010). In a Californian annual plant system, Levine & HilleRisLambers (2009) found positive low-density population growth rates and demonstrated the operation of niches using field-parameterized null models of population growth. Facelli et al. (2005) demonstrated that various temperature and water regimes could result in different arid shrubland communities in South Australia due to differences in species germination responses, implicating the temporal storage effect, and Sears & Chesson (2007) found experimental evidence for the spatial storage effect in two Arizona desert annuals. Recently, Kraft et al. (2015) found that individual functional traits were well correlated with relative fitness differences among species in a California annual grassland, whereas only combinations of multiple functional traits could describe stabilizing niche differences. These studies demonstrate that experimentation is a challenging though promising avenue for validation of coexistence mechanisms in natural communities, though clearly more evaluations are needed in a diversity of systems.

Chapters 3 and 4 of this thesis are experimental evaluations of frequency-dependent and density-dependent (i.e. density of individuals occupying a discrete spatial area) performance of native and non-native species that co-occur in invaded York gum-jam annual communities. Chapter 5 of this thesis consists of a field experiment which measures the performance of species experiencing inter- and intraspecific competition in natural assemblages. It also assesses community-level functioning by evaluating diversity effects (i.e. selection, complementarity, and dominance) based on relative yields of species in novel mixtures (Loreau & Hector 2001; Fox 2005). In the final data chapter, Chapter 6, I experimentally investigate how local-scale environmental gradients and non-native annual grasses simultaneously impact community structure in the field. In combination, all of these studies provide community-level assessments of the diversity of interactions that contribute to the formation of complex ecological communities as a result of land-use change. In addition, these studies serve as some of the first investigations into the coexistence processes that stabilize interactions among native and non-native species and lead to invaded yet diverse novel plant communities.

Chapter 2: Description of the York gum-jam annual plant communities of southwest Western Australia

The Southwest Australian Floristic Region is a global hotspot of biodiversity, containing an array of diverse plant community types (Myers et al. 2000). Climate in southwest Western Australia is typical of Mediterranean-type ecosystems, with cool winters and warm summers characterized by prolonged drought. Topography and soils of this region reflect long-term geological stability, where weathering of parent material has resulted predominantly in a low-relief landscape occasionally punctuated by granite outcrops (Beard 1981). Historically, a diversity of temperate eucalypt woodlands types were found extensively throughout the region. These woodlands span a mean annual precipitation gradient of 200 – 800 mm, forming a broad geographic transition between arid vegetation types of interior (eastern) areas and high rainfall forests in the southwest (Yates et al. 2000; Fig 2.1A).

Woodlands dominated by *Eucalyptus loxophleba* subsp. *loxophleba* (York gum) form one such association, and are often referred to broadly as York gum-jam (*Acacia acuminata*) woodlands (Fig 2.1B). York gum-jam woodlands are found on sandy loam soils that have historically low phosphorus content (Beard 1981; Lambers et al. 2008). Tree canopy cover is generally low, and understories usually support a mosaic of shrubs, perennial tussock grasses, and annual and perennial forbs. Understory annual herbaceous species (primarily Asteraceae) contribute substantially to the species richness of these woodlands, and are abundant during the winter and spring from approximately June to October.

Systematic land clearing associated with agricultural development during the 20th century has degraded floristic communities in this region through habitat loss and fragmentation, removing 93% of its native vegetation (Beard 1990; Fig 2.1A). Woodlands have been disproportionately affected in this process, with an estimated 97% of York gum-jam woodlands cleared during this period (Yates et al. 2000). Such levels of land clearing have resulted in widespread habitat loss for native woodland flora. As of 2000, 92% of the plant taxa listed as threatened in Western Australia occurred within the region where temperate eucalypt woodlands once dominated (Yates et al. 2000). Currently, the Western Australia Department of Parks and Wildlife, DPAW (formerly Department of Environment and Conservation, DEC) recognizes eucalypt woodland remnants in the wheatbelt as a threatened Priority Ecological Community “made up of large, and/or widespread occurrences, that may or may not be represented in the reserve system, but are under threat of modification across much of their range” (DEC 2010; DPAW 2014).

York gum-jam woodland remnants vary in size and condition, and are relegated to isolated nature reserves and private properties throughout the agricultural matrix (Fig 2.2). Many remnants have sustained extensive damage due to exogenous disturbances resulting from land use change. Habitat fragmentation has altered abiotic ecosystem processes primarily through changes in water and nutrient fluxes (Hobbs 1993). Increased runoff due to widespread removal of native vegetation has resulted in rapid groundwater recharge compared to background rates, causing naturally saline water tables to rise and damage woodland vegetation where surface salinization or inundation occurs (George et al. 1997; Yates et al. 2000). Nutrient enrichment has been demonstrated along the edges of many York gum-jam woodland remnants as a result of fertilizer drift, runoff, and leaching from adjacent agricultural fields (Hobbs & Atkins 1988; Prober & Wiehl 2011; Dwyer et al. 2014). Livestock grazing has homogenized understory vegetation in many areas by facilitating establishment of non-native species, altering soil resource availability via nutrient deposition, and changing soil structural properties (Scougall et al. 1993; Yates et al. 2000b; Prober et al. 2011). Historical fire frequency in York gum-jam woodlands is largely unknown. However, studies have shown that fire may affect remnant native eucalypt woodland species through changes in seedling recruitment (Yates et al. 1994) or facilitation of invasive species (Hobbs & Huenneke 1992).

Invasive non-native annual grasses and forbs have become a prominent component of most York gum-jam woodland remnants, especially in patches directly adjacent to croplands (Hobbs & Atkins 1988; Abensperg-Traun et al. 1998; Prober & Smith 2009; Fig 2.3). Fragmentation, along with nutrient enrichment and ungulate grazing, has facilitated the spread of non-native annuals into reserves by increasing propagule pressure along reserve edges (Hobbs & Atkins 1988; Scougall et al. 1993). Non-native annual grasses are particularly problematic, and pose a threat through direct effects on ecosystem properties (e.g. increased intensity and frequency of fire, changes in nutrient cycling), and indirectly through detrimental impacts on native species (reviewed in D’Antonio & Vitousek 1992). Despite the widespread occurrences of non-native species in disturbed and undisturbed York gum-jam woodland remnants, some invaded herbaceous communities appear to be more intact and seem not to be on a trajectory towards competitive exclusion (Fig 2.3; Prober & Wiehl 2011). In this thesis, I refer to non-native species simply as “non-native”, and denote their invasive status where appropriate.

Recently, Dwyer et al. (2014; 2015) and Lai et al. (2015) investigated patterns of regional and local community richness and composition in relatively intact annual communities versus communities bordering croplands in York gum-jam woodland reserves. These studies confirmed observations that intact communities support a greater diversity of species than those adjacent to reserve edges, and that non-native species are more commonly found near reserve edges. They also found that intact communities responded to favourable growing seasons by substantially increasing richness and community variation (α diversity), whereas edge communities were more compositionally entrenched from year to year. Variation in species composition was only somewhat explained by local-scale environmental factors (e.g. canopy cover, presence of grass litter, soil pH, soil P), supporting previous findings that elevated soil nutrients only moderately explain variation in species composition in long-ungrazed annual communities (Prober & Wiehl 2011). These results underscore the need to further investigate local-scale factors affecting community composition through targeted experimentation.

The diverse herbaceous understory communities of York gum-jam woodlands are an ideal system for ecological experiments testing coexistence mechanisms in novel plant communities. Generally, annual herbaceous plants are conducive to experimental manipulations, as they are small in stature, easily handled, have short life spans, respond to competition over short time frames, and compete for limited resources over small spatial scales. Furthermore, it is easy to assess a variety of fitness measures across all life stages of individuals. In addition, these communities support mixtures of native and non-native species, forming a compositional gradient from non-native-dominated to native-dominated assemblages, and abiotic gradients from intact to physically and chemically disturbed. The close proximity of novel communities to original reference communities is especially useful for studies on the contribution of species interactions to local community assembly.

Focal species chosen for the experiments in this thesis reflect both their natural high relative abundances and their co-occurrence over small (neighbourhood) scales. My goal was to choose species combinations which were realistic (if not simplified) representations of natural communities. This served to strengthen the generalizability of my findings, with the advantage of the species being readily available for study and manipulation in the field among multiple reserves and years.

Table 1.1 List of common focal York gum-jam annual species used in experiments in the thesis. Grass growth forms designated according to Prober & Wiehl (2011) and herb growth forms designated according to: Descriptions by the Western Australian Herbarium, Department of Parks and Wildlife. Text used with permission (https://florabase.dpaw.wa.gov.au/help/copyright). Accessed on Monday, 18 May 2015.

Name (Family)	**Origin**	**Growth form**
Aira cupaniana (Poaceae)	Non-native	Diminutive grass
Avena barbata (Poaceae)	Non-native	Robust grass
Bromus madritensis (Poaceae)	Non-native	Robust grass
Gonocarpus nodulosus (Haloragaceae)	Native	Slender herb
Hypochaeris glabra (Asteraceae)	Non-native	Rosetted herb
Pentameris airoides (Poaceae)	Non-native	Diminutive grass
Rhodanthe manglesii (Asteraceae)	Native	Erect slender herb
Trachymene cyanopetala (Araliaceae)	Native	Decumbent to semi-prostrate or erect
Trachymene ornata (Araliaceae)	Native	Slender herb
Trachymene pilosa (Araliaceae)	Native	Erect or ascending herb
Waitzia acuminata (Asteraceae)	Native	Erect or ascending herb
Waitzia nitida (Asteraceae)	Native	Erect herb

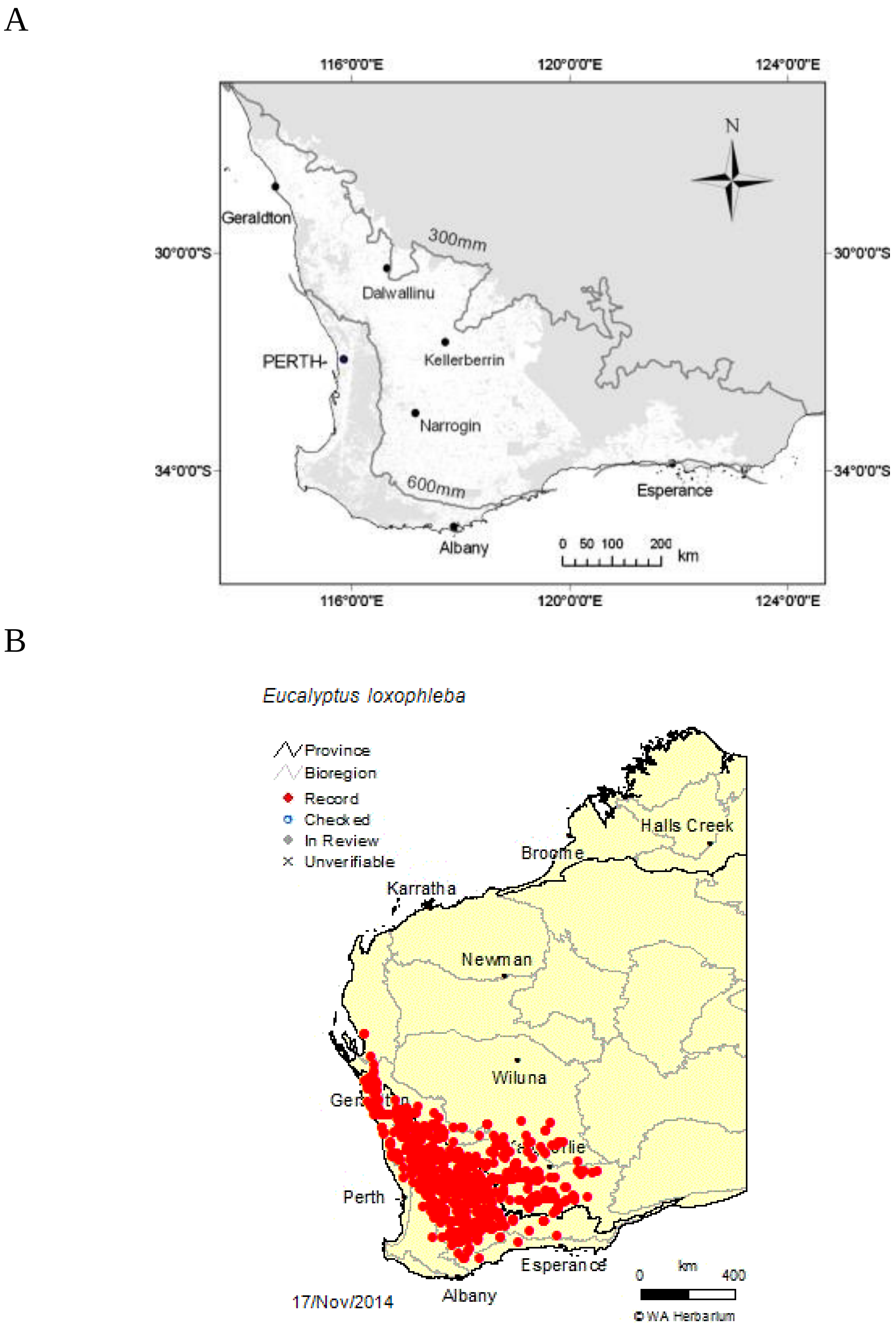

Fig 2.1 A) Map of SW Western Australia with the extent of vegetation clearing shown in white (reproduced from Prober & Smith (2009)). B) Distribution of York gum across SW Western Australia (from the Western Australian Herbarium). Image used with the permission of the Western Australian Herbarium, Department of Parks and Wildlife https://florabase.dpaw.wa.gov.au/help/copyright.

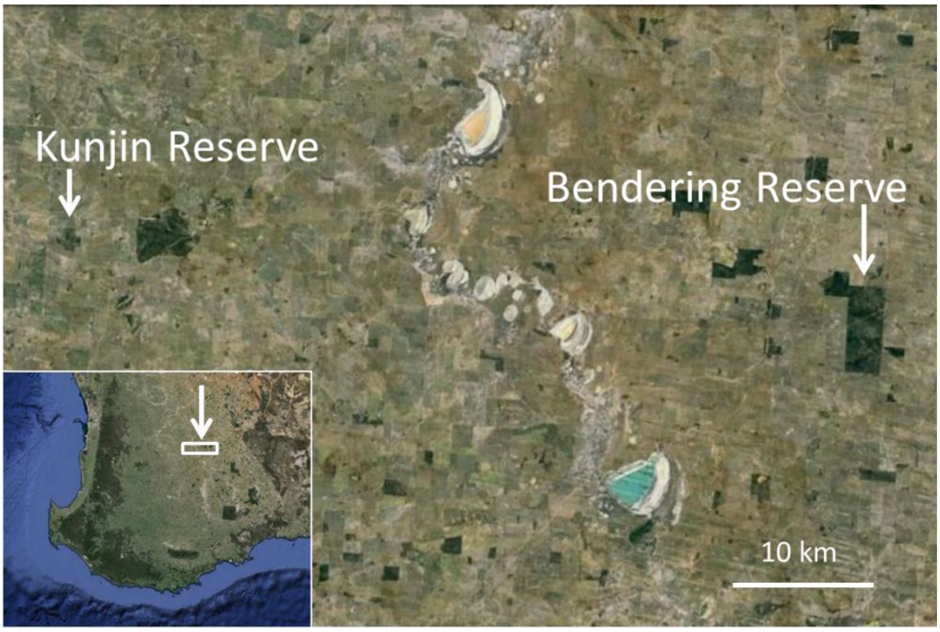

Fig 2.2 Kunjin and Bendering Reserves are remnants of the original vegetation that once covered southwest Western Australia prior to land clearing. My field studies were conducted in York gum-jam woodland patches within these reserves. Map data: Google.

Fig 2.3 Many annual communities in York gum-jam woodlands have undergone abiotic disturbance and invasion by aggressive annual grasses and broadleaf weeds (top) that result in local-scale native diversity declines, while other invaded communities still support diverse mixtures of both native and non-native annuals (bottom). Photos: author's own.

Chapter 3: Diverse outcomes of species interactions in an invaded annual plant community

Introduction

Substantial theoretical advancements in plant community ecology have been made over the past 15 years by conceptually formalizing the underpinnings of multispecies coexistence (Chesson 2000; Adler et al. 2007). Fundamentally, modern coexistence theory suggests that intra and interspecific variation in species interactions determine whether species may coexist over local scales (Chesson 2000). The details of species interactions post dispersal, germination, and establishment can, under this view of coexistence, still have diverse outcomes, ranging from negative, e.g. interference (Goldberg et al. 2001), resource exploitation (Dyer & Rice 1999), apparent competition (Dangremond et al. 2010), allelopathy (Hierro & Callaway 2003), to positive, e.g. microenvironmental amelioration (Soliveres et al. 2011), indirect facilitation (Levine 1999), and refuge from herbivores (Callaway et al. 2005). Though these types of interactions within and among species are commonly invoked as important determinants of local plant community structure in theoretical and empirical studies (Mouquet et al. 2003; Grace 2012; Spasojevic & Suding 2012), empirical evaluation of their realized importance to coexistence has not kept pace (Siepielski & McPeek 2010).

One aspect of modern coexistence theory that has substantial empirical and theoretical support is the concept of negative frequency-dependence (Harpole & Suding 2007; Levine & HilleRisLambers 2009). Specifically, theory predicts that species will exhibit weaker performance with increasing relative abundance in communities where stabilizing processes promote multispecies coexistence, i.e. negative effects of conspecific neighbours exceed negative effects of heterospecific neighbours (Chesson 2000). This can be achieved through a number of mechanisms that concentrate negative impacts among intraspecific competitors relative to interspecific competitors, such as resource competition, predation, and pathogen attack (Chesson & Kuang 2008). These phenomena can be purely spatial, as in the case of fitness-density covariance (Chesson 2000b) and aggregation models of coexistence (Bolker & Pacala 1997), or can be spatial and temporal in nature, as in the case of the storage effect (Chesson 2000b; Adler et al. 2006). In the absence of stabilizing processes, species are insensitive to conspecific effects relative to heterospecific effects and thus outcomes of interactions are determined by innate relative fitness differences among species, and the most competitively superior species will eventually dominate the community (Chesson 2000; Adler et al. 2007).

Quantifying all of the mechanisms important for coexistence in plant communities is inherently difficult, as important processes likely vary among species and operate on different spatiotemporal scales among communities (Chesson 2000; Levine & HilleRisLambers 2009). In general, a positive low-density growth rate (i.e. ability to increase in abundance in a community from rarity), combined with an intensification of negative intraspecific effects (such as competition) as species become common, is a requirement for multispecies coexistence (Adler et al. 2007). In the context of invasions, provided an introduced non-native species can increase from rarity in a recipient community post-dispersal or establishment (i.e. while interspecific effects exceed intraspecific effects), it will successfully invade (MacDougall et al. 2009). The net result of these relationships, negative frequency-dependence, is straightforward to measure experimentally. A simple approach is to directly compare intra-and interspecific impacts on co-occurring species (Adler et al. 2007). To this end, replacement series experiments can be used to measure species performance in monoculture to performance in mixtures of equal densities, where a portion of conspecific individuals are substituted with heterospecific individuals. Resulting changes in performance reflect the degree to which intraspecific effects (usually in the form of exploitation or interference competition, though density-dependent predation and parasitism have also been demonstrated) contribute to self-limitation, an essential component of coexistence (Chesson 2000). For example, by manipulating spatial aggregation of individuals, Stoll and Prati (2001) demonstrated that weaker competitors tended to increase in fitness in conspecific neighbourhoods while fitness of superior competitors decreased, suggesting that differences in species responses to competition could potentially promote coexistence. It should be noted that comparing intra- versus interspecific impacts in this way is analogous but not equivalent to measuring frequency-dependence. Measuring the impacts of intraspecific effects of a species in monoculture is essentially a measure of that species’ performance in a community where its relative frequency is at its maximum, 1.0. Measures of intraspecific effects inherently require species’ frequencies to be some smaller proportion of the community than 1.0; thus, comparing the impacts of inter- versus intraspecific competition can represent a coarse way of detecting frequency-dependent competition, where performance is compared at two frequency levels (1.0 and <1.0), rather than across a gradient of frequencies.

Past experiments designed to quantify the effects of stabilizing processes in plant communities have been criticized for their failure to examine results across a range of plant densities (Inouye 2001; Damgaard 2008). These criticisms stem from the potential for nonlinear responses to community density, which may skew links drawn between species performances in experimental and natural communities (Damgaard 2008; but see Levine et al. 2008). As with species composition, density-contingent outcomes of competitive interactions may be critical for coexistence. The importance and outcome of these interactions may change among species combinations, locations, and life stages of constituent species. It has been shown that the direction and magnitude of interspecific versus intraspecific competition among annuals may vary with total density depending on the life history stage examined (Leger & Espeland 2010). Goldberg et al. (2001), for example, demonstrated that community-level density is highly important for mediating both the intensity and type of interspecific interactions in a group of annual plants. In particular, competitive effects were most intense at the emergence stage and were characterized primarily by interference rather than exploitation (Goldberg et al. 2001). In addition, increasing total plant density has been shown to influence productivity of species mixtures by intensifying negative competitive effects in experimental assemblages of annual plants grown at different relative abundances (Polley et al. 2003) and spatial aggregations (Monzeglio & Stoll 2005).

While manipulative experiments sacrifice a certain element of realism, they are extremely useful for pinpointing the influence of specific processes in shaping communities relative to other assembly processes (Mason et al. 2011). This approach is particularly valuable for understanding how competitive dynamics vary with fundamental community properties such as evenness and the density of individuals (Polley et al. 2003). Finding a range of species densities while simultaneously holding community composition constant can be difficult in natural communities, making experiments useful for exploring these types of questions.

Using four annual plant species found in a fragmented woodland ecosystem in Western Australia, I assembled experimental communities to explore interactions under a variety of competitive conditions. Observational patterns from these communities suggest that certain local competitive processes may be important in determining community structure (Dwyer et al. 2015), particularly in communities assembling post-invasion. Targeted experimentation is needed, however, to clarify these processes. Here, I provide these empirical data while elucidating multispecies interactions and their relevance to coexistence in general. I designed this study to answer the following basic questions:

1) How do native and non-native species differ in their responses to intraspecific and interspecific competition?
2) Do native and non-native focal species vary in their density-dependence?
3) To what degree might the native and non-native species’ responses to competitor identity and density reflect their distributions and performance in natural communities?

I then discuss the answers to these questions in the broader context of multispecies coexistence.

Methods

Assembly of experimental communities

Experimental communities were made up of annual species commonly found in the understory of York gum (*Eucalyptus loxophleba*) – jam (*Acacia acuminata*) woodlands in southwestern Australia. This winter annual community type was formerly widespread, but extensive land clearing for the region's agricultural industry has resulted in fragmentation and degradation of remaining communities, particularly due to invasion by non-native annual grasses and broadleaf weeds (Prober & Wiehl 2011, Prober et al. 2011, Dwyer et al. 2014). Four commonly co-occurring York gum-jam woodland annuals were planted in monocultures, two-species, or three-species mixtures at different densities to assess competitive outcomes among growth forms and origins along a gradient of crowding. Species were chosen because they are some of the most common (if not the most common) native or non-native representatives of their growth form in York gum-jam understory annual communities, and because they are all found co-occurring and interacting at neighbourhood scales in natural communities (Dwyer et al unpublished data, pers. obs). The three-species mixture consisted of native slender erect herb *Waitzia nitida* (Asteraceae), non-native rosetted herb *Hypochaeris glabra* (Asteraceae), and robust non-native grass *Bromus madritensis* (Poaceae), and the two-species mixtures consisted of each constituent species pair. I included an additional two-species pair, *W. nitida* and diminutive non-native grass *Pentameris airoides* (Poaceae), to enable comparisons of competitive effects of the two grasses *P. airoides* and *B. madritensis*.

All communities were planted from seed at three density levels: low (21 individuals per pot: 1 plant per 3.85cm^2), medium (51 individuals per pot: 1 plant per 1.54cm^2), or high (81 individuals per pot: 1 plant per 0.97cm^2). The high density treatment was chosen based on a previous competition experiment composed of ecologically similar York gum-jam woodland annuals, in which 81 plants per pot created an environment of intense competition among individuals (D. Manietta, unpublished data). The low density treatment was chosen based on naturally occurring densities recorded in the field at peak biomass in 2011 in quadrats where focal species co-occurred (Dwyer et al. 2015), and scaled down to reflect the surface area of pots used in this experiment (78.5 cm^2). Equal proportions of each species were planted in every mixture (ratios of 1:1:1 or 1:1) to examine competitive outcomes influenced by density as opposed to relative frequency. Each species mixture (n=9) and density (n=3) combination was replicated three times, for a total of 81 experimental communities.

Seeds were collected from mature plants in several York gum-jam woodland remnants in October 2011 and then underwent a four week dry-after-ripening period at 40°C in a drying oven to alleviate seed dormancy and promote germination (important for a number of native Australian forb species; Hoyle et al. 2008). All seeds were then stored in darkness at room temperature until planting. Seed viabilities were assessed according to procedures in the AOSA/SCST Tetrazolium (TZ) handbook (Miller 2010), and were used to estimate the number of seeds needed of each species to reach target densities in each treatment. All pots were rinsed with 70% ethanol solution prior to use. Soil was obtained from The University of Queensland glasshouse facilities and prepared in order to closely resemble the texture and nutrient content of soil found beneath intact York gum-jam annual assemblages (< 5.0 mg/kg plant-available P; Dwyer et al. 2015). Soil was mixed as a combination of one part low-phosphorus native potting mix and three parts coarse sand and was passed through a 2-mm sieve to remove any large pieces of woody organic matter, as they are not a common feature of soils beneath herbaceous annual communities in this system (pers. obs.). Seeds of component species were mixed evenly and scattered on the soil surface before the first watering treatment. Each pot was hand-watered every four days (30 mL) during the first six weeks of seedling establishment, after which each pot was watered every seven days (35 mL). Throughout the establishment phase, communities were weeded regularly to maintain prescribed plant densities.

Experimental communities were grown in two temperature-controlled growth chambers (ThermoFisher Scientific, Adaptis 1000) equipped with fluorescent tubes (c. 650 µmol $m^{-2}s^{-1}$) at The University of Queensland. Pots were randomized between both chambers every week to account for any potential growth chamber or shelf differences. Temperature loggers (Thermodata Inc.) were used to monitor chamber temperatures at regular intervals (data not shown). Photoperiod was set to a 12 hour cycle, and temperatures ranged from 17.0°C (day) to 7.0°C (night) based on mean winter temperatures typical of the central wheatbelt region in July (BOM 2014) when annual plants typically establish (pers. obs.).

Several indices of plant performance were collected at the species level at four-day intervals during emergence (six weeks) and weekly thereafter. Abundance, reproductive potential (proportion of plants flowering and flower count as opposed to seed production, as natural pollination mechanisms are absent in growth chambers), and mortality were recorded for each species in each community. After about four months (120 days), peak aboveground biomass had been reached and was harvested and separated by constituent species for each community, and oven-dried for three days at 60°C before weighing.

Statistical analysis

Data analysis was conducted in R (v 3.1.2, R Development Core Team 2014) using packages lme4 (Bates 2014), nlme (Pinheiro 2014), and coxme (Therneau 2012). Species combination and density effects on plant performance were explored for each species. Density was treated in models as categorical (low, medium, high) when modelling species survival in monoculture over time and number of flowers per individual, and as a continuous variable when comparing mean biomass per individual or polyculture survival. This accounted for instances where target density was not reached (although equal proportions of each species were still maintained) and therefore comparisons of performance according to density categories among species would not have been valid. Monoculture survival was analysed using Cox proportional hazards mixed effects models with pot specified as a random effect to account for multiple observations (individuals) within each pot. Individuals were right-censored when they remained alive until harvesting. To enable comparisons of monoculture survival among species, survival analyses were followed by a mixed effects logistic regression of the proportion of surviving individuals at 15 weeks in monoculture at medium density, with pot specified as a random effect. Survival at 15 weeks in polyculture, as well as number of plants with reproductive potential (having buds or flowers at 14 weeks) were analysed using generalized linear mixed effects models with binomial errors and logit link function, and pot specified as a random effect to account for overdispersion (Elston et al. 2001). Number of flowers per individual for *H. glabra* and *W. nitida* were analysed using generalized linear mixed effects models with Poisson errors and a log link function, with plant nested within pot as a random effect to account for over-dispersion. Biomass data were ln-transformed to improve normality of residuals and analysed using linear mixed effects models with pot specified as a random effect to account for multiple observations per species within each community. For all polyculture survival and biomass models, two-way interactions among fixed effects were explored and were followed by additive models if no significant interactions were found.

Results

Survival responses to intraspecific competition

Plant survival (from emergence to harvest at 120 days) showed varying degrees of density dependence among species (Table 3.1, Fig 3.1). *W. nitida* survival declined throughout the experiment (Fig 3.1A), though differences in survival among density levels were not significant. At medium densities, *H. glabra* individuals showed a significantly positive association with death hazard (i.e. greater probability of mortality) compared to individuals grown at low densities (hazard ratio: 1.78, p=0.053) such that by the time 50% of *H. glabra* individuals died at low density, 70% had died at medium density (Fig 3.1B). *B. madritensis* had low mortality throughout the experiment at all conspecific density levels (Fig 3.1C). By contrast, *P. airoides* conspecific density was negatively, though weakly, associated with mortality (hazard ratio: 0.17, p=0.085; Fig 3.1D).

Analyses of survival in monoculture to 15 weeks at medium density confirmed differences in species responses to intraspecific competition. *W. nitida* survival was negatively impacted (estimate: -0.65, SE: 0.29, p=0.02), as was the survival of *H. glabra* (estimate: -0.96, SE: 0.22, p<0.0001). By contrast, proportion of *B. madritensis* surviving was much greater than for the other three focal species (estimate: 3.64, SE: 0.52, p<0.0001), while *P. airoides* was not significantly affected (estimate: -0.49, SE: 0.26, p=0.06).

Survival and reproductive responses to interspecific competition

Density-dependence and competitor identity influenced focal species survival to the end of the experiment in polyculture to varying degrees (Table 3.2, Fig 3.2; Appendices 3.1 – 3.4). *W. nitida* survival was negatively density dependent (p<0.0001) in polyculture, and was also depressed relative to monoculture except when grown with *P. airoides* (Fig 3.2A; p<0.0001). Non-native forb *H. glabra* survival was particularly sensitive to increasing plant density when grown with both *W. nitida* and *B. madritensis* simultaneously (*W. nitida + B. madritensis* * Density: p<0.0001; Fig 3.2B). By contrast, *B. madritensis* survival was relatively unaffected by competition (Fig 3.2C) compared to other species in this experiment, though greater replication may have increased my ability to detect effects that were weak but significant. *B. madritensis* was largely unaffected by either density (p=0.11) or the species composition of its competitive neighbourhood (Table 3.2). However, *B. madritensis* mortality did increase when grown with *W. nitida* at high densities (Fig 3.2C), though not significantly (p=0.52). Conversely, non-native grass *P. airoides* survival decreased when grown densely with *W. nitida* (*W. nitida* * Density: p=0.0007; Fig 3.2D).

Reproductive potential, measured as the proportion of initial individuals budding or flowering near the end of the experiment, did not mirror species survival responses to competitor identity and density (Table 3.3; Appendices 3.9 – 3.12). No *W. nitida* individuals invested in reproduction in the presence of *B. madritensis*. A reduced proportion of *W. nitida* individuals invested in reproduction when grown with *H. glabra* (p=0.0008). By contrast, a greater proportion of *W. nitida* individuals survived to invest in reproduction when grown with *P. airoides* (p<0.0001) than in monoculture. However, per capita flower count of *W. nitida* individuals was neither affected by community density nor competitor identity compared to low density monocultures (Table 3.4). *H. glabra* displayed significantly reduced reproductive investment when grown in the presence of *B. madritensis* (Table 3.3), but increased when grown with only *W. nitida* (p=0.009) compared to monoculture. Further analysis of flower count revealed that per capita flower production of *H. glabra* declined in high density communities (p=0.01), as well as communities containing both *B. madritensis* and *W. nitida* (p=0.01) compared to low density monocultures (Table 3.4). Density modified the reproductive response of *P. airoides*, where a smaller proportion of individuals invested in reproduction when grown with *W. nitida*, but only at high densities (p=0.006). The proportion of *B. madritensis* individuals surviving to invest in reproduction was negatively density dependent overall (p<0.0001), and unlike the other focal species was greater in all polycultures than in monoculture (Table 3.3).

Biomass responses to intraspecific competition

Species biomass responses in monoculture did not always reflect their survival responses (Fig 3.3). *W. nitida* individual biomass was insensitive to conspecific density (estimate: 0.01, SE: 0.01, p=0.53), and a similar trend was observed of *P. airoides* (estimate: -0.01, SE: 0.008, p=0.14). However, *H. glabra*'s mean biomass per individual decreased with increasing competition intensity (estimate: -0.01, SE: 0.004, p=0.02), as did *B. madritensis* (estimate: -0.02, SE: 0.003, p<0.001).

Biomass responses to interspecific competition

Biomass responses to interspecific competition also varied among species (Table 3.4, Fig 3.3; Appendices 3.5 – 3.8). Biomass of surviving *W. nitida* individuals was not influenced by initial planting density (p=0.89). However, *W. nitida* experienced greatly reduced biomass in both community types that contained non-native grass *B. madritensis* (*B. madritensis*: p=0.008, *B. madritensis + H. glabra*: p=0.0003; Fig 3.3A) relative to its biomass in monoculture or with *H. glabra* or *P. airoides* alone. I note that biomass values for *W. nitida* growing in mixtures containing *B. madritensis* are only available at low densities, as no *W. nitida* individuals survived in these mixtures at greater planting densities. Similarly, *H. glabra* had lower per plant biomass in both mixtures containing *B. madritensis* (*B. madritensis*: p=0.0003, *W. nitida + B. madritensis*: p=0.0007; Fig 3.3B), although its biomass when grown with *W. nitida* alone was similar to when grown with conspecifics (Table 3.4). Unlike *W. nitida*, *H. glabra* was negatively impacted as planting density increased (p=0.0006) across all species combinations. *B. madritensis* per plant biomass decreased in all communities with increasing density (p<0.0001; Fig 3.3C), and heterospecific competition resulted in greater biomass per individual compared to conspecific competition (*H. glabra*: p<0.0001, *H. glabra* + *W. nitida*: p<0.0001, *W. nitida*: p<0.0001; Fig 3.3C). For *P. airoides,* neither planting density nor growing with *W. nitida* significantly influenced biomass of surviving individuals relative to monoculture (Density: p=0.69, *W. nitida*: p=0.12), although the inability to detect relationships among these variables may have been due to low replication (Fig 3.3D).

Discussion

Several important factors emerged from this experiment that affected the relative strength of intra- vs interspecific competition among native and non-native annuals from York gum-jam woodland understories. The identity of competing species proved to be more informative than origin or stem density in explaining outcomes of intra- and interspecific competition. Changes in the relative strength of intra- versus interspecific competition more commonly occurred when the identity of competitors was switched than when stem density increased. Overall, the direction and type of response to competition varied dramatically among species, which I relate to natural co-occurrence patterns as discussed below.

Responses to intraspecific competition

Though this experiment took place in a lab setting, all species involved commonly co-occur at the scale of interaction neighbourhoods in natural York gum-jam systems (Dwyer et al. unpublished data), suggesting that natural communities may result in part from the combined impacts of the distinct ecological processes observed in this experiment. Species showed different degrees of conspecific density dependence, from negative to positive and complete density-independence depending on the species and the component of fitness measured. I identified a spectrum of responses to high conspecific density, from limited self-thinning but reduced individual biomass (*B. madritensis*) to substantial self-thinning but consistent individual biomass (*W. nitida*) and responses intermediate to these (*H. glabra* and *P. airoides*).

I suspect that growth form was largely responsible for survival trends. Non-native annual grasses demonstrated little to no evidence for self-thinning, either displaying density independence (*B. madritensis*) or positive density dependence (*P. airoides*). By contrast, *W. nitida* exhibited strong contest competition (Crawley 1990), resulting in taller though no more massive survivors under intense intraspecific competition (pers. obs.) and potentially compensatory growth, suggesting that competition for light may be key in regulating competitive outcomes for forbs in this system. This finding is consistent with field studies of these same species (Dwyer et al. 2015).

The fact that *B. madritensis* survival was uniformly high as well as insensitive to conspecific density in this experiment is not surprising given how successful this species is in most of its introduced range (IUCN/SSC Invasive Species Specialist Group, 2005). The lack of self-limitation on survival at any density may be advantageous to *B. madritensis* when introduced into new communities. *B. madritensis* naturally forms dense swards (Salo 2004), which may confer an advantage over native forbs such as *W. nitida*, mediated by competition for light (Dwyer et al. 2015). *B. madritensis* was not, however, immune to intraspecific competition. Rather, the effects of intraspecific competition took a different form compared to the forbs in this study. Specifically, *B. madritensis* invested less in reproduction and individuals were smaller on average in high density treatments. These findings are consistent with other studies of this species (Wu & Jain 1979) and its congeners (Lowe et al. 2003; Vasquez et al. 2008). Whether such decreases in biomass and reproductive output are sufficient to offset high survival rates is undoubtedly circumstance-specific. Given *B. madritensis'* extreme success as an invader, it seems unlikely that such limitation is common, at least outside of its native range.

In contrast to *B. madritensis*, the diminutive non-native grass *P. airoides* did not have strong responses in biomass or reproductive output across a conspecific density gradient. Interestingly, the only significant impact of intraspecific competition was positive, with more plants surviving to later dates in the higher and medium density than low density treatments. Although survivorship decreased across all density levels throughout the experiment, the fact that density reduced rather than exacerbated mortality is suggestive of intraspecific facilitation. Intraspecific positive interactions have been demonstrated in both annual (e.g. Leger & Espeland 2010) and perennial species (e.g. Fajardo & McIntire 2011) and often result from the amelioration of environmental stress outweighing the competitive effects of conspecific aggregation. Environmental stress gradients were not imposed in this study, but it is possible that soils beneath denser *P. airoides* communities may have been more mesic due to reduced evaporation at the soil surface (Callaway 2007). Although intraspecific competition does not seem to contribute to limit *P. airoides* productivity or reproduction, other factors might control its abundance in the field.

Overall, both forbs, whether native or non-native, were more heavily impacted by intraspecific competition than either of the non-native annual grasses, which was particularly evident in their higher density-dependent mortality. This potential for self-limitation is reflected in observed patterns of co-occurrence over local scales in the field based on natural species abundances (Chapter 5 of this thesis; Lai et al. 2015). *W. nitida* is a widespread species positively associated with native annual plant species richness in York gum-jam woodlands (Lai et al. 2015) and its congener *W. acuminata* tends to perform better in mixed assemblages than in monoculture in the field (Chapter 5 of this thesis). While I do not have field survival data for *W. nitida* at the spatial scale of the pots used in this growth chamber experiment, at a 30 x 30 cm quadrat scale in a natural community, mortality rates of *W. acuminata* at peak biomass ranged from 30-40% in monoculture at densities lower than this growth chamber experiment (Ch 4 of this thesis). In 2012, *W. acuminata* mortality at peak biomass in the field averaged approximately 30% in monocultures of similar density to the low density treatment in this experiment (Wainwright, unpublished data). Studies of annual plant recruitment dynamics in other semi-arid systems have reported lower seedling mortality rates than these (e.g. Espigares & Peco 1995; Rebollo et al. 2001; but see Pec & Carlton 2014). I suspect the high rates of seedling mortality observed for the forbs in this experiment were due to medium and high densities being denser than natural communities. Still, mortality rates as high as those observed in this experiment are consistent with other natural semi-arid annual plant communities, especially when environmental stress is high (Espigares & Peco 1995). Like many annuals native to semi-arid systems, the abundance of *W. nitida* is potentially co-regulated by biotic interactions and dormancy mechanisms buffering the effects of interannual climate variation (Chesson 2000; Erickson et al. unpublished data). *H. glabra,* while also fairly ubiquitous in York gum-jam woodlands, is unlike many other non-native annuals in this system in that it is not associated with soil eutrophication, nor is it associated with reduced species richness (Lai et al. 2015). Because it is non-dormant and does not form a seed bank (Erickson et al. unpublished data), I suspect that density-dependent processes such as herbivory (pers. obs.) are involved in regulating its abundance in the field.

Responses to interspecific competition

As in the case of intraspecific competition, responses to interspecific competition varied by species and could not be generalized across the performance variables measured. Among the three focal species for which all combinations were tested (*B. madritensis, H. glabra*, and *W. nitida*), I noticed a general competitive hierarchy. Native forb *W. nitida* had only neutral or positive effects on heterospecifics, invasive forb *H. glabra* suppressed *W. nitida* only, and non-native grass *B.*

madritensis suppressed both *H. glabra* and *W. nitida*. My results suggest that per capita competitive effects of the robust non-native grass were stronger than the other species in this experiment, even at low density.

Survival of *H. glabra*, however, was greater in the presence of *B. madritensis* when *W. nitida* was added, suggestive of an indirect facilitation via reduction in competition from *B. madritensis*, though only at low density. This may be offset, however, by a reduction in reproductive output per surviving individual. *W. nitida* individuals had significantly reduced investment in reproduction when the neighbourhood contained *H. glabra* as opposed to conspecifics at the population level, though per capita flower count was unaffected. By contrast, no individuals invested in reproduction when grown in the presence of *B. madritensis*. It is possible that *W. nitida* may be able to locally persist in the presence of *B. madritensis* or *H. glabra* provided that their maximum field densities remain lower than those investigated in this experiment. Natural densities, however, are often as high as or higher than those used in this study, especially in areas that have undergone physical disturbance or eutrophication (Dwyer et al. 2015). Thus, stable coexistence of these species is unlikely in natural assemblages.

Interestingly, for a given density of conspecifics, *W. nitida* survival was greater with *P. airoides* present, suggesting a role of *P. airoides* may not only be to provide release from intraspecific competition, but to facilitate at least this native species. Recently, more emphasis has been placed on the role that positive interactions play in structuring plant communities (Brooker et al. 2008). The potential role of *P. airoides* as a facilitator has not been previously documented to my knowledge, and is investigated further in Chapter 4 of this thesis. A competition study on functionally similar species *Aira caryophyllea* and *Aira praecox* noted that these small annual grasses had negligible effects on their neighbours, whether they were conspecific or heterospecific (Pemadasa & Lovell 1974). In addition, field surveys spanning the York gum-jam woodland range indicate that *P. airoides* and *Aira cupaniana*, another functionally similar non-native grass, are positively associated with native species richness both at regional and local scales (Lai et al. 2015). Further study on interactions between *P. airoides* or *Aira* species in combination with other native species besides *W. nitida* are needed, however, to draw any general conclusions on its effects on whole community dynamics.

The ability to maintain high survivorship regardless of the competitive environment may underscore *B. madritensis*'s global status as a problematic invader (IUCN/SSC 2005). Like many non-native annual grasses in semi-arid ecosystems, *B. madritensis* may not only grow and establish more rapidly than natives (DeFalco et al. 2003), but can also exert negative competitive effects on native species through interference and resource depletion (Brooks 2000). Furthermore, in natural systems *B. madritensis* has the potential to promote positive feedbacks to abundance through alteration of disturbance regimes (Brooks 1999; Brooks 2000 et al. 2000; D'Antonio & Vitousek 1992). While the average size of *B. madritensis* individuals was reduced by interspecific crowding, individuals were still larger on average and more likely to invest in reproduction when grown in mixed stands than in monoculture. Overall, this suggests that *B. madritensis* was more negatively impacted by conspecific than heterospecific competition, though the absolute effects of either form of competition were small relative to those observed for other species in this study. Overall, *B. madritensis* displayed a general competitive superiority in all mixed stands in this study, indicative of a fitness advantage that could contribute to its observed dominance over native annuals in the field. In natural communities, however, this advantage might not necessarily lead to competitive exclusion in areas that have not simultaneously experienced disturbance (Hobbs & Huenneke 1992; D'Antonio & Chambers 2006; Theohardes & Dukes 2007).

Conclusion

Here, I have documented a range of dynamics that can simultaneously contribute to community structure. There are clearly myriad potential outcomes of interactions among different species over small scales, depending both on species-specific attributes and (to a lesser extent among these focal species) the density of the community.

Rather than focusing on the outcomes of one type of interaction using species pairs, here I have observed a diverse suite of interaction outcomes in monocultures, pairs, and three-species mixtures. My results suggest that indirect interactions and positive interactions may be more prevalent than their current documentation in the literature suggests. Further, this study provides insight into the diverse processes relevant to the assembly of novel communities comprising native and non-native species. Future research should be directed towards clarifying the importance of these interactions relative to other processes in promoting or preventing multispecies coexistence in a variety of recently invaded plant communities.

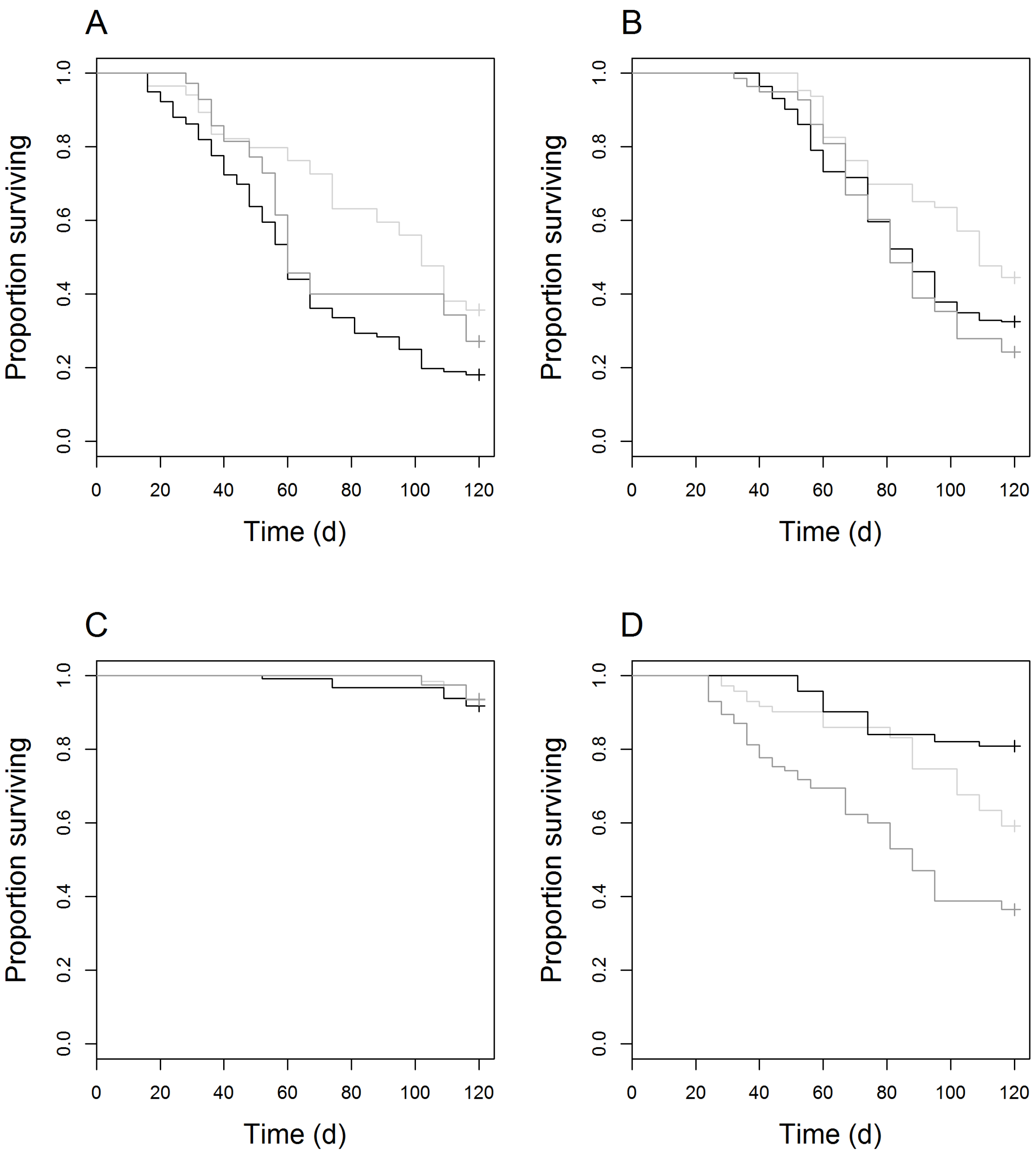

Fig 3.1 Survival curves for A) *W. nitida*, B) *H. glabra*, C) *B. madritensis*, and D) *P. airoides* monocultures from emergence to harvest at 120 days. Lines represent three levels of conspecific density (light gray = low density, gray = medium density, black = high density).

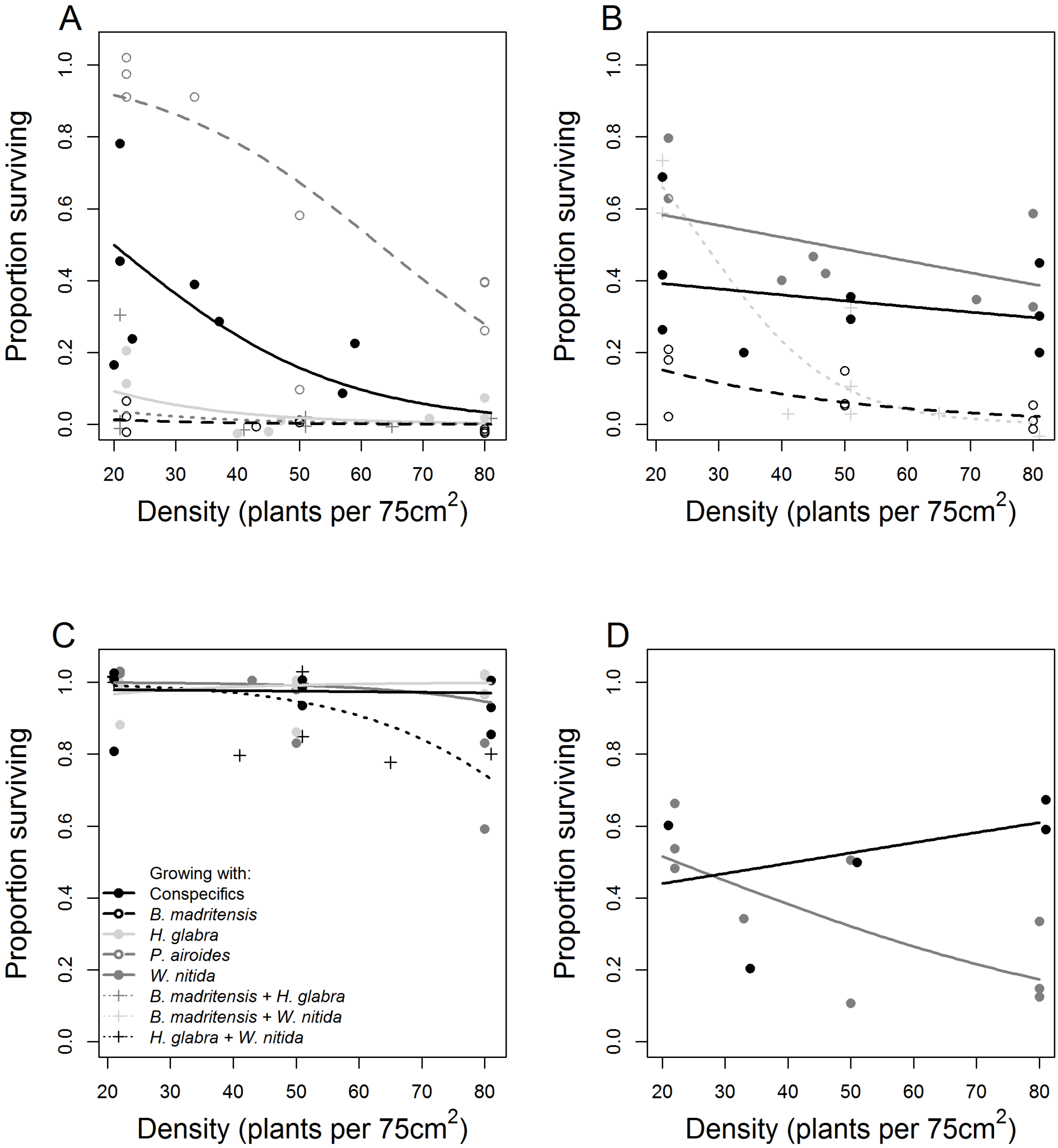

Fig 3.2 Proportion of initial community surviving to end of experiment by planting density, for A) *W. nitida*, B) *H. glabra*, C) *B. madritensis*, and D) *P. airoides*. Dashed and dotted lines within each plot correspond to different competitor combinations (described in panel C), while solid black lines represent each species in monoculture.

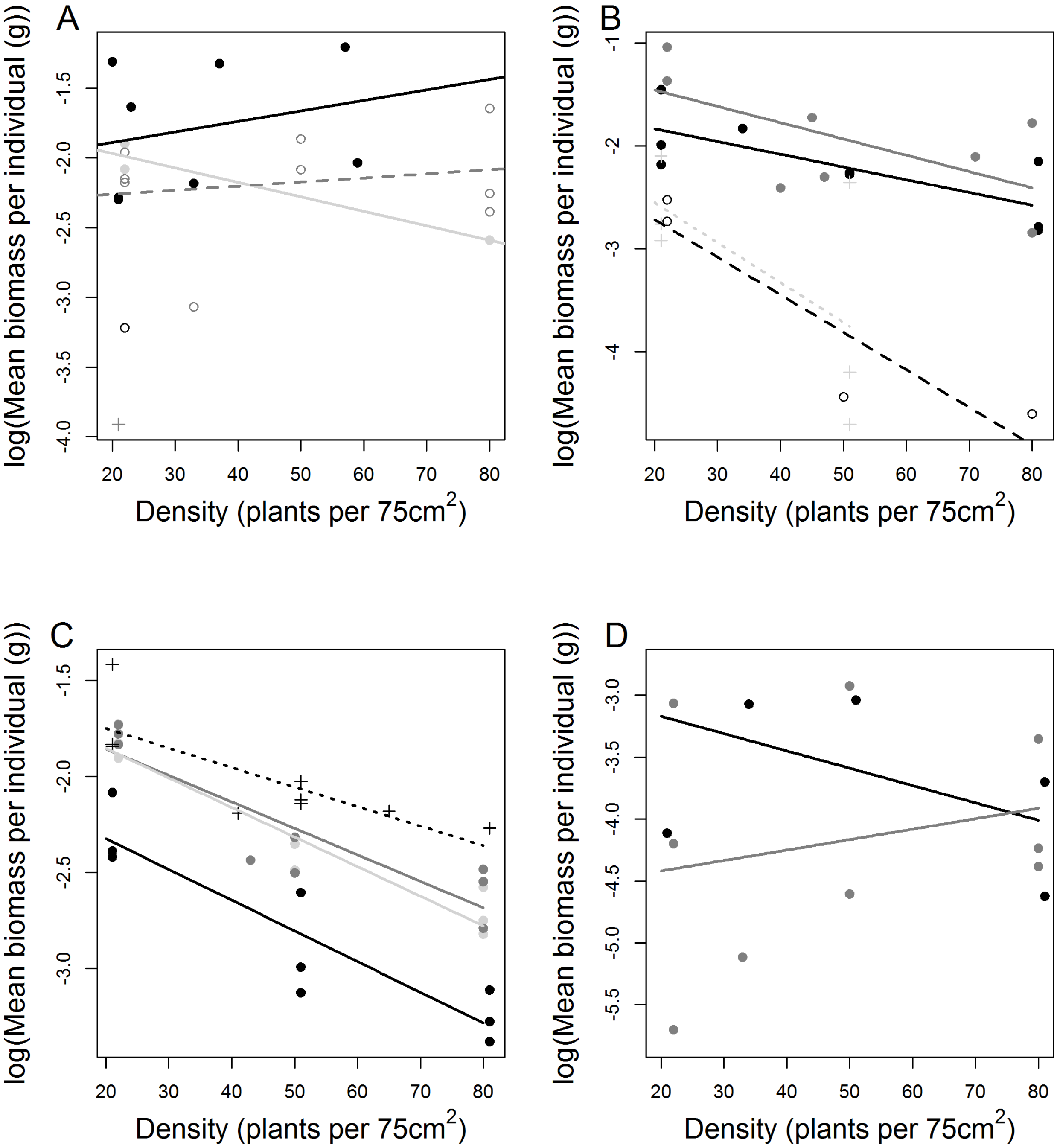

Fig 3.3 Mean biomass per individual by planting density for A) *W. nitida*, B) *H. glabra*, C) *B. madritensis*, and D) *P. airoides*. Dashed and dotted lines within each plot correspond to different competitor combinations, while solid black lines represent each species in monoculture following the same description as legend in Fig 3.2.

Table 3.1 Coefficients and (SEs) of proportional hazard rates from mixed effects Cox proportional hazards models of species survival in monoculture by density. Reference level is low density, and asterisks denote levels of significance (*: p≤0.05, **: p<0.01, ***: p<0.001).

Focal species:	***B. madritensis***	***H. glabra***	***P. airoides***	***W. nitida***
Fixed effects:				
Med density	0.13(1.24)	0.58(0.3)*	0.87(0.98)	0.28(0.44)
High density	0.46(1.21)	0.39(0.29)	-1.80(1.04)	0.62(0.43)
Random effects (variance estimates):				
Among pot	1.45	0.07	1.20	0.20

Table 3.2 Model coefficients and (SEs) from mixed effects models of focal species survival at 15 weeks in polyculture by initial planting density. A dash corresponds to instances when the focal species combination did not occur, “NS” corresponds to cases where no interaction terms were significant and thus an additive model was used, and “NA” corresponds to cases where interactions could not be estimated from the data. Asterisks denote level of significance (*: p≤0.05, **: p<0.01, ***: p<0.001).

Focal species: **Fixed effects:**	***B. madritensis***	***H. glabra***	***P. airoides***	***W. nitida***
Intercept (Conspecifics):	5.39 (1.18)***	-0.29 (0.41)	-0.47 (0.41)	1.11 (0.54)*
Total plant density	-0.03 (0.02)	-0.01 (0.01)	0.01 (0.01)	-0.06 (0.01)***
Growing with:				
B. madritensis	-	-0.71 (0.87)	-	-4.272 (1.28)***
B. madritensis + H. glabra	-	-	-	-3.21 (-0.99)**
H. glabra	1.14 (1.14)	-	-	-2.28 (0.73)**
P. airoides	-	-	-	2.39 (0.58)***
W. nitida	-0.63 (0.96)	0.90 (0.70)	1.07 (0.66)	-
W. nitida + B. madritensis	-	3.01(0.95)**	-	-
W. nitida + H. glabra	-1.03 (0.97)	-	-	-
B. madritensis * Density	NS	-0.03 (0.02)	-	NA
B. madritensis + H. glabra * Density	NS	-	-	NA
H. glabra * Density	NS	-	-	NA
P. airoides * Density	NS	-	-	NA
W. nitida * Density	NS	-0.01 (0.01)	-0.03 (0.01)***	NA
W. nitida + B. madritensis * Density	NS	-0.09 (0.02)***	-	NA
W. nitida + H. glabra * Density	NS	-	-	NA
Random effects (variance estimates):				
Among pot	2.52	0.15	0.14	0.88

Table 3.3 Model coefficients and (SEs) from mixed effects models of focal species reproductive investment (proportion of initial plants budding or flowering) at 14 weeks in polyculture by initial planting density. A dash corresponds to instances when the focal species combination did not occur, "NS" corresponds to cases where no interaction terms were significant and thus an additive model was used, and "NA" corresponds to cases where interactions could not be estimated from the data. Asterisks denote level of significance (*: p≤0.05, **:p<0.01, ***: p<0.001).

Focal species: **Fixed effects:**	***B. madritensis***	***H. glabra***	***P. airoides***	***W. nitida***
Intercept (Conspecifics)	-2.93 (0.82)***	-0.35 (0.31)	-0.40 (0.44)	-0.38 (0.28)
Total plant density	-0.05 (0.01)***	-0.02 (0.005)***	-0.004 (0.008)	-0.03 (0.006)***
Growing with:				
B. madritensis	-	-2.81 (0.63)***	-	NA (0)
B. madritensis + H. glabra	-	-	-	NA (0)
H. glabra	3.01 (0.87)***	-	-	-1.87 (0.56)***
P. airoides	-	-	-	1.13 (0.28)***
W. nitida	1.65 (0.93).	0.67 (0.26)**	0.73 (0.79)	-
W. nitida + B. madritensis	-	-1.67 (0.47)***	-	-
W. nitida + H. glabra	2.54 (0.88)**	-	-	-
B. madritensis * Density	NS	NS	-	NS
B. madritensis + H. glabra * Density	NS	NS	-	NS
H. glabra * Density	NS	NS	-	NS
P. airoides * Density	NS	NS	-	NS
W. nitida * Density	NS	NS	0.04 (0.02)**	NS
W. nitida + B. madritensis * Density	NS	NS	-	NS
W. nitida + H. glabra * Density	NS	NS	-	NS
Random effects (variance estimates):				
Among pot	1.04	0.10	0.26	0.06

Table 3.4 Model coefficients and (SEs) from mixed effects models of flower count of native *W. nitida* and non-native *H. glabra* at 14 weeks in polyculture by initial planting density. A dash corresponds to instances when the focal species combination did not occur and "NA" corresponds to cases where interactions could not be estimated from the data. Asterisks denote level of significance (*: p≤0.05, **:p<0.01, ***: p<0.001).

Focal species: **Fixed effects**	***H. glabra***	***W. nitida***
Intercept (conspecifics, low density)	1.44 (0.21) ***	1.26 (0.18) ***
Medium density	0.30 (0.24)	0.08 (0.23)
High density	-0.62 (0.26) *	-0.03 (0.22)
Growing with:		
B. madritensis	-0.52 (0.53)	NA(0 individuals flowered)
H. glabra	-	-0.37 (0.46)
P. airoides	-	-0.37 (0.46)
W. nitida	0.35 (0.20)	-
B. madritensis + W. nitida	-1.05 (0.43) *	-
Random effects (variance estimates):		
Among pot	0.12	0.05
Within pot	0.15	0.27

Table 3.5 Model coefficients and (SEs) from mixed effects models of focal species ln-transformed mean biomass per individual in a given community across densities. No significant interaction terms were found for any species. Dashes denote to instances where the focal species combination did not occur. Asterisks denote level of significance (*: p≤0.05, **: p<0.01, ***: p<0.001).

Focal species: **Fixed effects:**	***B. madritensis***	***H. glabra***	***P. airoides***	***W. nitida***
Intercept (conspecifics)	-2.10 (0.09)***	-1.20 (0.32)**	-3.31 (0.44)***	-1.81 (0.22)***
Total plant density	-0.01 (0)***	-0.02 (0.01)***	0 (0.01)	0 (0)
Growing with:				
B. madritensis	-	-1.50 (0.35)***	-	-1.43 (0.47)**
B. madritensis + H. glabra	-	-	-	-2.12 (0.47)***
H. glabra	0.49 (0.08)***	-	-	-0.41 (0.30)
P. airoides	-	-	-	-0.40 (0.22)
W. nitida	0.54 (0.08)***	0.28 (0.28)	-0.71 (0.42)	-
W. nitida + B. madritensis	-	-1.24 (0.32)***	-	-
W. nitida + H. glabra	0.73 (0.08)***	-	-	-
Random effects (variance estimates):				
Among pot	0.03	0.30	0.64	0.02
Within pot	0.004	0.04	0.09	0.17

Chapter 4: Interactions between a common native forb and non-native annual grasses

Introduction

It is commonly assumed that invasion by non-native species negatively impacts native resident species; however, many invaded communities worldwide retain high native species diversity, even at local scales (Levine 2000). Following biological invasions, mixtures of native and non-native species may form stable “novel” communities, reflecting new species combinations and/or modified environmental conditions (Hobbs et al. 2009). It is the capacity for non-native species to negatively impact native species and communities that generally receive the most research attention (Levine et al. 2003; Vila & Weiner 2004). The outcomes of these interactions can be variable, however, and do not necessarily reduce native species diversity. In reality, non-native species exert a spectrum of effects on resident species (Shackelford et al. 2013), and interact with and impact one another as well as the native community. The complex suite of interactions that occur within novel communities provide an excellent opportunity to gain a greater understanding of species coexistence, community diversity, ecological resilience and invasion success. To understand why some novel communities become near monocultures of non-native species and others remain diverse, we first must understand how native and non-native species interact over small scales in novel communities (Hobbs et al. 2006).

Invasions by non-native species have long interested ecologists investigating the role of interactions in community formation (Elton 1958; Richardson & Pysek 2008). Generally, the most highly-cited literature on plant invasions is contains accounts of non-native species incurring substantial damage to the ecological integrity of vulnerable ecosystems (Mack et al. 2000; D’Antonio & Vitousek 1992; Vitousek et al. 1997) including threats to native biodiversity (Wilcove et al. 1998). The invasion literature is dominated by descriptions of non-native species displacing native species, often invoking competitive exclusion (Levine et al. 2003; Vila & Weiner 2004 and references therein). In many systems and for many species pairs, non-natives do out-compete natives by reducing native species’ fitness via resource competition or suppression (Dyer & Rice 1999; Brown & Rice 2000; Bakkar & Wilson 2001; Kueffer et al. 2007). These negative impacts are, however, often exacerbated by some form of exogenous disturbance or abiotic change that precedes, accompanies, or results directly from the invasion (Hobbs & Huenneke 1992; Davis et al. 2000; Seabloom et al. 2003; MacDougall & Turkington 2005) rather than due to intrinsic properties of the invader (Daehler 2003). Though native population declines may occur due to competition with invasive species, examples of extinctions resulting from competition with invasive species are at present exceedingly rare in plants, especially in non-island systems (Sax & Gaines 2003; Vellend et al. 2013), though longer-term extinction trajectories are a possibility (Gilbert & Levine 2003). As a result, ecologists have recently suggested that species functional attributes and impacts are perhaps more useful foci for management and conservation than species origins (Brown & Sax 2004; Davis et al. 2011; Drenovsky et al. 2012; Thompson 2014; Lai et al. 2015).

In contrast to early ecological theory that predicted negative impacts of invading non-native species (Elton 1958; MacArthur 1984), several observational studies of invaded communities show positive correlations between native and non-native species richness at a variety of spatial scales (Stohlgren et al. 1999; Levine 2000; Sax 2002; Cleland et al. 2004; Harrison et al. 2006), giving rise to the "invasion paradox" (Fridley et al. 2007). Several factors have been implicated in relation to these positive relationships, including abiotic conditions and disturbance histories (Levine & D'Antonio 1999), high propagule supply (Levine 2000; D'Antonio et al. 2001), and environmental heterogeneity (Davies et al. 2005; Melbourne et al. 2007). Intrinsic biological processes may also contribute to positive native - non-native richness relationships. These processes include relative fitness and niche differences among invasive and native species that permit coexistence post invasion (MacDougall et al. 2009).

Given the overwhelming historical focus on the negative impacts of non-native species on native communities and species, it is perhaps not surprising that evidence for neutral or even positive impacts of non-native species, such as facilitation, has only recently started to emerge (Rodriguez 2006). Facilitation among plant species occurs when one or more direct (or indirect) interactions (reviewed in Callaway 2007) confer greater fitness to one or more species in the presence of a "benefactor" species than when the benefactor species is absent. Facilitation among native and non-native species has recently been highlighted (Rodriguez 2006; White et al. 2006; Shlaepfer et al. 2011) and may in fact contribute to positive relationships between native and non-native species richness (Stachowicz 2001; Bruno et al. 2003). Direct facilitation is thought to play a more prominent role in stressful than benign environments, primarily through habitat amelioration (Callaway et al. 2002; Cavieres et al. 2006) and is predicted to become more important as human-induced environmental change progresses (He 2013). Facilitation has been observed among non-native plant species, e.g. "invasional meltdown" (Simberloff & Von Holle 1999; Jordan et al. 2008), and there are accounts of non-native species facilitated by natives (Maron & Jeffries 1999; Lenz & Facelli 2003; Belnap & Sherrod 2009). There are far fewer published examples of non-native species facilitating native species, especially in terrestrial plant systems. However, there is no obvious reason that positive interactions between native and non-native species should not occur under certain circumstances. Published examples include a few cases in which non-native species facilitate native recruitment (Kanowski et al. 2008; Elgar et al. 2014) and productivity (Pec & Carlton 2014), or promote native fitness through environmental engineering, such as by increasing soil nutrient levels (Quinos et al. 1998; Knight et al. 2007) and alleviating moisture stress after natural disturbance (Titus & Tsuyuzaki 2002). To fully understand the variable outcomes of biological invasions, there is a need to study the full range of interactions between native and non-native species, including those that are positive in nature.

Here, I experimentally tested for facilitative interactions between a native annual forb (*Waitzia acuminata*, Asteraceae) and two species of non-native annual grass (*Aira cupaniana* and *Pentameris airoides*, Poaceae) which commonly co-occur in semi-arid woodland fragments of southwest Western Australia. Preliminary observations from both field and laboratory studies suggest that *W. acuminata* survival and/or biomass is greater when growing alongside either of these non-native grass species than when grown alone (Chapters 3 and 5 of this thesis). Using a combination of field and laboratory experiments and assessment of several performance measures, I test for facilitation by the non-native grass species and the differences among all species in their responses to intra- versus interspecific competition. I also estimate the magnitude of any frequency-dependence of these interactions. Both experiments are guided by the following two questions:

1. Do the common non-native grasses *A. cupaniana* and *P. airoides* facilitate the native forb *W. acuminata*?
2. How do patterns of intra- versus interspecific competition relate to the potential long-term coexistence of these focal species in natural communities?

I then discuss the results in the context of coexistence among these species in natural communities.

Methods

Study system

Our three focal species are common in annual understory communities of formerly extensive York gum (*Eucalyptus loxophleba* subsp. *loxophleba*) – jam (*Acacia acuminata*) woodlands, a fragmented semi-arid woodland type that persists in the agricultural wheatbelt region of southwest Western Australia. The canopy of York gum-jam woodlands is sparse, and understory vegetation typically comprises dense annual and perennial forb assemblages and scattered shrubs and tussock grasses. The annual component germinates and grows mainly from June to October during the winter-spring rainy season, and senesces by the onset of the summer dry season.

W. acuminata is an erect herb, occurring in all Australian states with the exception of Tasmania (Australia's Virtual Herbarium/AVH). Both of the non-native annual grasses are commonly referred to as "feather grasses" due to their slender, diminutive stature. *A. cupaniana* is native to the Mediterranean region, though its distribution is now global, and *P. airoides* is native to South Africa but with a widespread Australian distribution (AVH). Both grasses were presumably introduced to the region during periods of agricultural development in the late 19th and early 20th century (Burvill 1979). Such early introductions are supported by herbarium records dating back to 1893 and 1922 for *P. airoides* and *A. cupaniana*, respectively (Avon Wheatbelt Bioregion, AVH). Both species are now ubiquitous within woodland fragments across the south-western agricultural region, and *W. acuminata* co-occurs with both grass species over regional and local (sub-meter) spatial scales in York gum-jam woodland remnants (Fig 4.1; Dwyer et al. 2014; 2015).

York gum-jam annual local-scale communities range in composition from completely non-native-dominated to predominantly native (Dwyer et al. 2014). Communities dominated by non-native species tend to occur in heavily grazed areas (Prober et al. 2011) and in the absence of grazing along woodland edges adjacent to roads and agricultural fields where robust non-native annual grasses (e.g. *Avena barbata*) and broadleaf weeds (e.g. *Arctotheca calendula*) exploit disturbed conditions (Hobbs & Atkins 1988; Prober & Wiehl 2011), often to the detriment of native species including *W. acuminata* (Dwyer et al. 2014). However, in typical woodland interior communities where abiotic conditions are more intact, a different suite of non-native annuals not associated with disturbance tends to compose the non-native portion of the annual community. Occurrences of *A. cupaniana* and *P. airoides* are strongly negatively associated with that of robust annual grasses and broadleaf weeds, and positively associated with native species richness (Lai et al. 2015).

Field experimental design

The field component of this study took place at Bendering Nature Reserve in southwestern Australia (32 °23' 7.88" S, 118 °23'5.66"E) during the winter-spring growing season (July – November) of 2013, in an intact York gum-jam woodland area in the reserve interior. *W. acuminata* and *A. cupaniana* were both locally abundant and present at varying relative frequencies in natural mixtures. In early August, 10 30 x 30 cm quadrats were located in areas containing two-species mixtures of *W. acuminata* and *A. cupaniana*. All non-focal species were weeded out of the quadrats, though mixtures were chosen such that non-focals were present at very low abundances and minimal weeding was required. Quadrats containing monocultures of *W. acuminata* were also located (n=12) at the same woodland site to enable investigation of facilitation and comparisons of the strength of intra vs interspecific competition for *W. acuminata*. I treated *W. acuminata* as the focal species in this field study and allowed its density to vary while keeping the density of *A. cupaniana* relatively constant at between 120 – 180 individuals per quadrat. Initial *W. acuminata* densities in 2-species mixtures and monocultures were binned into two density levels (low = 10±5 and high=20±5 individuals, Table 4.1).

To assess whether quadrat-scale environmental heterogeneity was responsible for differential performance of *W. acuminata* individuals, I recorded *E. loxophleba* litter percent cover, *A. acuminata* litter percent cover, herbaceous litter percent cover, percent soil moisture halfway through the growing season (late September) and percent overhead tree canopy cover for each quadrat. In addition, I collected dry soil from each quadrat at the end of the growing season which was stored in darkness at room temperature in sealed beakers until chemical analysed for nitrate, ammonium, phosphorus, and potassium content. To measure whether N-cycling rates were different between *W. acuminata* monocultures and plots containing *A. cupaniana*, I deployed three anion-exchange membrane strips in each quadrat for six weeks to estimate nitrate adsorption rates, which were determined according to methods described in Jasrotia & McSwiney (2008) and Vogt (2013b). Abundances of *W. acuminata* and *A. cupaniana* were recorded regularly in each quadrat over the course of the growing season. To assess aboveground biomass of *W. acuminata*, all focal individuals were harvested in December 2013 once both species had gone to seed, oven dried at 60˚C for one week and then weighed.

Growth chamber experimental design

The growth chamber component of this study tested for facilitation of *W. acuminata* by *A. cupaniana* and *P. airoides*, and to measure the relative strength of intra vs interspecific competition for all three focal species. *W. acuminata* was grown with either *A. cupaniana* or *P. airoides* in two-species combinations at three relative frequencies (proportion of individuals in a mixture) as described in Table 4.2. Monocultures of each species were also planted at each density to directly compare species' performance measures (survival, productivity, and reproductive investment) with and without interspecific competition at a given intraspecific density.

All of the two-species (*W. acuminata* + grass) communities were planted from seed at a target density of 60 total plants per pot (78.5 cm^2 surface area), with the number of each species varying according to the frequency treatment. This density was chosen based on densities commonly observed in the field. Species' relative frequencies (*W. acuminata*:grass ratio) varied from 1:5, 1:1 to 5:1.

Seeds were collected from mature plants in York gum-jam woodland remnants in October 2011 at Bendering Reserve (*W. acuminata* and *A. cupaniana*) and Kunjin Reserve (32 °21'19.31"S, 117 °45'42.32"E); *W. acuminata* and *P. airoides*) and then after-ripened for four weeks at 40°C in a drying oven to alleviate dormancy (important for a number of native Australian forb species; Hoyle et al. 2008). All seeds were then stored in darkness at room temperature until planting. All pots were rinsed with 70% ethanol solution prior to use. Soil was obtained from The University of Queensland glasshouse facilities and prepared in order to closely resemble the texture and nutrient content of soil found in intact York gum-jam annual assemblages (< 5.0 mg/kg plant-available P; Dwyer et al. 2015). Soil was mixed as a combination of one part low-P native potting mix and three parts coarse sand. Seeds of component species were mixed evenly and scattered on the soil surface before the first watering treatment. Each pot was hand-watered every four to five days (30 mL) during the first six weeks of seedling establishment, after which each pot was watered every seven days (35 mL). Throughout the establishment phase, communities were weeded regularly to maintain prescribed plant densities.

Experimental communities were grown in two temperature-controlled growth chambers (ThermoFisher Scientific, Adaptis 1000) equipped with fluorescent tubes (c. 650 $\mu mol\ m^{-2}s^{-1}$) at The University of Queensland. Pots were randomized between both chambers every week to account for any potential growth chamber or shelf differences. Photoperiod was set to a 12 hour cycle, and temperatures ranged from 17.0°C (day) and 7.0°C (night), based on mean winter temperatures typical of the central wheatbelt region in July (BOM 2014) when annual plants typically establish (pers. obs.).

Once the prescribed densities had been reached and no further seeds germinated, the abundance of each species was monitored regularly until the harvest date. When plants reached peak biomass at four months since planting, all pots were harvested for aboveground and belowground biomass. Aboveground biomass and number of flowers (for *W. acuminata*) was recorded at the individual level (averaged within a pot), while the number of individuals flowering was recorded at the species level in each pot.

Statistical analysis

Data analyses was conducted in R (v 3.1.2, R Development Core Team 2014) using packages lme4 (Bates et al. 2014), nlme (Pinheiro et al. 2014), and multcomp (Horthorn et al. 2008), described in detail below.

W. acuminata *survival, productivity, and reproductive investment in the field*

To explore whether abiotic differences among plots may have potentially influenced changes in *W. acuminata* performance measures, several key environmental variables were ln- or square-root-transformed as appropriate to improve the normality of their distribution and were compared between monoculture and mixture plots using t-tests with Bonferroni corrections for multiple comparisons: ln(nitrate), ln(ammonium), ln(phosphorus), ln(potassium), nitrate adsorption rate, percent soil moisture, and ln(percent tree canopy cover), sqrt(*E. loxophleba* litter percent cover), *A. acuminata* litter percent cover, ln(Herbaceous litter percent cover)).

W. acuminata performance measures (survival, biomass per individual and flower count per individual) from the field experiment were analysed using mixed effects models with community type (mixture with *A. cupaniana* or monoculture) and *W. acuminata* abundance (continuous) and their interaction specified as fixed effects. In all models, the community type x *W. acuminata* abundance interaction term was not significant, and so additive models were used instead.

W. acuminata survival in the field was modelled as a binary response (1 = alive at harvest, 0 = dead at or before harvest) as a function of treatment (mixture with *A. cupaniana* or monoculture) using a mixed-effects logistic regression with binomial errors and logit link function. Plot was included as a random effect. *W. acuminata* biomass responses were ln-transformed and modelled using linear mixed effects models with plot specified as a random effect to account for multiple observations per plot. *W. acuminata* flower counts per plant were modelled using a generalized linear mixed effects model with Poisson errors and log link function. Plot was included as a random effect, and plant (within plot) was also included to account for overdispersion (Elston et al. 2001).

W. acuminata *survival, productivity, and reproductive investment in growth chambers*

To investigate potential facilitation of *W. acuminata* by *A. cupaniana* or *P. airoides* in growth chambers, I compared *W. acuminata* performance measures (survival, individual plant biomass, proportion of surviving individuals flowering, and the number of flowers per flowering individual) with and without the grass species present while holding *W. acuminata* density constant. To avoid confounding the effects of grass presence versus its relative abundance, these response variables were modelled within each *W. acuminata* abundance category separately (10, 30, or 50 *W. acuminata* individuals) as grass abundances varied with *W. acuminata* abundance to maintain overall community densities. Responses were analysed using mixed effects models where fixed effects included identity of competing individuals (*W. acuminata* if monoculture, and *A. cupaniana* or *P. airoides* if 2-species mixture). Community (pot) was specified as a random effect to account for multiple observations used per pot. This analysis allowed investigation of general differences in *W. acuminata* performance measures due to addition of grass across a range of conspecific abundances. *Post-hoc* tests of differences among all 3 species combinations (*W. acuminata*, *W. acuminata* + *A. cupaniana*, and *W. acuminata* + *P. airoides*) were then conducted on all responses.

The various responses in the growth chamber experiment were modelled using the same transformations and error structures as described for the field experiment (e.g. binomial errors for survival etc.). Flowering of surviving plants was treated as a binary response and modelled as for binary survival responses.

Species responses to intra vs interspecific competition

To determine the relative impacts of intra vs interspecific interactions on focal species performance, I analysed survival, mean biomass per plant (as grass biomass was measured at the species level per pot), proportion flowering, and number of flowers produced (*W. acuminata* only) across a range of species' relative frequencies in a community. *P. airoides* monocultures only reached 50 instead of the targeted 60 individuals, so relative frequency = 1.0 for this species reflects a density of 50 rather than 60 individuals. For both grass species, the competitive neighbourhood always consisted of *W. acuminata*. However, for *W. acuminata* the competitive neighbourhood consisted of one of either grass species. Because both community types containing *W. acuminata* as a focal species shared the same data where *W. acuminata* relative frequency was equal to 1.0, separate models were run for *W. acuminata* with either grass competitor.

Response variables were modelled as a function of species' relative frequencies (continuous). Survival, flowering probability and flower number were all modelled using the same error structures as described above. Mean biomass per plant was square-root transformed instead of ln-transformed because the latter over-corrected the skew in this response variable. Again, pot was specified as a random effect where required to account for multiple observations per pot and for overdispersion (Poisson model).

To enable direct comparisons of *W. acuminata* performance measures in neighbourhoods of *P. airoides* versus *A. cupaniana,* I also modelled these responses without the shared data (i.e. excluding pots with *W. acuminata* relative frequencies of 1.0; Appendix 4.2). For these models the fixed effects were competitor identity (*P. airoides* or *A. cupaniana*), relative frequency of *W. acuminata*, and their interaction.

Results

W. acuminata *survival, productivity, and reproductive investment in the field*

No significant differences were detected in environmental variables between mixture and monoculture plots (Appendix 4.1). Overall, *A. cupaniana* had a facilitative or neutral effect on *W. acuminata* in the field depending on the performance measure considered. Survival of *W. acuminata* from seedling to adult was significantly greater for *W. acuminata* individuals growing in the presence of *A. cupaniana* than those found in monoculture across all conspecific densities (p=0.01; Table 4.3; Fig 4.3A; Appendix 4.3). All surviving *W. acuminata* plants flowered. The aboveground biomass and the number of flowers produced per surviving individual declined significantly with increasing conspecific density (biomass: p=0.02, number of flowers: p=0.005; Table 4.3; Fig 4.3B and 4.3C; Appendices 4.4 & 4.5).

W. acuminata *survival, productivity, and reproductive investment in growth chambers*

In general, *W. acuminata* was neutrally or positively affected by *A. cupaniana* in the growth chamber, while the effects of *P. airoides* were neutral or negative.

W. *acuminata* survival was reduced at low conspecific abundance (10 individuals) only when in mixture with *P. airoides* (p=0.007, Table 4.4, Fig 4.4A; Appendices 4.6 – 4.8). By contrast, *W. acuminata* biomass per individual was not affected by grass presence compared to conspecifics alone at any abundance (Fig 4.4B; Appendices 4.9 – 4.11), though *post-hoc* pairwise comparisons revealed that at high conspecific abundance, *W. acuminata* individuals were significantly larger when growing with *A. cupaniana* than in monoculture (estimate: 0.64 (0.27), adjusted p=0.04). The proportion of *W. acuminata* survivors flowering was significantly lower with *P. airoides* present when its abundance was high (Table 4.4, Fig 4.4C, p=0.02; Appendix 4.14) but was otherwise unaffected (Appendices 4.12 & 4.13). Of the individuals that did flower, the number of flowers produced was significantly lower when growing with *P. airoides*, but only when *W. acuminata* was at low abundance (Table 4.4, Fig 4.4D, p=0.02; Appendices 4.15 – 4.17).

Species responses to intra vs interspecific neighbourhoods

Survival was not related to relative frequency for any species (Table 4.5; Fig 4.5A; Appendix 4.18), but frequency-dependence was evident in other performance measures to varying degrees.

W. acuminata individual aboveground biomass (averaged per pot) declined as its relative frequency increased in communities where *A. cupaniana* composed the competitive neighbourhood (p<0.0001; Table 4.5; Fig 4.5B; Appendix 4.19). By contrast, *P. airoides* exerted stronger interspecific competition on *W. acuminata* plant biomass (p=0.02, Appendix 4.2). Neither grass species' mean biomass per plant was significantly related to relative frequency (Table 4.5; Fig 4.5B; Appendix 4.19).

The proportion of *A. cupaniana* individuals that flowered was unaffected by its relative frequency in mixture. A positive relationship was found, however, between the proportion of *P. airoides* individuals flowering and its relative frequency in mixture (p=0.02; Table 4.5; Fig 4.5C; Appendix 4.20). The proportion of surviving *W. acuminata* that flowered declined significantly as it increased in frequency, but only in communities containing *A. cupaniana* (Table 4.5, Fig 4.5C, p=0.03; Appendix 4.20). A similar relationship was found for *W. acuminata* flower counts per plant, which declined with increasing relative frequency in communities containing *A. cupaniana* (p=0.002; Table 4.5, Fig 4.5D; Appendix 4.21).

Discussion

This study reveals that two functionally similar non-native grass species interact in a variety of ways, from positive to negative, with a native forb. Interactions with *A. cupaniana* were neutral or positive and interactions with *P. airoides* were suppressive or neutral, implying that invaders with similar growth forms do not necessarily have similar impacts on resident species. Both grasses responded neutrally or positively to conspecific abundance, which may promote their invasiveness.

Overall, the prevalence and contingencies of positive interactions between native and non-native species merit further attention when assessing invasion impacts on native communities.

Positive and neutral interactions in the field

In the field, I found that *W. acuminata* survival was significantly greater in plots containing the non-native annual grass *A. cupaniana. W. acuminata* biomass and flower production were impacted less by the presence *A. cupaniana* than by conspecifics, suggesting that the effects of intraspecific competition are much stronger than interspecific interactions for *W. acuminata* productivity and reproductive investment when growing in mixture with *A. cupaniana*. This trend was robust across a range of *W. acuminata* abundances, indicating that the positive effect of *A. cupaniana* was not contingent on conspecific competition intensity. The generality of this interaction should be investigated further by determining whether *A. cupaniana* similarly affects other co-occurring native and non-native species, or if its effects are unique to *W. acuminata*. Additionally, the consequences of this facilitation should be evaluated relative to co-occurring species at the population and community level.

Positive interactions between non-native *A. cupaniana* and native *W. acuminata* could arise through a number of processes, such as plant-soil feedbacks. Preliminary observations suggest that *W. acuminata* does not regularly form mycorrhizal mutualisms (A. Nance, pers. comm.), though facultative mycorrhizal associations or benefits from other microorganisms in soils beneath *A. cupaniana* could potentially facilitate *W. acuminata* through indirect positive plant-soil feedbacks (reviewed in Callaway 2007). In addition, nutrient cycling rates may also differ in soils beneath patches of annual grasses from soils characteristic of native communities where annual grasses have not occurred historically (Hobbie 1992; Prober et al. 2005). For example, Pec (2014) found that the survival of a native annual forb in a California coastal sage scrub community was potentially facilitated by the senescence of co-occurring non-native annual grasses. *W. acuminata* has a more delayed phenology than *A. cupaniana*, so it is possible that some senescence of *A. cupaniana* individuals may have been beneficial to *W. acuminata* during its active growth phase by providing a nutrient pulse. Additionally, *A. cupaniana* litter is less persistent than that of other common non-native annual grasses and native herbaceous species in this system (pers. obs.) and may be less recalcitrant, potentially serving as a nutrient source for *W. acuminata* individuals the following year (Facelli & Pickett 1991), though I measured differences in levels of key nutrients between mixtures and monocultures in the field at the end of the growing season only (Appendix 4.1).

Within the experimental site, naturally-occurring mixtures of *A. cupaniana* and *W. acuminata* were located in more open patches with lower overhead tree canopy cover than *W. acuminata* monocultures. Environmental variables associated with overhead tree canopy cover effects on understory plant communities (i.e. coverage of sclerophyllous litter, soil moisture, and nutrient levels) did not differ between *W. acuminata* monocultures and mixtures with *A. cupaniana*, suggesting the relationship may be correlated with unmeasured variables. Environmental and biotic covariates of *A. cupaniana* presence occurring at finer sub-plot or larger site-level scales study merit further investigation, as they may have impacted *W. acuminata* survival.

Diverse impacts of non-native grasses in growth chamber

In growth chambers, *A. cupaniana* had a neutral or positive effect on *W. acuminata* performance measures across a range of relative abundances. Surviving *W. acuminata* individuals were significantly larger when *A. cupaniana* was present at high conspecific density than without, indicative of growth facilitation at high density. These results support the overall trend of neutral or positive interactions between these two species in the field, although *A. cupaniana* impacted different performance measures in the growth chamber than in the field (production as opposed to survival), potentially because environmental conditions were less stressful in growth chambers. The fact that this interaction was found in a laboratory setting indicates that this neutral to positive relationship may occur independently of microenvironmental variation or other factors associated with *A. cupaniana* in the field.

W. acuminata survival decreased in communities containing *P. airoides* compared to monocultures, particularly when it was much less abundant than *P. airoides*. The same pattern held true for *W. acuminata* biomass and reproductive investment. These results are in opposition to the facilitative effect *P. airoides* demonstrated on survival of *W. nitida* (Ch 3 of this thesis), a congener of *W. acuminata*. The difference in the effects of *P. airoides* on *Waitzia* survival may have been due to the fact that in the previous experiment, at low *W. nitida* abundance (~10 individuals per pot of the same dimensions as in this study) where the facilitation effect occurred, *P. airoides* was present at equally low abundance. It is therefore possible that if fewer *P. airoides* individuals had been in mixture with *W. acuminata*, a facilitative effect may have occurred. Additionally, though *W. acuminata* is functionally very similar to *W. nitida*, *W. acuminata* may have been more susceptible to interspecific competition from *P. airoides.*

Species responses to intra vs interspecific competition

The only occurrence of negative frequency-dependence in mixture was for *W. acuminata* biomass and reproductive investment, which both declined with increasing frequency in mixtures with *A. cupaniana*. These results indicate that intra- rather than interspecific interactions determine *W. acuminata* productivity in this mixture, corroborating observations of these species in the field. Conversely, interspecific competition was more evident in mixtures with *P. airoides*. In fact, the results for biomass indicate that the strength of inter- and intraspecific competition were similar in these mixtures. This suggests that *W. acuminata* may not increase from rarity in a neighbourhood of *P. airoides* as rapidly as in a neighbourhood of *A. cupaniana*. In natural communities, however, microenvironmental heterogeneity may buffer *W. acuminata* from intense competition with *P. aidoides* in certain microsites (Melbourne et al. 2007).

Both grasses showed neutral or positive relationships between performance measures and their relative frequency in mixture. Combined with insensitivity to interspecific competition, neutral or positive density dependence may underlie the success of these species as invaders in this system. High propagule pressure may further contribute to their successful invasion (Holle & Simberloff 2005) through production of large quantities of readily germinable seed compared to native species in this system (Erickson et al. unpublished data; Lai et al. 2015). Neither *P. airoides* nor *A. cupaniana* are associated with disturbed conditions, unlike many other non-native annual grasses in this system (Lai et al. 2015). Despite being relatively abundant, both species are positively associated with native species richness and are not associated with elevated soil P (indicative of anthropogenic eutrophication in this system (Lai et al. 2015; Dwyer et al. 2015)), suggesting that factors other than P-enrichment may contribute to their persistence and ubiquitous distribution in predominantly native species-rich communities.

Conclusions

This study presents evidence of a native species benefiting from interactions with a non-native “benefactor” species. Positive interactions of this nature are seldom documented, despite their potential prevalence in invaded plant communities. The results of this study imply that under certain conditions, these interactions may promote stable coexistence between native and non-native species in plant communities.

Caution should be exercised, however, when attempting to relate local-scale positive and neutral pairwise interactions to effects on whole communities. The long-term trajectory of positive interactions and their implications for community structure are likely complex and depend on factors occurring over larger spatial and temporal scales than were measured in this study. In particular, it has been suggested that invasive plants may promote extinction in native plant communities not by competitive exclusion, but by reducing the size of native refugia and disrupting native metapopulation connectivity, processes which may occur over long timescales and be masked by current trends of native persistence (Gilbert & Levine 2013). Small-scale microsite conditions may also differentially favour certain species and alter the strength of interactions between native and non-native species. While two-species mixtures certainly occur naturally in this plant community, they do not always interact in isolation. Although the facilitative effect was strong across the beneficiary species' abundances in this study, temporal environmental heterogeneity could alter these dynamics. Intra- and interannual variation in rainfall can affect the type and strength of interactions in herbaceous plant communities through changes in species relative and absolute abundances (Pitt & Heady 1978; Hobbs & Mooney 1991) and phenologies (Quevedo-Robledo et al. 2010). Additionally, the frequency and magnitude of species interactions, as well as the performance measures affected, may change with environmental stress in complex ways (Tielborger & Kadmon 2000). The strength of positive interactions is generally predicted to be greatest under stressful environmental conditions (Brooker & Callaghan 1998; Callaway 2002; He 2013). If interactions between these native and non-native species are mediated by environmental stress, their outcome may ultimately depend on whether the stress is resource-based (i.e. water stress) or non-resource based (i.e. temperature stress; Maestre et al. 2009). Clearly, further experimentation is required to assess the prevalence and contingencies of positive interactions as a mechanism promoting the coexistence of native and non-native species in invaded communities.

These findings underscore the need for approaches to understanding invaded plant communities that are more inclusive of variable species interactions and the ways they may respond to further environmental change. Recently, non-native dominance has been highlighted as a better option than species richness for assessing the extent and condition of invaded plant communities (Seabloom et al. 2013). Our results suggest that even the relative abundances of non-native species may not accurately predict their impact on native species or the function of communities post-invasion. The impacts of invasion cannot be easily predicted or generalized, even when comparing the impacts of very similar non-native species.

Fig 4.1 A natural mixture of native forb *W. acuminata* and senescent non-native annual grass *A. cupaniana* at Bendering Reserve. Photo: author's own.

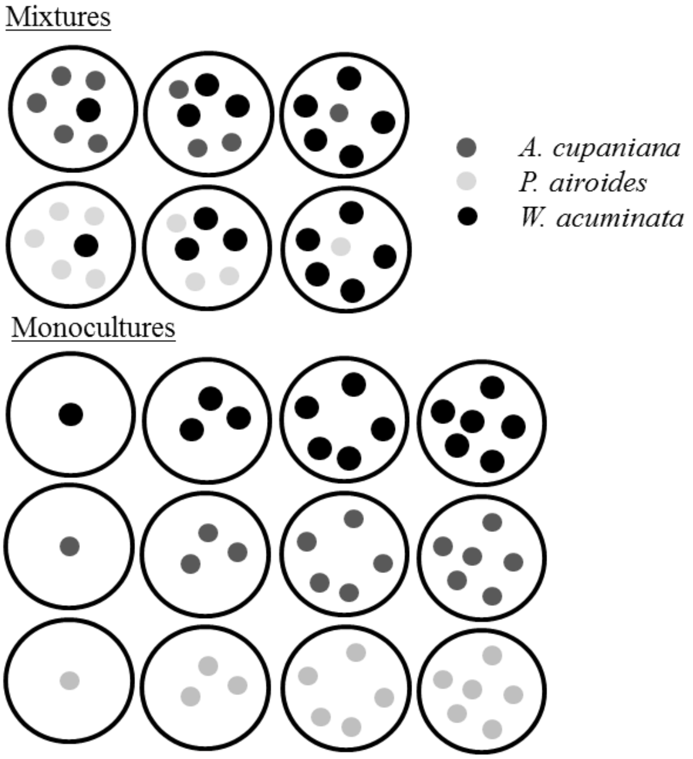

Fig 4.2 Diagram of growth chamber experimental design, where each circle represents a treatment combing the relative frequency and identity of each component species (coloured dots) in mixture and monoculture. Each dot corresponds to 10 individuals of the designated species.

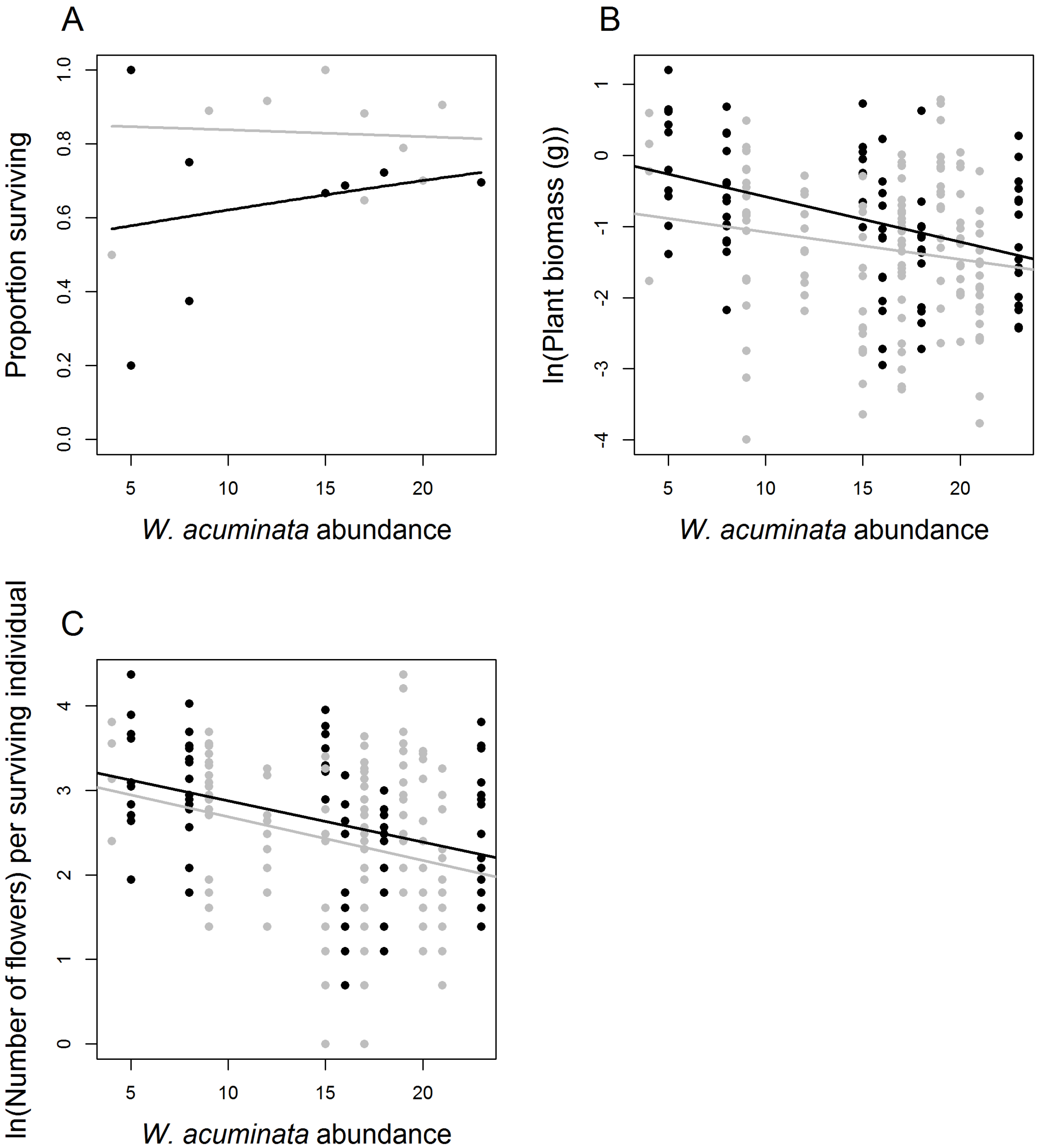

Fig 4.3 *W. acuminata* proportion of individuals surviving (A), aboveground biomass per individual (B), and flower count per plant (C) at Bendering Reserve by conspecific abundance (x-axis), growing in the presence of *A. cupaniana* (grey) or among conspecifics only (black).

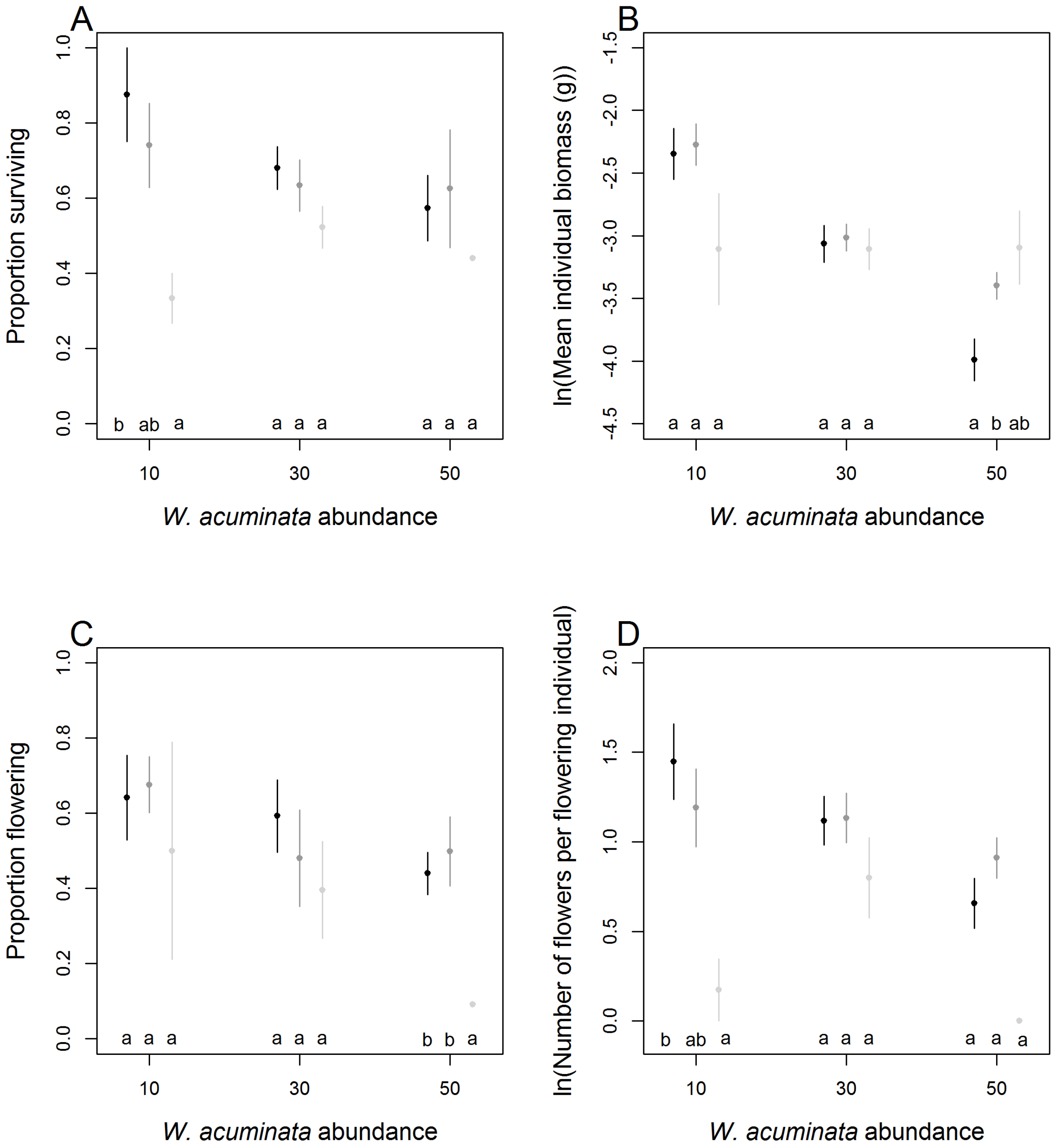

Fig 4.4 *W. acuminata* (A) proportion of individuals surviving, (B) aboveground biomass per plant, (C) proportion of surviving individuals flowering, and (D) flower count per flowering individual by *W. acuminata* abundance category (10, 30, or 50 individuals) in monoculture (black), in mixture with *A. cupaniana* (gray), and in mixture with *P. airoides* (light gray): Letters denote significant differences among all species combinations within a given abundance category (x-axis).

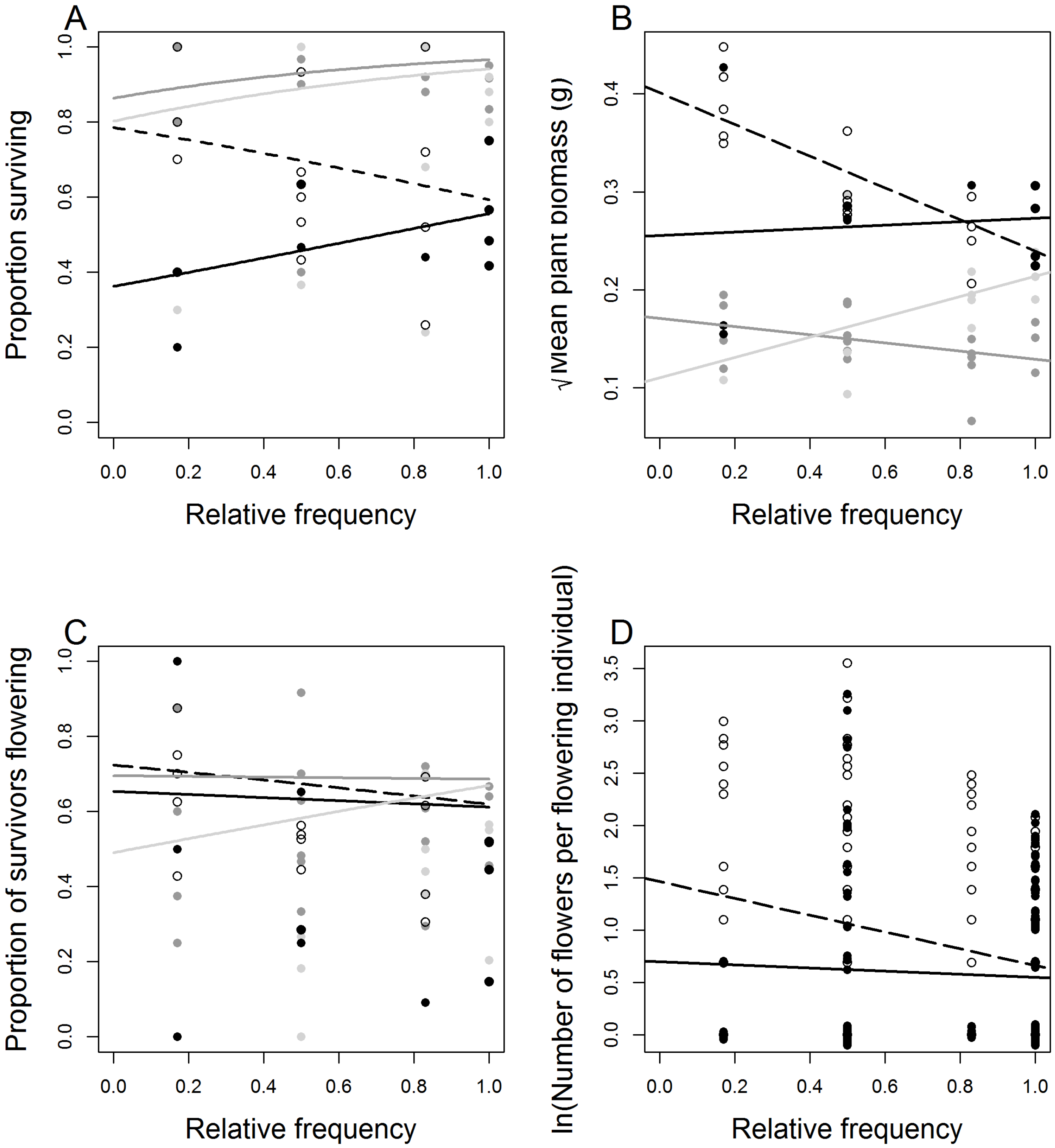

Fig 4.5 Species performance measures of (A) proportion of individuals surviving, (B) mean biomass per individual, (C) proportion of survivors flowering, and (D) flower count for flowering *W. acuminata* individuals. Species responses are plotted by their relative frequencies in a community of 60 individuals, where *W. acuminata* (with *A. cupaniana*) = black dashed/open point, *W. acuminata* (with *P. airoides*) = black solid, *A. cupaniana* (with. *W. acuminata*) = gray, and *P. airoides* (with *W. acuminata*) = light gray. Both lines for *W. acuminata* share the same data points at relative frequency= 1.0.

Table 4.1 Treatment description for field experiment. The first column specifies whether the community (quadrat) was a 2-species mixture or a monoculture, the second and third column specifies species' abundances in each quadrat categorized by either high or low *W. acuminata* density, and the fourth column lists the number of replicates for each community type x *W. acuminata* abundance combination.

Community type	**Number of each species**		**n**
	W. acuminata	***A. cupaniana***	
W. acuminata + *A. cupaniana*	Low (10±5) High (20±5)	120-180 120-180	5 5
W. acuminata monoculture	Low (10±5) High (20±5)	- -	4 4

Table 4.2 Treatment description for growth chamber experiment. The first column specifies whether the community (pot) was a 2-species mixture or a monoculture, followed by columns specifying species' relative frequencies by the ratio of abundances in each community and the number of replicates (n) for each community type x relative frequency combination.

Community type	**Abundance of each species**			**n**
	W. acuminata	***A. cupaniana***	***P. airoides***	
W. acuminata + *A. cupaniana*	10 30 50	50 30 10	- - -	5 6 4
W. acuminata + *P. airoides*	10 30 50	- - -	50 30 10	3 3 1
W. acuminata monoculture	60 50 30 10	- - - -	- - - -	4 3 5 4
A. cupaniana monoculture	- - - -	60 50 30 10	- - - -	3 3 3 4
P. airoides monoculture	- - - -	- - - -	60 50 30 10	NA 3 4 7

Table 4.3 Coefficients and (SEs) from mixed-effects models of *W. acuminata* performance (proportion of individuals surviving, aboveground individual biomass, and flower count per surviving individual) in the field when growing with or without *A. cupaniana*. Dashes indicate no random effects included in model. Asterisks denote level of significance (*: p≤0.05, **: p<0.01, ***: p<0.001).

	Response of *W. acuminata*		
Fixed effects:	Proportion individuals surviving	ln(Individual biomass (g))	ln(Flower count per surviving individual)
Intercept (Monoculture)	0.38 (0.52)	-0.07 (0.34)	3.41 (0.27)***
A. cupaniana present	0.88 (0.34)*	-0.38 (0.25)	-0.17 (0.20)
Conspecific density	0.02 (0.03)	-0.06 (0.02)*	-0.05 (0.02)**
Random effects (variance estimates):			
Among plot	0.05	0.20	0.11
Within plot	NA	0.75	0.41

Table 4.4 Coefficients and (SEs) from mixed effects models of *W. acuminata* performance (proportion of individuals surviving, biomass per individual, proportion flowering, and flower count per flowering individual) in growth chamber experiment when growing with or without *A. cupaniana* or *P. airoides*. Models are presented for low, medium, or high *W. acuminata* abundance (10, 30, and 50 *W. acuminata* individuals respectively). Dashes indicate non-significant interaction terms (additive model). Asterisks denote level of significance (*: p≤0.05, **: p<0.01, ***: p<0.001).

	Response of *W. acuminata*			
Fixed effects	**Proportion individuals surviving**	**Ln(Individual biomass (g))**	**Proportion individuals flowering**	**Flower count per flowering individual**
10 *W. acuminata*				
Intercept (monoculture)	2.54 (0.94)**	-2.35 (0.19) ***	0.38 (0.36)	1.55 (0.21)***
A. cupaniana present	-1.27 (1.07)	0.07 (0.26)	0.35 (0.50)	-0.18 (0.28)
P.airoides present	-3.34 (1.23)**	-0.76 (0.48)	-0.38 (0.79)	-1.51 (0.64)*
Random effects (variance estimates):				
Among pot	1.18	<0.0001	<0.0001	<0.0001
Within pot	NA	1.17	NA	0.61
30 *W. acuminata*				
Intercept (monoculture)	0.79 (0.27)**	-3.06 (0.14)***	0.36 (0.29)	1.25 (0.22)***
A. cupaniana present	-0.20 (0.36)	0.05 (0.18)	-0.49 (0.37)	-0.01 (0.29)
P. airoides present	-0.69 (0.43)	-0.04 (0.22)	-0.65 (0.46)	-0.16 (0.38)
Random effects (variances estimates):				
Among pot	0.19	<0.0001	0.12	0.12
Within pot	NA	1.42	NA	0.61
50 *W. acuminata*				
Intercept (monoculture)	0.31 (0.76)	-3.98 (0.20)***	-0.29 (0.27)	0.81 (0.20)***
A. cupaniana present	0.62 (1.03)	0.65 (0.27)	0.12 (0.36)	0.23 (0.26)
P.airoides present	-0.56 (1.52)	0.89 (0.43)	-2.04 (0.84)*	-0.95 (0.75)
Random effects (variances estimates):				
Among pot	1.65	0.06	0.08	0.23
Within pot	NA	1.80	NA	0.05

Table 4.5 Coefficients and (SEs) from mixed effects models of focal species performance (proportion surviving, mean individual biomass, proportion flowering, and number of flowers for flowering *W. acuminata*) in the growth chamber experiment by relative frequency (ranging from 0.18 in 2-species mixture to 1.0 in monoculture). Asterisks denote level of significance (*: p≤0.05, **: p<0.01, ***: p<0.001).

Response variable:	**Fixed effects**		**Random effects (variance estimates):**	
	Intercept	**Relative frequency**	**Among pot**	**Within pot**
W. acuminata* (with *A. cupaniana):				
Proportion surviving	1.29 (0.60)*	-0.92 (0.86)	1.04	-
ln(biomass per individual)	0.40 (0.02)***	-0.16 (0.03)***	0.001	0.0002
Proportion flowering	0.66(039)	-1.10 (0.52)*	0.18	-
ln(Flower count)	1.67 (0.21)***	-0.93 (0.30) **	0.05	0.71
W. acuminata (*with *P. airoides):				
Proportion surviving	-0.57(0.43)	0.79(0.53)	0.12	-
ln(biomass per individual)	0.26 (0.05)***	0.02 (0.07)	0.005	0.0009
Proportion flowering	1.02 (1.03)	-3.4 (1.93)	0.46	-
Ln(Flower count)	0.98 (0.45)*	-0.34 (0.55)	0.08	0.65
***A. cupaniana* (with *W.acuminata*):**				
Proportion surviving	1.84(1.08)	1.48(1.56)	2.88	-
Sqrt(mean biomass per individual)	0.17(0.02)***	-0.04(0.02)	0.0009	0.0001
Proportion flowering	0.24(0.43)	-0.04(0.59)	0.27	-
***P. airoides* (with *W. acuminata*):**				
Proportion surviving	1.40(2.65)	1.37 (2.65)	7.12	-
Sqrt(mean biomass per individual)	0.11 (0.05)*	0.10 (0.63)	0.0025	0.0004
Proportion flowering	-2.87 (1.10)**	2.98 (1.30)*	0.39	-

Chapter 5: The contribution of interactions to community structure in novel and original annual plant assemblages

Introduction

Human-aided introductions of non-native species are an increasingly common component of environmental change in many ecosystems (Vitousek et al. 1997; Mack et al. 2000). In some cases, these introductions have been followed by rapid spread and establishment of non-native species in recipient communities. As a consequence of these invasions, many plant communities are forming that are composed of mixtures of both native and non-native species, and have no historical counterpart (Hobbs et al. 2006). Describing the ecological significance of these novel communities is an important task in modern ecology (Sax et al. 2007). In particular, where intervention techniques are infeasible or where invasions do not clearly warrant intervention, it is critical to quantify whether and how these invaded communities function differently from the original communities they are replacing (Hobbs et al. 2009).

The literature on plant invasions is replete with accounts of non-native species displacing natives at local scales, often invoking competitive exclusion as the mechanism (e.g. Brown & Rice 2000; Bakkar & Wilson 2001). However, a reduction in native diversity or abundance due to competition from non-natives is only one potential outcome of invasion (MacDougall et al. 2009). Neutral or even positive effects of invaders on resident communities may be more common than previously appreciated (Rodriguez 2006; Ricciardi & Cohen 2007; Davis et al. 2011). Depending on the relative niche and fitness differences among native residents and non-native invaders, non-native species can invade and coexist with native residents, with no associated negative effect on native species richness (Levine & D’Antonio 1999; MacDougal et al. 2009). This concept is supported by the observation that, contrary to predictions made by early invasion theories, areas of high native species richness often also contain the highest non-native species richness (Stohlgren et al. 1999) due to ecological factors that spatially covary with diversity (Levine & D’Antonio 1999), high propagule pressure (Levine 2000), environmental heterogeneity (Davies et al. 2005), and in some cases positive interactions (Bruno et al. 2003).

Over small scales, coexistence among native and non-native species may be determined by the net results of interactions among individuals. Specifically, the extent to which species limit themselves, relative to how they limit co-occurring species, may determine whether species are likely to coexist locally (Chesson 2000). Intraspecific limitation can be achieved through a variety of processes such as species-specific climatic optima, resource competition, predation, and pathogen attack (Chesson 2000; Chesson & Kuang 2008). These processes are collectively termed “stabilizing mechanisms” because species limit themselves when abundant, but can increase from rarity (Chesson 2000). Where stabilizing mechanisms are absent or small, fitness inequalities among species become the main predictor of local coexistence (Chesson 2000). Where species’ fitness inequalities are sufficiently large to overcome stabilization, the best competitor will eventually dominate the community (Chesson 2000; Adler et al. 2007). One approach for quantifying the net results of these interactions is by directly comparing the relative impacts of intra-and interspecific competition on the performance of co-occurring species (Adler et al. 2007). Quantifying these relative differences can expose the processes which promote or prevent coexistence among native and non-native species.

In addition to determining local coexistence, biotic interactions among co-occurring species can influence the overall productivity of communities. Productivity, e.g. biomass production over a discrete time interval, is often measured as a proxy for plant community functioning (Tilman 2001; Knapp et al. 2014). Differences in total productivity among communities may reflect underlying differences in diversity, including species or functional group composition (Hooper & Dukes 2004). A recent meta-analysis of empirical studies (Cardinale et al. 2011) showed that mixtures tend to yield greater biomass than predicted based on biomass of component species in monoculture. This over-yielding is attributed to the net result of processes operating in mixture that do not operate in species’ monocultures, termed “diversity effects”, which include over-yielding driven by particular species (selection effects (Loreau & Hector 2001), dominance effects or trait-depdendent complementarity (Fox 2005)), and the residual driven by all species simultaneously (complementarity effect (Loreau & Hector 2001)). Selection effects are indicative of particular species driving community over-yielding (Loreau & Hector 2001), while dominance effects provide information about the extent to which these species-specific responses occur at the expense of other co-occurring species (dominance) or not (trait-dependent complementarity; Fox 2005). By contrast, complementarity among species has been suggested as an indicator of niche partitioning among species which confers species an advantage when faced with interspecific competition in mixtures as opposed to intraspecific competition in monocultures (Loreau & Hector 2001). While selection, dominance, and complementarity are not in themselves coexistence mechanisms (see exchange between Carroll et al. (2011) and Loreau et al. (2012)), they indicate differences in functioning among communities (Hooper & Dukes 2004; Cardinale et al. 2007). Much of this evidence comes from micro- and mesocosm experiments, but investigation of diversity effects in naturally-assembled communities has been minimal to date, despite the obvious potential to reveal important insights. For example, investigation of diversity effects is likely to reveal whether invaded communities function differently from original communities due to changes in species composition.

We conducted a field experiment to examine the role that intra- and interspecific interactions play in the local coexistence and productivity of species in extensively invaded annual plant communities where non-native species do not appear to be reducing native species richness. In addition to measuring the importance of interactions to species-level productivity, we explored differences in community-level productivity between novel communities (i.e. native and non-native species) and original reference communities (i.e. purely native species). Novel and original communities were considered over a variety of spatial scales in order to holistically evaluate the processes underlying their formation. This study was guided by the following questions:

1. Does the relative importance of intra- and inter-specific competition among common species shift according to origin (i.e. non-native vs. native)?
2. What is the relative importance of local competitive dynamics, local environmental gradients (P and water availability) and interannual climate variation in determining individual plant productivity?
3. Does the relative importance of diversity effects (e.g. complementarity, selection, and dominance effects) differ between novel and original communities?

Methods

Study system

Experimental studies were undertaken during the 2012 and 2013 winter-spring growing seasons at Bendering Nature Reserve (32 °23’ 7.88” S, 118 °23’5.66”E) and Kunjin Reserve (32 °21’19.31”S, 117 °45’42.32”E) in Western Australia. The reserves are surrounded by agricultural fields and paddocks and had not been grazed for at least 40 years prior to the study (Prober & Wiehl 2011). Neither reserve has been burned during the past 40 years, and their earlier fire histories are unknown.

My study system is the diverse annual understory communities of formerly common York gum (*Eucalyptus loxophleba* subsp. *loxophleba*) and jam (*Acacia acuminata*) woodlands, often referred to as York gum-jam woodlands. The canopy of York gum-jam woodlands is generally sparse, and understories typically support relatively dense assemblages of annual and perennial forbs.

Understory annuals contribute substantially to the floral species richness of these woodlands, and are abundant during the winter-spring rainy season which lasts from June to October.

Disturbance associated with land clearing and agricultural intensification continues to degrade remaining patches of York gum-jam woodlands, particularly due to invasion of non-native annual grasses, legumes and forbs (Hobbs & Atkins 1988; Yates et al. 2000; Dwyer et al. 2015). Currently, York gum-jam annual communities range in composition from completely non-native-dominated to predominantly native (Dwyer et al. 2015), presenting an ideal system for studying interactions in novel species mixtures given their close proximity to native-dominated reference mixtures.

A suite of non-native annuals in this system are associated with areas of soil eutrophication adjacent to agricultural fields where they exploit elevated resources (particularly phosphorus) and often competitively exclude natives (Hobbs & Yates 1988; Standish et al. 2008). However, some non-native species have invaded these woodlands in the absence of eutrophication and other forms of ongoing disturbance (Prober & Wiehl 2011; Dwyer et al. 2015). These non-native annuals were presumably introduced to the region during periods of agricultural development in the late 19th and early 20th century (Burvill 1979), but are currently not associated with reduced community diversity (Lai et al. 2015) and do not appear to be on the trajectory towards community dominance. It is the function of these relatively "stable" mixtures of native and non-native annuals that I investigate in this study. Here, I focus on non-historical species composition as a key aspect of ecosystem novelty without confounding effects of nutrient addition on species performance. However, in general, novel plant communities (including many of those found in York gum-jam woodlands) fall along gradients of departure from historical abiotic and biotic conditions, which are seldom independent from one another (Hobbs et al. 2009).

Individual plant performance at interaction neighbourhood scale

To gauge the relative impacts of inter- versus intraspecific competition on native and non-native species, we examined individual plant performance of three focal species at the neighbourhood scale: *Aira cupaniana* (Poaceae, non-native), *Trachymene cyanopetala* (Araliaceae, native), and *Waitzia acuminata* (Asteraceae, native). These species were chosen due to their widespread occurrence throughout the York gum-jam woodland range and the fact that they regularly occur in mixture with other species at small spatial scales across a variety of microenvironments. These focal species were located growing within mixtures of natives or non-natives and their performance was compared to single plants growing without competitors in their interaction neighbourhood. In

August 2013, 35 30 x 30 cm quadrats were marked out per focal species in York gum-jam woodlands at Kunjin and Bendering Reserves. *A. cupaniana* quadrats were located at Kunjin Reserve only. In each quadrat, we weeded out non-focal species according to competitive background treatment type (native or non-native), recorded the identity and abundance of non-focals, and selected up to three individuals of the focal species which were designated with coloured string. We then quantified the interaction neighbourhood of each of these focal plants by placing a 10 cm diameter metal ring at ground level around each focal individual, and recording the identity and abundance of all plants rooted within the ring.

We then collected seeds from each focal plant when ripened as a measure of reproductive output. As not all seed heads on any given *W. acuminata* plant were mature at the time of harvest, we estimated total seed production per plant of this species by multiplying the total number of seed heads by the number of seeds from one seed head for each plant. Overhead tree canopy cover was then recorded for each quadrat to include as an environmental covariate in analyses.

Individual performance at quadrat scale

This field component examined differences in productivity of individuals and entire communities in novel and original annual assemblages. The study was conducted at Bendering Reserve in 2012 and 2013 and spanned a below-average and above-average rainfall year (total annual rainfall 237.8 mm in 2012, 444.2 mm in 2013, compared to a 373 mm 104-year average; Station ID 10536, BOM 2014). I examined the performance of four common annual plant species native to York gum-jam woodlands: *Gonocarpus nodulosus* (Haloragaceae), *Rhodanthe manglesii* (Asteraceae), *Trachymene* sp. (Araliaceae), and *W. acuminata* (Asteraceae) and two non-native species commonly found in areas of high native diversity rather than in non-native-dominated communities: *Hypochaeris glabra* (Asteraceae) and *A. cupaniana* (Poaceae). Focal species were all common in the interior of Bendering Reserve in areas that had not experienced obvious anthropogenic modification. There are three common species of *Trachymene* at Bendering Reserve (*T. cyanopetala*, *T. ornata*, and *T. pilosa*). Though as flowering adults these species are distinguishable, they are difficult to tell apart as seedlings. As experimental plots were set up at the seedling stage, it was not possible to uniformly select one of these three species. As a result, I used data from plots containing only *T. pilosa* in analyses, as replication was highest among plots containing this species. However, analyses performed using all data from plots containing any of the three *Trachymene* species are included as supplementary material to this chapter for comparison (Appendices 5.4 & 5.5) and yielded similar results to analyses using only *T. pilosa* data.

In early winter, communities (n_{2012}=91, n_{2013}=80) were marked out across five experimental blocks. All blocks were at least 100 m apart and all were within the interior of the reserve. Communities were located using 30 cm x 30 cm quadrats. All quadrats had a 10 cm perimeter buffer, which was thinned (as per the treatment quadrat) and weeded regularly to eliminate edge effects within the sampling area. To assess differences in species performance in original and novel annual plant assemblages in each block, quadrats were placed in areas that naturally contained seedlings of a mixture of the four focal native species (original), a mixture of two native and two non-native species (novel), or a monoculture of one of the six focal species (Appendix 5.1). Each species combination, including monoculture, was present in at least four of the five blocks.

Seedling density was targeted at 80 individuals per plot in monocultures of all species in 2012. Given their distinct growth form compared to the other annuals in this study (slender annual grass as opposed to annual herb), monoculture densities for *A. cupaniana* were targeted at 80 10-plant "patches" per plot. Stem densities for all species were obtained by thinning individuals when target densities were occasionally exceeded and by weeding non-focal species. In 2013, densities of *G. nodulosus* and *W. acuminata* were markedly lower than in 2012 and lower than the other focal species. Thus, calculating diversity effects was not feasible in 2013, as all focal species were not present in equivalent relative abundances without extensive thinning of the more abundant species, which would have reduced my ability to detect the effects of natural levels of competition.

Abundances were recorded bi-weekly for each species in every quadrat from the beginning of the experiment until aboveground biomass harvesting for calculations of species monoculture and mixture yields began (September 2012 and October 2013). Because species phenologies varied throughout the growing season, a staggered biomass harvest approach was used in both years where individual plant aboveground biomass was removed as its seeds matured. Approximately 10-20 individuals per species per quadrat were removed throughout each species' maturation period each year to eliminate harvesting bias towards early-maturing individuals. Cover analyses of quadrat photos indicated that effects of plant removal on shading of remaining plants were negligible (data not shown). In addition, plants were only removed after seeds were fully mature and collected (at the time of natural dispersal) and vegetative tissues were on the verge of senescence and thus would have had negligible impact on subsequent belowground processes, regardless of removal. In some instances for *H. glabra*, *R. manglesii*, and *W. acuminata*, fine mesh bags were tied around flower heads when seeds were nearly ripe to prevent loss of seeds due to sudden wind dispersal. Biomass for each plant was stored in an envelope, dried at 60°C for one week, and then weighed.

We collected soil data for each quadrat to determine the relative influence of important abiotic gradients on plant performance in mixture and monoculture. I chose to use soil moisture (10 cm probe, TDR method) and extractable phosphorus (P, Colwell method) in my analyses, as they are two of the most important factors constraining annual performance in this system (Prober & Wiehl 2011; Dwyer et al. 2015).

Community performance at the quadrat scale

Diversity effects on production in original and novel assemblages in 2012 were calculated by comparing deviations in species biomass yields when grown in mixture versus monocultures using the quadrats at Bendering Reserve described in the preceding section. I adopted Loreau & Hector's additive partitioning method (2001) based on the Price equation in evolutionary genetics (Price 1995), as well as Fox's modification (2005) of the selection effects calculated by this method. The additive partitioning method separates the simultaneous contributions of complementarity and selection effects to departures in observed yields of species in mixture from that expected based on their monoculture yields (weighted by their relative abundances in mixture). Positive complementarity occurs when, on average, all species increase yields in mixture, indicative of niche partitioning or positive interactions. Positive selection effects occur when species with particular traits, e.g. the greatest biomass per individual, are the greatest contributors to over-yielding, indicated by positive covariance between species monoculture yields and changes in relative yields in mixture. I then calculated dominance effects and trait-dependent complementarity, which are surrogates for the selection effect (Fox 2005) that determine whether increases in species' yields in mixture are at the expense of other species (Fox 2005). Diversity effects were calculated as follows:

$$\Delta Y = Y_O - Y_E = \Sigma RY_{Oi}M_i - \Sigma RY_{Ei}M_i$$
$$= N\Delta\overline{RY}\,\overline{M} + N\mathrm{cov}(\Delta RY, M)$$
$$= N\Delta\overline{RY}\,\overline{M} + N\mathrm{cov}(M, RYo - RYo/RYTo) + N\mathrm{cov}(M, RYo/RYTo - RY_E)$$

Where ΔY equals the deviation of expected total yield (Y_E) from observed total yield of mixture (Y_O; or the total biomass of the mixture), and N equals the number of species in the mixture. M_i is the monoculture yield of species i (total biomass of the monoculture), and the expected relative yield of species i in mixture (RY_{Ei}) simply equals the (unitless) proportion of total individuals in the mixture that species i represents. The expected biomass yield of species i in mixture (Y_{Ei}) is thus

$RY_{Ei}M_{i.}$, or the proportion of their total monoculture biomass expected in mixture based on their relative abundance in mixture. The observed relative yield of species i (RY_{Oi}) is the species observed biomass in mixture (Y_{oi}) divided by its total monoculture biomass, or Y_{oi}/M_i. Because a subset of each species' biomass was harvested in each plot, total biomass per species per plot was estimated by multiplying the mean individual biomass by the total number of individuals of that species in a plot. Because *H. glabra* sometimes occurred at lower densities than the other focal species, its expected relative yield was calculated with reference to its own monoculture density. All other calculations were as described above.

The complementarity effect of a mixture is calculated as the number of species multiplied by the average deviation in all species relative yields ($\overline{RY_O\text{-}RY_E}$, or $\overline{\Delta RY}$) multiplied by the average of all species' monoculture yields ($\overline{M}$). The selection effect is calculated as number of species multiplied by the covariance between species' monoculture yields and their deviation in relative yield, or N(covΔRY, M). The dominance effect, which accounts for changes in certain species' relative yields that occur at the expense of others, is calculated as Ncov(M, RYo/RYTo – RY_E), where RYTo equals the sum of observed relative yields for all species in a mixture. By contrast, trait-dependent complementarity, calculated as Ncov(M, RYo – RYo/RYTo), measures changes in certain species relative yields that do not occur at the expense of other species yields.

Statistical analysis

All statistical analyses were conducted using R statistical software (v 3.1.2., R Development Core Team 2014). Three quadrats in 2012 (one *A. cupaniana* monoculture, two novel mixtures), and two novel mixtures in 2013 were excluded from analyses due to species misidentification, high mortality, or animal damage.

Species' seed production responses to neighbourhood type (native or non-native), neighbour density, and site (Kunjin or Bendering) in interaction neighbourhoods were estimated using generalised linear mixed effects models with Poisson errors and log link function (package lme4, Bates et al. 2014). To simultaneously assess the influence of a local environmental gradient on species fecundity, overhead woody canopy cover was included as a quadrat-scale covariate. Target plant nested within quadrat was specified as a random effect to account for over-dispersion (Elston et al. 2001) and spatial dependence of observations. Where significant relationships between seed set and non-native neighbourhood were found, I investigated whether the identity of the non-native species further explained variation in focal species seed set in non-native neighbourhoods, as non-native species in this system are diverse in their impacts on resident species (Lai et al. 2015; Ch. 3 of this thesis). I scored whether each observation had a robust non-native annual (high-biomass non-native annuals associated with disturbed conditions, Prober & Wiehl 2011; Lai et al. 2015) species present in its neighbourhood as a binary value, and modelled the focal species ln-transformed seed count in non-native neighbourhoods using a linear mixed model with random effect of quadrat.

Individual plant biomass was assessed separately for each species. I used linear mixed effects models (package nlme, Pinheiro et al. 2014) to assess differences in ln-transformed biomass values in the different community types (novel or original where appropriate, with monoculture as reference). *W. acuminata*, *G. nodulosus*, and *R. manglesii* were modelled using data from all original mixture plots regardless of the *Trachymene* species present. To simultaneously assess the influence of local abiotic gradients, I also included fixed effects of soil moisture and soil P content. Quadrat nested within block was specified as a random effect in all individual plant biomass models to account for spatial nesting of observations. To explore whether biomass of each species differed between 2012 and 2013, I utilised monoculture data for species whose relative abundances remained similar between years to avoid confounding density effects on biomass values. For this analysis I used linear mixed effects models with random effects for quadrat.

To assess mixture yield deviations from expected yields and diversity effects, I used one-sample t-tests to test the null expectation of no deviation and no diversity effects (H_o: $\mu=0$) for each mixture type in 2012. Separate models were run for each mixture type, and block was specified as a random effect.

We followed these analyses with examinations of species contributions to mixture biomass deviations. Specifically, I used mixed effects models for each mixture type in 2012 to test for differences among species in their deviations of observed from expected relative yields, where block was specified as a random effect. Because species showed unequal variances in their deviation values, I used weighted variance functions in each model that allowed variances to differ among species (varIdent function within lme models; Pinheiro & Bates 2000). These models were followed by simultaneous *post-hoc* contrasts (package multcomp, Hothorn et al. 2008) testing whether each species deviation in was significantly different from zero.

Results

Individual fecundity at neighbourhood scale

Of the three focal species in this component of the field experiment, native forb *W. acuminata* was the only species whose seed production was impacted by competition compared to single plants (mean(SE) seeds per individual: single plant= 2204.39 (557.71); native neighbourhood= 824.72 (90.20), p=0.05; non-native neighbourhood= 845.65 (112.26), p=0.02; Table 5.1). Within non-native neighbourhoods, the effect of presence or absence of robust non-native species was not significant. None of the focal species were impacted by neighbour abundance except *W. acuminata* (p=0.002; Table 5.1; Appendices 5.6 – 5.8).

T. cyanopetala seed production was not significantly related to any of the explanatory variables. For this species, seed production per individual was similar between single plants and those in either non-native or native neighbourhoods (mean (SE) seeds per individual: single plant= 69.07 (9.46), native neighbourhood= 48.85 (3.94), non-native neighbourhood= 77.89 (8.32); Table 5.1, Appendix 5.7).

For *A. cupaniana*, seed production declined with increasing canopy cover (p=0.01, Table 5.1, Appendix 5.6) but this was not impacted further by the composition of its neighbourhood (mean (SE) seeds per individual: single plant=92.17(29.46); native neighbourhood= 57.78 (7.98); non-native neighbourhood= 88.83 (13.38)).

Individual biomass at quadrat scale

Overall, variation in individual plant biomass between years was greater than variation due to compositional differences or microenvironmental variation within years (Fig 5.1).

Neither soil moisture nor P at the quadrat level were significant predictors of individual plant biomass in either year (Appendices 5.2 and 5.3). Extractable soil P ranged from < 2.00 – 16.00 mg/kg (mean: 4.22 ± 0.22 mg/kg) in 2012 and from < 2.00 - 13.00 mg/kg (mean: 4.01 ± 0.32 mg/kg) in 2013, typical of soils in York gum-jam woodland interiors (Dwyer et al. 2014). The fact that P was unrelated to productivity likely reflects my intentional focus on relatively undisturbed communities, whereas P-enriched soils tend to occur along reserve edges adjacent to fertilized cropland (Dwyer et al. 2014; 2015). Soil moisture ranged from 2.00 – 10.76% (mean: 4.06 ± 0.12%) in 2012 and from 2.67 – 8.67% (mean: 4.9±0.16%) in 2013.

H. glabra and *T. pilosa* were the only species whose mean individual plant biomass was affected by the quadrat-level community species composition (Appendices 5.2 and 5.3). In both years, *H. glabra* plants were significantly smaller when found in mixtures compared to monocultures (2012: p=0.04; 2013: p=0.04), and in 2012, *T. pilosa* plants were smaller in mixture than in monoculture (p=0.03)

Individual plant biomass of all focal species increased from 2012 to 2013 (Fig 5.1). For species whose relative abundances did not shift between years (*A. cupaniana, H. glabra*, *R. manglesii*, *T. pilosa),* comparisons of plant biomass in monocultures of equivalent densities between years revealed that the increase was statistically significant for *A. cupaniana* (year estimate (SE): 0.62 (0.21), p=0.008), *H. glabra* (year estimate (SE): 0.92(0.22), p<0.001), and *T. pilosa* (year estimate (SE):1.60(0.23),p<0.001).

Community productivity at the quadrat scale

On average, only original communities displayed significant diversity effects, though total community biomass did not exceed that which was predicted by component species biomasses in monoculture in 2012 (Table 5.2, Fig 5.2). When data were included for communities containing all *Trachymene* species, original community overyielding became significant (Appendix 5.4; p=0.05). In original communities, selection (p=0.008) and dominance effects (p=0.02) occurred rather than complementarity among species (Table 5.2, Appendix 5.4). Mixed effects models of selection and dominance effects revealed that neither were related to soil moisture or P (data not shown). In novel communities, neither differences between observed and expected yields nor the contributions of diversity effects to these differences were significantly different from zero (Table 5.2).

Given the apparent contribution of selection and dominance effects in original mixtures, I explored differences between observed and expected relative yields of component species in both mixture types (Fig 5.3, Table 5.3). *W. acuminata* over-yielded compared to other species in novel communities (p=0.02), and marginally significantly in original communities (p=0.055), though in analyses using data from all original mixtures this trend was strengthened (p=0.01; Appendix 5.5). By contrast, *H. glabra* under-yielded compared to other species in novel mixtures (Table 5.3, novel: p=0.0007). *Post-hoc* analyses revealed *W. acuminata* and *H. glabra* to be the only species with changes in relative yield significantly different from zero (*W. acuminata* novel: adjusted p=0.04, *H. glabra* : adjusted p<0.001).

Discussion

With a few exceptions, the effects of intra- versus interspecific competition seem to be fairly equivalent among the focal species in this study. The presence of competitors did not affect plant reproductive output at the neighbourhood scale except for *W. acuminata*, whose seed set was reduced in both non-native and native neighbourhoods. In terms of plant productivity, the effects of shifting between intra- and interspecific competition were negligible for most focal species except *H. glabra* and *W. acuminata*, which performed better in monoculture and in mixture, respectively. Species productivity was not further influenced by microenvironmental conditions at the local scale. Diversity effects calculated in 2012 ranged from negative to positive, but positive selection and dominance effects were found as opposed to complementarity among species in original communities. I describe these results and their implications for community structure in novel and original communities in detail below.

Individual fecundity at neighbourhood scale

Overall, I found little evidence of strong competition at the neighbourhood scale on focal species' total seed production, except for native *W. acuminata*, which was negatively impacted by both native and non-native neighbourhoods. I cannot make direct inferences about the relative strength of intra- vs interspecific competition for this species at this scale because I cannot disentangle the impacts of conspecific abundance from total neighbour abundance. Still, competition from both conspecific and heterospecific neighbours in both non-native and native communities clearly influences *W. acuminata* fitness in the field. These results align with previous experiments where congener *W. nitida* fitness was particularly susceptible to both intra- and interspecific competition at this scale (Ch 3 of this thesis).

Within non-native neighbourhoods, *W. acuminata* seed production was further unrelated to whether robust non-native annuals were present. This was somewhat surprising, given the observed effects of many of these species on *W. acuminata* survival, biomass, and overall native species richness in previous studies (Ch 3 of this thesis; Dwyer et al. 2014; 2015). Furthermore, non-native neighbourhoods (exploitative and non-exploitative non-natives, and conspecifics) and native competitors (including conspecifics) appeared to suppress *W. acuminata* individuals to a similar degree. Clearly, competitive effects cannot be generalized according to species origins, and for some species, the distinction between their performance in non-native and native assemblages may be trivial. In addition, these robust non-native annuals tend to competitively exclude native species under artificially P-enriched conditions, but may not be as competitive in the low-P areas which were the focus of this study (Dwyer et al. 2015; Lai et al. 2015).

Within Kunjin Reserve, non-native annual grass *A. cupaniana* produced fewer seeds in shadier plots, but this was not affected further by the composition or abundance of potential competitors within neighbourhoods. This suggests that for *A. cupaniana*, microenvironmental variation may have a larger impact on fecundity than biotic interactions at this reserve.

Individual performance at quadrat scale

For aboveground biomass at the individual plant level, there was no significant effect of species composition or microenvironment for most species. The lack of response to shifting between intra- and interspecific competition for most species aligns with studies in other annual plant communities, where only highly competitive species are likely to experience substantial negative competition in areas of conspecific aggregation (Goldberg & Barton 1992; Wassmuth et al. 2009). Some minimal thinning at the beginning of the growing season (of non-focal species and of focal species when they exceeded target densities) may have weakened effects of competition. However, species continued to self-thin beyond the abundances prescribed by the experiment, suggesting that we did not thin them beyond the point where competition would have been observable.

An exception was *T. pilosa*, individuals of which were significantly smaller in mixture than in monoculture in 2012. It is possible that the combined effects of greater water availability and lower densities of competitors *W. acuminata* and *G. nodulosus* alleviated the environmental stress and competitive suppression experienced by *T. pilosa* in mixture relative to monoculture in the more environmentally favourable year. The other notable exception was for *H. glabra*, individuals of which were significantly smaller in size when found in mixed communities compared to monocultures in both years. *H. glabra* is a successful invader with a widespread distribution in York gum-jam woodlands (Western Australian Herbarium 2014), though its competitive impacts were minimal in this study. This species is also widely distributed in North America, with studies also showing low competitive impacts between *H. glabra* and natives within its North American introduced range (Cal-IPC 2005; USDA 2014). In a growth chamber study (Ch 3 of this thesis), *H. glabra* individuals were also found to be smaller in mixture compared to monoculture, but only when the mixture contained the highly competitive non-native grass *Bromus madritensis*. Here, it is possible that combined effects of competition from native *W. acuminata*, *G. nodulosus*, and *A. cupaniana* resulted in significantly lower biomass per individual for *H. glabra* in mixture than in monoculture. The fact that *H. glabra* aboveground biomass was unrelated to microenvironmental conditions suggests that both competition and other factors may come into play in determining its fitness in natural communities. For example, *H. glabra* produces large quantities of non-dormant seeds with high germination rates compared to the native species in this study (Erickson et al. unpublished data), which likely aids in its ability to proliferate and may compensate for the weak competitive ability observed in this study.

Interannual rainfall patterns produced a larger response in species' productivities than local microenvironmental conditions within years. The total amount and duration of the winter-spring growing season rainfall increased substantially between 2012 and 2013, contributing to an increase in the average sizes of individuals to varying degrees among the focal species. In addition, differences in climate conditions between years translated not only to biomass increases, but may have shifted focal species absolute and relative abundances, as indicated by the results for *G. nodulosus* and *W. acuminata*. Interannual climate variation in semi-arid ecosystems plays a large role in regulating winter annual plant community structure (Pitt & Heady 1978; Venable 2007) that must complete seedling through adult life cycle phases within one discrete growing season each year. Winter annuals therefore display large degrees of intraspecific demographic and phenotypic variation among generations, depending on the timing and availability of resources in a given year (Fox et al. 2006; Venable 2007; Angert et al. 2007; Levine et al. 2008). Interannual climate variability is implicated in long-term patterns in winter annual plant population dynamics, whereby the timing and magnitude of growth differ among species through differential responses to favourable conditions (Chesson et al. 2004; Angert et al. 2009). In conjunction with spatial heterogeneity of resources, temporal environmental heterogeneity has been found to contribute to community structure in winter annual plant communities by mediating which species interact under specific conditions (Rees et al. 1996; Chesson et al. 2000; Chesson et al. 2004). In a previous study on York gum-jam woodland annuals, Dwyer et al. (2014) found that an increase in the amount of growing-season rainfall relative to the previous year led to substantial intraspecific variation in abundance (both absolute and relative) and an increase in community-level biomass. While *W. acuminata* individuals experienced the greatest size increase between 2012 and 2013 of all focal species, it is not possible to separate the contributions of reduced intraspecific competition (via naturally lower abundances) from increased soil moisture availability. For species whose abundances remained relatively constant between years (*A. cupaniana, H. glabra, Trachymene, R. manglesii*), all but *R. manglesii* experienced significant increases in mean plant biomass in monocultures of equal densities between years, indicating that increased water availability may have differentially driven changes in plant productivity between years. Thus, temporal climate variation may have been an important determinant of species productivities and community structure during the two-year span of this experiment, though these dynamics were not the initial focus of the study. Future research in this system should be directed towards investigating the influence of long-term climate variability on population dynamics and hence community structure.

Community performance at the quadrat scale

In 2012, original communities yielded greater biomass than was predicted by component species monoculture yields on average, although there was substantial variation within this trend. This over-yielding was unrelated to soil moisture or P, two of the most important factors constraining productivity in this plant community (Prober & Wiehl 2011; Dwyer et al. 2015), suggesting biotic interactions may have been an important underlying cause.

Selection and dominance effects were greater contributors to over-yielding in original communities than complementarity among species. Specifically, *W. acuminata* experienced greater increases in relative yield when released from intraspecific competition than any other species. These results align with my observations for this species at the neighbourhood scale, suggesting that *W. acuminata* performance (seed production and biomass) may be regulated, at least in part, by intraspecific competition. Mean plant biomass was greater in both mixture types than in monoculture in 2012, though these increases were not significant when considered across all quadrats and blocks (see preceding section). This suggests the responses of certain mixtures may have driven the mean tendency to over-yield. The species- and plot-level averaging required by the additive partitioning method may have obscured a substantial amount of variance among individual biomass values, which could explain the positive selection effects due to *W. acuminata* at the plot level in original mixtures, but a lack of signal at the individual level.

By contrast, *H. glabra* experienced significantly lower yields in mixture than in monoculture, in keeping with results at the individual plant level. Thus, although *W. acuminata* and *H. glabra* are the two most productive species in the novel communities and exhibited the strongest responses when shifting from intra- to interspecific neighbourhoods (i.e. strong positive and negative selection effects, respectively), the opposing directionality of their responses resulted in a zero net effect in novel communities. These artefacts of the additive partitioning method highlight the need to examine community responses into constituent species-specific responses when comparing overall functioning in two community types.

Conclusion

The performance of most species did not change with the composition of either the immediate or local neighbourhood, suggesting that other factors combine with competition to constrain species' abundances. Climate variation among years, for example, produced communities with very different relative abundances and sizes, and affected plant productivities more than microenvironmental variation within either year. Though I did not directly calculate species niche and relative fitness differences, the prevalence of weak or non-existent competitive interactions suggests that small differences among the majority of co-occurring species are sufficient to overcome any fitness differences and permit coexistence. The main exceptions were non-native and native forbs *H. glabra* and *W. acuminata*. Though *H. glabra* appears to benefit from intraspecific congregation relative to interspecific, other processes such as herbivory (pers. obs.) might limit its abundance in diverse communities where it has established and persisted. By contrast, *W. acuminata* was negatively affected by intraspecific competition at small scales, consistent with findings in other experimental studies that spatial aggregation reduces productivity in conspecific neighbourhoods for only the most productive species (Monzeglio & Stoll 2005; Vogt et al. 2010).

The finding of over-yielding in original but not novel mixtures was due to the inclusion of an ostensibly weak non-native competitor, *H. glabra*. This may reflect my intentional focus on novel communities in intact woodland areas that have retained high native species richness and are not characterized by obvious ongoing anthropogenic change. Had I chosen to examine novel communities in degraded woodland areas, for example where eutrophication has occurred, the composition and relative abundance of non-native species would have differed (Dwyer et al. 2014; 2015). Taller non-native annual grasses and forbs are the dominant invaders under these nutrient enriched conditions (Prober & Wiehl 2011) and they exclude native resident species mainly via strong competition for light (Dwyer et al. 2015). The most common non-natives in my study, by contrast, exert weaker effects on natives than those most commonly found in degraded communities within the same and similar reserves, and other annual plant systems (Pemadasa & Lovell 1974;Cal-IPC 2005; Chapter 3 and 4 of this thesis; Lai et al. 2015).

Overall, my results suggest that provided both the relative and cumulative differences between native and non-native species are small, some aspects of community function may be retained between original and novel plant communities, at least in the absence of extreme anthropogenic abiotic changes. The dynamics of invaded communities may be scale and context-dependent, however. Species long-term persistence may rely on a host of factors in addition to plant-plant interactions, such as dispersal processes, climatic factors, and interactions with other trophic levels. Future research should be directed towards determining the relative importance of these factors compared to direct competition in maintaining diverse communities of ecologically similar species.

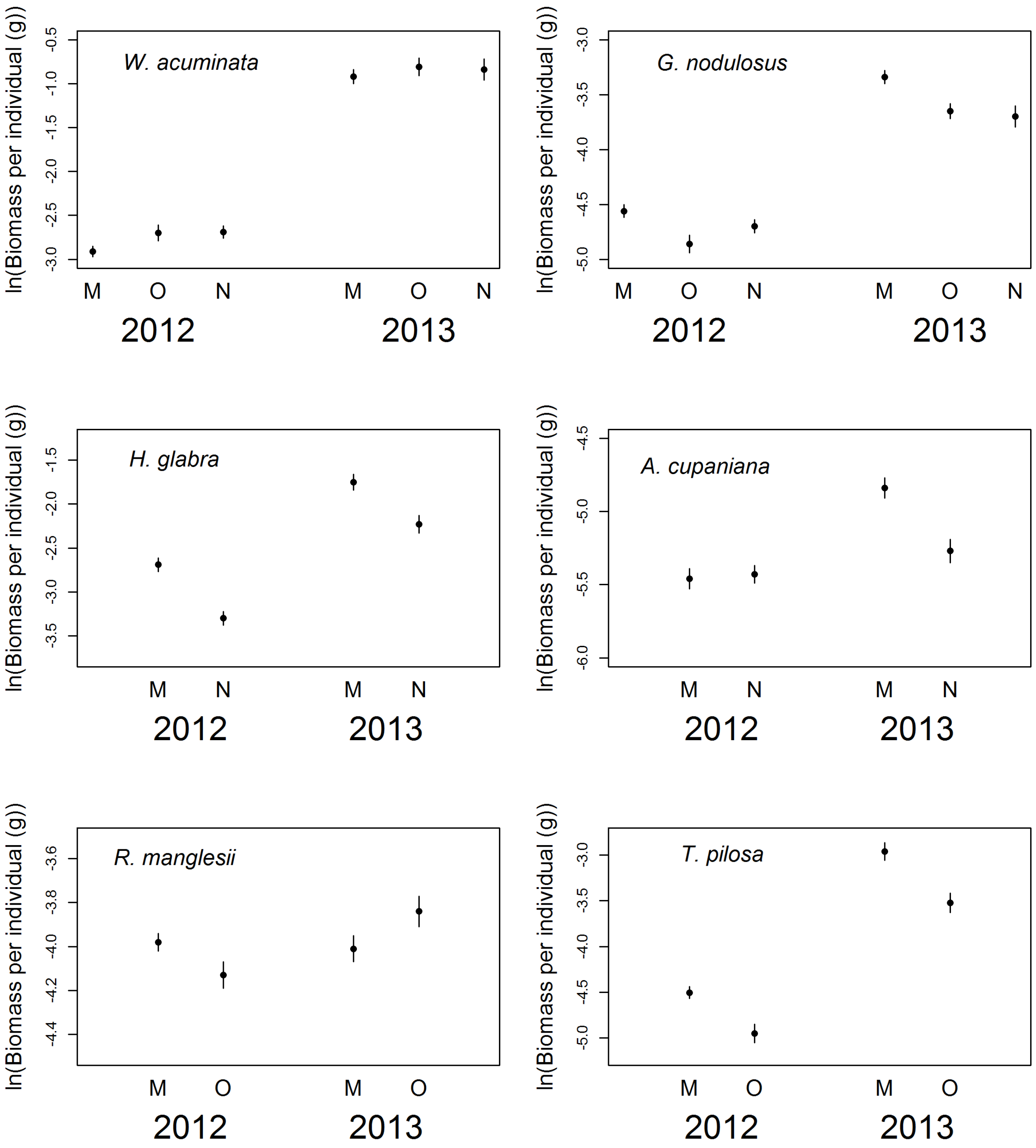

Fig 5.1 Species ln-transformed biomass per individual by community type (monoculture=M, original mixture= O, or novel mixture = N) in 2012 and 2013.

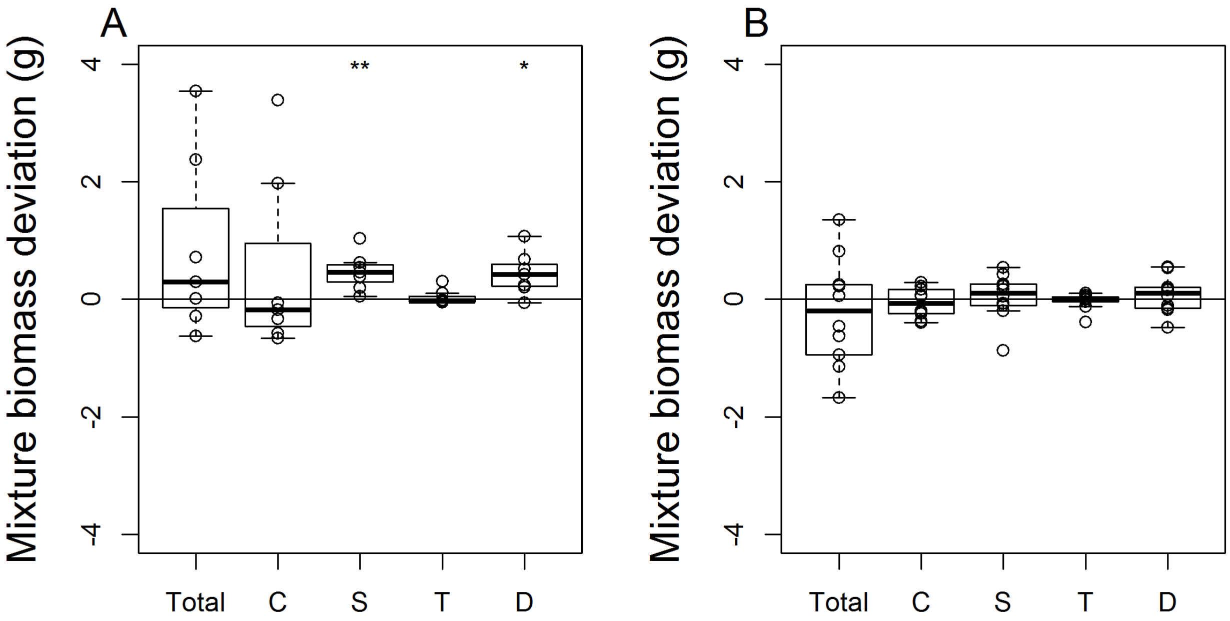

Fig 5.2 Deviations in observed mixture biomass yield from expected mixture yield based on constituent species' abundance-weighted monoculture yields in original (A) and novel (B) communities in 2012. Total= sum of all species biomass deviations from expected values, C= deviation due to complementarity effects, S= deviation due to selection effects, T= deviation due to trait-dependent complementarity, and D= deviation due to dominance effects. Asterisks denote level of significance (H_o: $\mu=0$; *: $p\leq0.05$, **: $p<0.01$, ***: $p<0.001$).

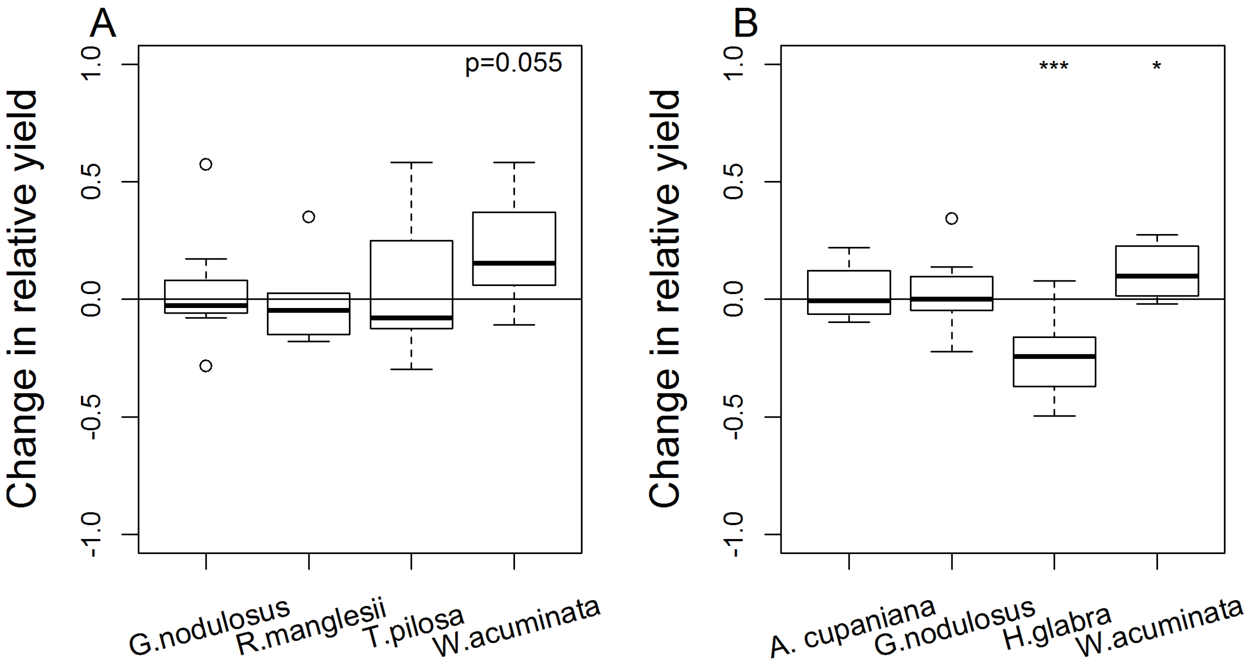

Fig 5.3 Deviations in observed species yields in mixture from their expected yields based on abundance-weighted monoculture yields in 2012 in original (A) and novel (B) communities. Asterisks denote level of significance (H_o: $\mu=0$; *: $p \leq 0.05$, **: $p<0.01$, ***: $p<0.001$).

Table 5.1 Coefficients and (SEs) from mixed effects models of focal species seed production in interaction neighbourhoods within quadrats in 2013 by neighbourhood identity (relative to single individual plants), neighbour abundance, reserve (Kunjin relative to Bendering), and overhead woody canopy cover (%). Asterisks denote level of significance (*: $p \leq 0.05$, **: $p<0.01$, ***: $p<0.001$).

Focal Species:	***A.cupaniana***	***T. cyanopetala***	***W. acuminata***
Fixed effects:			
Intercept (single plant, Bendering)	4.64(0.38)***	4.10 (0.32)***	7.20 (0.28)***
Neighbour abundance	-0.01 (0.02)	-0.03 (0.02)	-0.08 (0.02)**
Non-native neighbours	-0.16 (0.40)	0.14(0.25)	-0.52 (0.24)*
Native neighbours	-0.43 (0.39)	-0.28(0.24)	-0.49(0.25)*
Site (Kunjin)	NA	-0.27(0.21)	-0.16(0.16)
Canopy cover	-0.03 (0.01)*	0.005 (0.009)	0.008(0.008)
Random effects (variance estimates):			
Among neighbourhood	0.13	0.20	<0.0001
Within neighbourhood	0.34	0.38	0.93

Table 5.2 Means and 95% confidence intervals of observed plot-level biomass deviations from expected yields and constituent diversity effects in novel and original species mixtures in 2012. Asterisks denote level of significance (H_o: $\mu=0$; *: $p \leq 0.05$, **: $p<0.01$, ***: $p<0.001$).

	Mixture type	
Response:	**Novel (n=10)**	**Original (n=7)**
Deviation from expected yield	-0.21 (-0.50-0.07)	0.86 (-0.55 – 2.28)
Complementarity	-0.06 (-0.14 – 0.02)	0.51 (-0.93 – 1.94)
Selection	0.04 (-0.08 – 0.16)	0.47** (0.18 – 0.77)
Dominance	0.08 (-0.02 – 0.17)	0.44* (0.10 – 0.78)
Trait-dependent complementarity	-0.03 (-0.08 – 0.01)	0.03 (-0.09 – 0.15)

Table 5.3 Coefficients and (SEs) from mixed effects models of species deviations from expected relative yields when grown in either community type compared to monoculture in 2012. A dash corresponds to instances where a focal species was not present in a community type. Asterisks denote level of significance (*: p≤0.05, **: p<0.01, ***: p<0.001).

Species:	**Mixture type**	
	Novel (n=10)	**Original (n=7)**
A. cupaniana	0.03 (0.05)	-
G. nodulosus	0.03 (0.06)	0.05 (0.12)
H. glabra	-0.23 (0.06)***	-
R. manglesii	-	-0.008 (0.08)
T. pilosa	-	0.08 (0.13)
W. acuminata	0.12 (0.05)*	0.22 (0.11)
Random effects (variance estimates):		
Among block	0.003	0.014
Within block	0.01	0.066

Chapter 6: Effects of non-native annual grass litter and local environmental gradients on annual plant community structure

Introduction

Understanding the mechanisms that promote the persistence of non-native plant species is complementary to understanding the factors that enhance invasion resistance. The introduction of non-native propagules in conjunction with various forms of exogenous disturbance may trigger invasions by creating opportunities for non-native species to establish aided by altered resource levels or reduced competition from native species (Hobbs & Huenneke 1992; MacDougall & Turkington 2005). However, it is less clear which abiotic and biotic processes permit non-native species to persist once these disturbances have ended (D'Antonio & Chambers 2006). Identifying these processes and their contingencies may reveal the barriers to recovery of invaded plant communities, while also providing insight into general abiotic and biotic conditions for species coexistence (Hobbs & Norton 1996; Palmer et al. 1997; D'Antonio & Chambers 2006).

In many plant communities in Mediterranean-type ecosystems, introduced annual grasses and forbs persist after disturbance has ceased by inhibiting the establishment of native competitors (D'Antonio & Vitousek 1992; Seabloom et al. 2003; Grman & Suding 2010). One mechanism of this inhibition is the suppression of native species by accumulation of residual non-native annual grass biomass, or litter. Annual grass litter may inhibit other species by imposing direct and indirect barriers to growth and activity at various life stages. This inhibition can begin as early as dispersal by physically preventing native seed from reaching the soil surface (Fowler 1986). Annual grass litter may also alter native species germination patterns and their productivity through modifications to the microenvironment, such as changes in nutrient levels, water availability, increasing soil temperature, facilitating pathogen attack, and decreasing light penetration to the soil surface (reviewed in Facelli & Pickett 1991). Once native germination has occurred, annual litter can further prevent or suppress seedling growth (Lenz et al. 2003). Neutral or facilitative interactions between non-native grass litter and conspecific seedlings have also been found to promote a positive feedback to their abundance that may compound over time and facilitate non-native grass dominance in some systems (D'Antonio & Vitousek 1992; Lenz et al. 2003; Coleman & Levine 2007).

Natural environmental features of recipient plant communities may modify the impacts of non-native species over small spatial scales. In particular, overstory vegetation may contribute substantially to variation in understory floristic composition in savannah grasslands (Belsky 1993; Scholes & Archer 1997), eucalypt woodlands in southeastern Australia (Prober et al. 2002a), and eucalypt woodlands Western Australia (Prober & Wiehl 2011; Dwyer et al. 2015). The effects of trees on understory vegetation are twofold, encompassing both aboveground and belowground processes. Tree canopies reduce direct solar radiation, which may alleviate water stress in understory plant assemblages (Weltzin & Coughenour 1990; Dwyer et al. 2015). Prober & Wiehl (2011) found that both tree species and tree proximity were significant sources of variation in soil properties such as bulk density, total nitrogen, and pH in semi-arid eucalypt woodlands. Topsoils beneath trees are often more fertile than soils found in open patches as a result of nutrient deposition and physical disturbance from faunal congregation, as well as nutrient concentration near tree root systems, runoff zones, and areas of litter accumulation (Belsky 1994; Facelli & Brock 2000; Prober et al. 2002a). However, inhibitory effects of trees on understory vegetation have also been documented in semi-arid eucalypt woodlands (Lamont 1985) and may be due to allelopathic effects of tree leaf litter (May & Ash 1990) or resource drawdown by tree roots (Lamont 1985; Belsky 1994).

The extent to which non-native annual grass litter interacts with tree proximity to impact resident annual plant community structure and invasion dynamics remains unclear. To explore these processes simultaneously, I conducted a field study in a semi-arid eucalypt woodland in southwest Western Australia in which I experimentally added non-native annual grass litter at varying distances from established trees. I measured the relative influences of non-native grass litter and several naturally-occurring abiotic gradients on resident plant community structure. This study was guided by the following questions:

1. How does tree proximity affect microenvironmental conditions important for annual plant performance and community structure?
2. What are the effects of litter addition on these microeonvironmental conditions?
3. How does the presence of non-native annual grass litter, in combination with underlying environmental gradients, affect annual plant community structure?

Methods

Study system

Our study was undertaken in a woodland remnant in Kunjin Reserve (32 °21’19, 31”S 117 °45’42.32”) in the central-southern wheatbelt region of Western Australia. Kunjin Reserve experiences a typical mediterranean-type climate, with mild wet winters and prolonged summer drought. The generally sparse canopy is dominated by York gum (*Eucalyptus loxophleba* subsp. *loxophleba*) and jam (*Acacia acuminata*) trees, and understory plant communities are composed of relatively dense assemblages of annual and perennial forbs, and occasional shrubs and perennial tussock grasses (Dwyer et al. 2015). The annual component is prominent during late winter and spring from June to October. Annual grasses are not native to York gum-jam woodlands, and as such their litter is not a natural feature in the absence of invasion, and litter from native annuals is relatively sparse.

Experimental design

To test effects of non-native annual grass litter on annual plant community structure, I added litter to native-dominated areas within Kunjin Reserve at the end of the 2012 growing season, and assessed plant community structure during the 2013 growing season. I also assessed how community structure varied naturally along canopy cover and soil gradients related to distance from *E. loxophleba* and *A. acuminata* trees, the two dominant trees in this woodland type.

A total of 6 pairs of transects were established in Kunjin Reserve in November 2012. Each pair consisted of one transect running north away from a single tree and the second transect running south away from the same tree (*A. acuminata*: n=2, *E. loxophleba* n=4). Along each transect five pairs of 0.5 x 0.5 m plots were placed every 1 to 3 m to avoid perennial bunchgrasses, which are very sparse at Kunjin Reserve relative to annuals but would have dominated study plots in which they occurred due to their comparatively large size. The same plot spacing was used for north and south transects in each pair. The litter treatment was applied to one plot per pair. Litter plots were alternated with each consecutive plot pair to prevent an east-west bias in the findings. Plot pairs were separated by 0.5 m to minimise variation in underlying abiotic conditions and plant community composition while avoiding edge effects of the litter on control plots. This scale is consistent with herbaceous species turnover in these communities (Dwyer et al. 2015). Trees were chosen to have relatively homogenous annual plant composition around them.

All litter treatment plots received stem and leaf litter of non-native annual grass *Avena barbata*, an introduced grass which persists in many York gum-jam woodlands (Prober et al. 2011; Dwyer et al.

2015). The litter was collected from a nearby roadside, cleaned of seeds, and oven-dried at 60°C for one week before application. The litter was applied to each treatment plot and loosely held in place with a thin layer of bird netting, which was left in place for the entire experiment. Control plots also received a layer of bird netting to minimize differences between treatment and control plots not due to the presence of grass litter. The bird netting was unlikely to affect plant emergence, as I chose a 2 cm mesh aperture, large enough for all annual seedlings in this system to grow through. The *A. barbata* litter was added in November 2012 after community senescence and natural seed release in the experimental plots. I chose to add 65 g of litter to each 0.5 x 0.5 m treatment plots based on the mean mass of litter sampled in areas invaded by *A. barbata* of the same dimensions from Kunjin Reserve. I considered this amount dense enough to prevent seeds that subsequently dispersed into litter addition plots from reaching the soil surface. Therefore, any annual plants present in litter addition plots in 2013 were assumed to have germinated from the seed bank or the soil surface when litter was added in November 2012. By contrast, annuals that occurred in control plots in 2013 could have germinated from the seed bank, or could have dispersed into plots over the summer and autumn of 2012-13. Thus, any compositional differences between litter and control plots in the 2013 growing season were a combined result of the litter acting as a dispersal barrier as well as its effects on plant germination and establishment. *A. barbata* was present in only three of 120 plots (distributed among two transects) prior to experimental litter application, and each of the three plots contained only one individual of *A. barbata*. No pre-treatment litter (non-native annual, native annual or native sclerophyll) was removed or redistributed from plots prior to the experiment.

Data collection

Plant community data from nine plots were discarded due to animal damage, but this damage was distributed among treatments and among the six transects. In August 2013, plant community structure was evaluated by recording the identity and abundance of all plant species using a 30 x 30 cm quadrat centred within each 0.5m x 0.5m plot to eliminate edge effects. In early October 2013, plots were harvested at peak biomass, dried in drying ovens located in the glasshouse facilities at the University of Western Australia, and weighed to assess treatment effects on productivity.

In addition to measures of plant performance across experimental treatments, several abiotic variables were measured for each plot both prior to and post-litter application. Soil samples (0-10 cm depth and excluding litter and debris) were collected from the centre of each plot before litter application and again during biomass harvests, and analysed for nutrient content (nitrate, Colwell phosphorus (P), and Colwell Potassium (K)) according to methods described in Prober & Wiehl (2011). To measure whether N-cycling rates were different between litter addition and control plots, I deployed six ion-exchange membrane (IEM) strips in each plot for seven weeks, corresponding to three cation and three anion membrane strips, for estimating ammonium and nitrate adsorption rates, which were determined according to methods described in Jasrotia & McSwiney (2008) and Vogt (2013a, 2013b). Soil moisture was measured in each plot using a soil moisture probe (0-10 cm, TDR method) partway through the growing season in September 2013. Canopy cover of *E. loxophleba* and *A. acuminata* was measured as an average of cover facing north, east, and west of each plot using a spherical crown densiometer (Forestry Supplies Inc.). Cover to the south was not included in analyses because it does not contribute to shading during the winter growing season in these communities.

Data analysis

All analyses were conducted in R (v 3.1.2, R Development Core Team 2014). To account for spatial dependence of responses, I included spherical correlation structures (Diggle et al. 2002) in all models except those of focal species abundances and verification of pre-treatment litter cover.

To verify that pre-treatment litter amounts (herbaceous, *E. loxophleba*, and *A. acuminata*) did not inherently differ between control and litter plots, I used linear mixed-effects models (package nlme (Pinheiro et al. 2014)) to model cover of each litter type in each plot by treatment assigned to the plot, with random effect specified as plot pair nested with transect to account for spatial dependence of observations. Cover values were sqrt-transformed (herbaceous litter) or ln-transformed (*E. loxophleba* and *A. acuminata*) prior to analyses to meet model assumptions of normality. Then I examined natural (pre-treatment) variation in important abiotic variables along transects by fitting generalized additive mixed models (package gamm4 (Wood 2012)) of canopy cover, soil nitrate, soil phosphorus (P), and soil potassium by distance to tree, with a random effect of plot pair nested within transect. Because the number of *E. loxophleba* and *A. acuminata* transects were unequal, differences in relationships of abiotic variables to tree proximity according to tree species could not be statistically estimated in one model. Thus, separate models were fit for transects of either tree species. A number of these variables were log normally distributed and were therefore ln-transformed or logit-transformed. To visually estimate the non-linear trends of these abiotic variables by tree proximity, smoothed splines of model-predicted values were plotted with one SE interval around each spline. To investigate natural directional differences in soil moisture and nitrate adsorption rates around trees, I used a mixed effects model of ln-transformed soil moisture and nitrate adsorption values from control plots only by aspect (north or south), with plot nested within block specified as a random effect. In addition, I modelled the relationship between pre-treatment native sclerophyllous litter and overhead canopy cover using mixed effects models of plot-level ln-transformed *E. loxophleba* and *A. acuminata* litter percent cover by overhead canopy cover, with random effects of plot nested within block to account for spatial dependence and overdisperson (Elston et al. 2001).

This was followed by investigation of how litter addition impacted these variables, using mixed effects ANOVAs with fixed effects of treatment (litter addition or control) and tree species and random effect of transect. These analyses were followed by multiple comparisons of responses among tree-treatment combinations (package multcomp (Hothorn et al. 2008)).

Then, I analysed how litter addition and pre-treatment abiotic variation explained aspects of community structure and plant performance using mixed effects models, using fixed effects of treatment (categorical: litter addition or control) and continuous measures of pre-treatment abiotic variables, and a random effect of transect. First I related treatment and abiotic variables to community-level measures of species richness and non-native and native plant density. Then, I chose four common focal species and assessed the impact of treatment and abiotic variables on their abundance and mean biomass per individual: *Waitizia acuminata* (native, Asteraceae), *Millotia myosotidifolia* (native, Asteraceae), *Arctotheca calendula* (non-native, Asteraceae), and *Vulpia myuros* (non-native, Poaceae).

We rarefied species richness values to investigate the effect of litter on richness while accounting for differences in plant density among plots (Appendix 6.1). Plant density was square-root transformed to meet assumptions of normality. Focal species abundances were analysed using generalized linear mixed effects models with Poisson errors and a log link function (package lme4 (Bates et al. 2014)) and plot-level random effect nested within transect to account for spatial dependence and overdispersion. Biomass responses of focal species were ln-transformed to improve normality of residuals before linear mixed effects models were fitted.

Results

Pre- and post-treatment natural variation

Pre-treatment litter cover did not differ between control and treatment plots (herbaceous litter$_{\text{control}}$ = 9.3±1.5%), herbaceous litter$_{\text{litter}}$ (11.3±1.4%; p=0.21), *E. loxophleba* litter$_{\text{control}}$ (19.7±3.5%), *E. loxophleba* litter$_{\text{litter}}$ (19.3±3.1%; p=0.51), *A. acuminata* litter$_{\text{control}}$(9.0±2.9%), *A. acuminata* litter$_{\text{litter}}$ (11.1± 3.1%; p=0.51). Environmental variables varied along transects depending on the distance from tree, aspect, and tree species (Fig 6.1). *A. acuminata* canopies were smaller than those of *E. loxophleba* canopies, reflected in percent canopy cover values (Fig 6.1A). Nitrate increased with distance to *A. acuminata* trees, but only to the north (Fig 6.1B). By contrast, there were no strong trends in nitrate values around *E. loxophleba* trees (Fig 6.1B). Phosphorus values declined with distance to *E. loxophleba* trees only (Fig 6.1C). No discernible trends were found for potassium around either tree species (Fig 6.1D). Soil moisture measured in control plots was significantly greater to the south of trees than to the north (south estimate: 0.17, SE: 0.04, p=0.0001), though this was not the case for nitrate adsorption rates and aspect (south estimate: 0.36, SE: 0.76, p=0.64). Percent cover of native sclerophyllous litter was significantly positively correlated with overhead tree canopy cover (*E. loxophleba* estimate (SE): 0.02 (0.003), p<0.0001; *A. acuminata* estimate (SE): 0.03 (0.004), p<0.0001).

Litter addition did not affect the measured abiotic variables with the exception of soil moisture (Fig 6.2A), which increased with litter addition (estimate: 0.07, SE: 0.02, p=0.0001). *Post-hoc* comparisons revealed that while this increase in soil moisture in litter addition plots was apparent in transects of both tree species, the effects were strongest under *E. loxophleba* (adjusted p= 0.002) potentially due to greater treatment replication than under *A. acuminata*.

Species richness and plant density

Rarefied species richness was unaffected by the litter treatment (Table 6.1, Fig 6.3A; Appendix 6.3). However, total plant densities declined with litter addition (p=0.02), as well as canopy cover (p=0.004). This trend was driven by native species, which declined in abundance with litter addition (p=0.04, Fig 6.3B) and canopy cover (p=0.02), while non-native plant density was unrelated to any explanatory variable in this study.

Abundance and biomass of focal native and non-native species

W. acuminata abundance declined with litter addition and canopy cover (p=0.03 and p<0.0001 respectively, Table 6.2, Appendix 6.2 & 6.4), and phosphorus (p=0.01). *M. myositidifolia* abundance was positively associated with phosphorus (p=0.05, Table 6.2, Appendix 6.4). *A.*

calendula and *V. myruos* abundance decreased with canopy cover (p=0.04 and p=0.003, respectively; Table 6.2, Appendix 6.2 & 6.4). Mean individual biomass was not significantly influenced by any of the abiotic variables, with the exception of *M. myositidifolia*, individuals of which were smaller in areas of higher potassium (p=0.01, Table 6.2, Appendix 6.5).

Discussion

In general, plant community structure and productivity of focal species were more strongly influenced by soil and canopy cover gradients than the presence of litter. However, native species were significantly less abundant where litter was added across all natural gradients. Combined with evidence from regional scale studies, these results suggest that one of strongest effects of non-native annual grass litter in this system may be the prevention of germination and establishment of native annuals. If the impacts of litter were to compound over multiple years, even stronger negative impacts on native plant communities may result than were observed in this study.

Natural microenvironmental gradients

Higher soil moisture to the south of trees likely reflected greater shading by trees during the winter and spring in this system. Native sclerophyll litter was concentrated at the bases of trees, confirming that the effects of tree litter on understory communities may not be as strong in open areas relative to shaded areas. Nitrate was higher to the north of trees, especially in open patches adjacent to *A. acuminata*, which was surprising given previous findings in this system of greatest total N near trees (Prober and Wiehl 2011). As nitrate adsorption rates were unrelated to aspect, this may have been due to inherent soil differences leading to lower N leaching rates to the north of jam trees (Austin et al. 2004; Prober et al. 2005).

Litter effects on microenvironmental conditions

The most pronounced effect of *A. barbata* litter on measured abiotic variables was to elevate soil moisture, consistent with findings in other systems (reviewed in Facelli & Pickett 1991). Higher soil moisture in litter addition plots was likely due to reduced evaporation from the soil surface (Fowler 1986; Facelli et al. 1999). Non-native grass litter also has the potential to modify microenvironmental conditions over longer timescales than this study. In temperate eucalypt woodlands, these long-term effects may include increased levels of soil organic carbon (Dwyer et al. 2015) and increases in internal soil nitrogen cycling rates (Prober et al. 2002b; 2009).

Microenvironmental and litter effects on community structure

Overall, canopy cover and soil nutrient gradients were more informative predictors of plant community structure than the presence of litter. Canopy cover in particular proved to be among the strongest drivers of understory annual community responses. Total and native annual plant abundance declined in shadier areas closest to trees, confirming previous observations of negative relationships between annual plants and York gum-jam overstories (Prober & Wiehl 2011). While I did not isolate the specific mechanisms driving canopy cover effects on understory communities, there are factors correlated with overhead canopy cover that may have contributed to this pattern. For example, the results show that the canopy effect was likely not due to increased nutrient content closer to trees. Rather, I suspect that increased volume of sclerophyllous leaf litter closer to tree trunks may have been important for driving abundance declines, as the percent of *A. acuminata* and *E. loxophleba* leaf litter was positively correlated with overhead canopy cover. *Eucalyptus* species may exert inhibitory effects on understory vegetation in low rainfall systems, including allelopathic stem flow or leachates from leaf litter (May & Ash 1990), though we did not test for such compounds in soil analyses.

Of the soil nutrients measured, only P had a significant negative relationship with focal species abundances. Consistent with previous findings in York gum-jam woodlands (Dwyer et al. 2015), native *W. acuminata* declined in abundance as P increased. While phosphorus can be toxic to perennial species in this historically P-limited region (Lambers et al. 2008), it is unknown how it affects herbaceous annuals other than through competitive exclusion by exploitative annuals that thrive on P-enriched soils (Dwyer et al. 2014), which was not the case in this study. On the other hand, native forb *M. myosotidifolia* was positively associated with P. On the regional scale, however, the relationship between *M. myosotidifolia* and P is not significant (Dwyer et al. unpublished data).

Unlike previous studies (Lenz et al. 2003), there was no detectable effect of *A. barbata* litter on species richness. Additionally, though this system is water-limited, the increase in soil moisture in the plots may not have been large or sustained for long enough to produce an effect on plant biomass. However, there was a significant negative effect of litter on plant density, driven by declines in the abundance of native species where litter was present. While this study examined the effects of litter deposition over one year, significant population declines of native species may, over time, lead to localised extinction. Even though the litter was added after the completion of natural seed dispersal in this plant community, it may have prevented or delayed small, wind-dispersed native seeds from subsequently reaching the soil surface (Fowler 1986). This seed barrier effect of accumulated litter has been implicated in observational studies in several invaded York gum-jam woodland remnants (Dwyer et al. 2015). Non-native grass litter was associated with an increase in mean seed mass and a narrowed seed mass distribution, indicative of exclusion of relatively small-seeded native species (Dwyer et al. 2015). Of seeds that did germinate, the *A. barbata* litter may have additionally acted as a mechanical barrier to emergence of native germinants (Facelli & Pickett 1991). The litter may also have promoted seedling herbivory (Facelli 1994) or granivory (Brown et al. 1979).

Altered soil microclimate conditions beneath grass litter may have further reduced the abundance of native annuals by rendering the soil microenvironment unfavourable for germination. Temperature, light availability, and soil humidity cycles play key roles in regulating the germination of annuals in this system (Erickson et al. unpublished data) and in other semi-arid plant communities in Australia (Bell 1999) and worldwide (Baskin et al. 1993; Levine et al. 2008). In addition, an increase in moisture may have corresponded to elevated rates of infection of seedlings by fungal pathogens (Goldberg & Werner 1983; Facelli et al. 1999).

The fact that the abundance of non-native annuals was not affected by *A. barbata* litter likely reflects inherent physiological differences between common native and non-native annuals in this system. To begin with, many common non-native annuals in York gum-jam annual plant communities exhibit more consistent and greater rates of germination than native annuals (Perez-Fernandez et al. 2000; Wainwright & Cleland 2013; Mayfield et al. unpublished data). Non-native species in York gum-jam annual communities typically have larger seeds that may assist germination and penetration through dense layers of litter compared to smaller-seeded natives (Carson & Peterson 1990; Facelli & Pickett 1991; Dwyer et al. 2015). In other locations, non-native annual grass litter has had positive effects on conspecifics by direct feedback mechanisms promoting their abundance or through reductions in interspecific competition (Evans & Young 1970; Lenz et al. 2003; Coleman & Levine 2007). The combination of insensitivity or even positive responses to non-native grass litter may thus be a factor promoting non-native annual grass persistence in invaded communities (Lenz et al. 2003) including York gum-jam woodlands.

Conclusion

Here, I have documented the simultaneous contributions of underlying abiotic gradients and experimental non-native annual grass litter addition to the structure of an annual plant community. Notably, I have isolated the short-term aboveground effects of litter deposition from belowground effects of non-native annual grass presence. I have shown that canopy cover and soil nutrients are important drivers of community structure regardless of whether non-native annual grass litter is present. In addition, I have demonstrated that aboveground litter addition has the potential to reduce native species abundances even over short timeframes, implying that litter presence alone could eventually lead to localized extinction of native species.

Of course, the presence of a naturally-occurring layer of non-native annual grass litter in this system is inherently tied to altered environmental conditions that promoted the establishment of a dense non-native grass canopy. My results thus represent effects on the microenvironment and community composition driven solely by litter, without the effects of live grass presence or the environmental conditions that may have promoted live grass presence and thus litter deposition. In reality, the proximate effects of robust non-native annual grasses (especially *A. barbata*) on native annuals are much more extensive. Live *A. barbata* individuals are known to be highly competitive for light and may also rapidly deplete soil moisture (Dyer & Rice 1999; Lenz & Facelli 2005; Coleman & Levine 2007; Standish et al. 2008). Further, annual grass invasion is often reinforced by eutrophication or ungulate grazing, which may be selectively detrimental to native species (HilleRisLambers et al. 2010; Prober et al. 2011). An increasing volume of litter may accumulate over time in given microsites (Facelli & Pickett 1991; Facelli & Carson 1991), and so my study almost certainly underestimated the potential long-term effects on native community structure. Still, over one year, the presence of litter significantly impacted the native annual plant community in this study. Thus, my results demonstrate that litter may degrade native plant communities in the absence of ongoing disturbance. Combined, the direct effects of grass competition and disturbance may interact with litter deposition to dramatically change community composition in favour of non-native annual grass persistence.

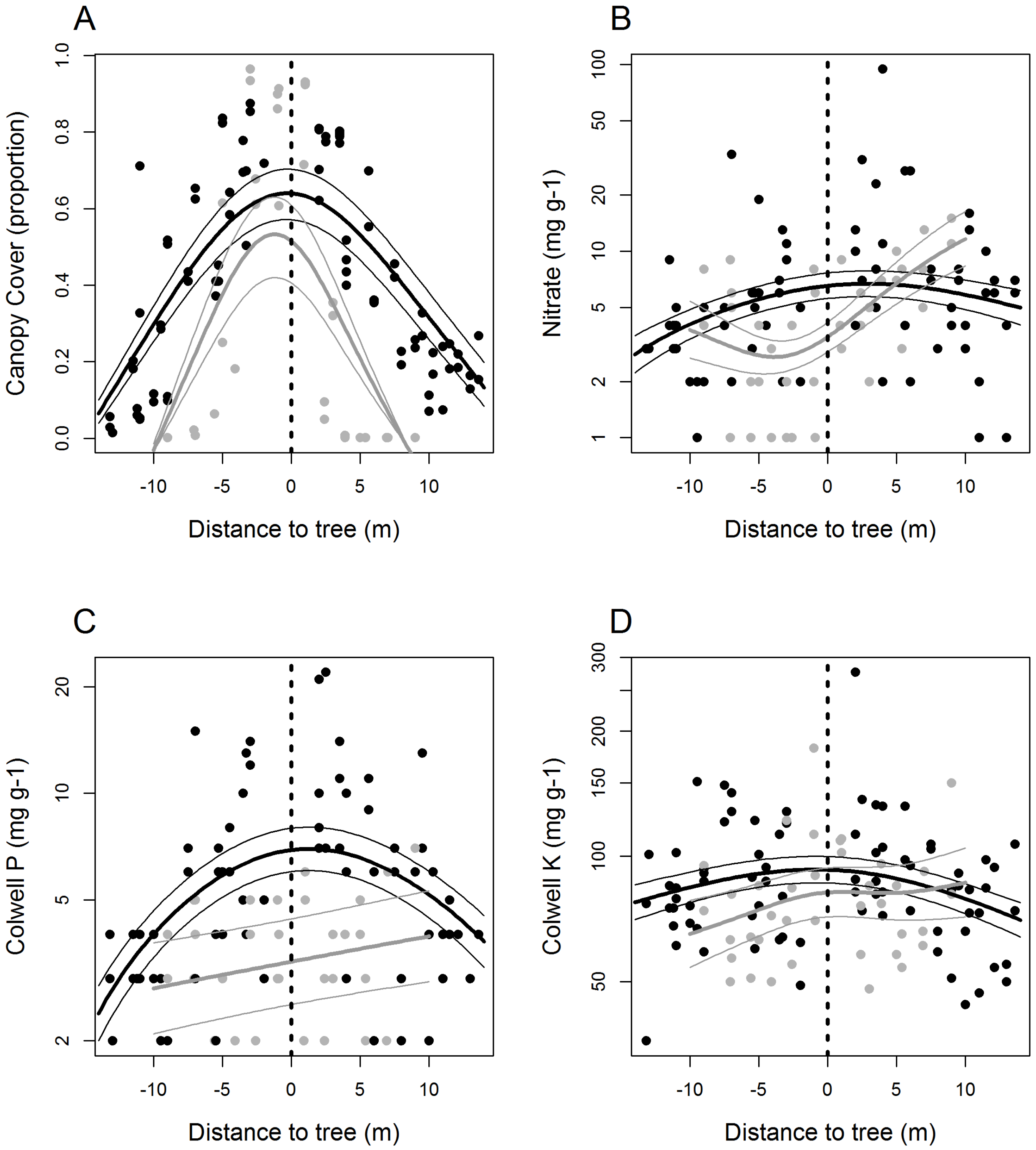

Fig 6.1 Smoothed splines (±1 SE) of transformed environmental variables with proximity to tree (grey: *A. acuminata*, black: *E. loxophleba*) measured in experimental plots in 2012 prior to litter addition. Position along the x-axis denotes position along the south (negative) - north (positive) transect relative to the tree at the origin.

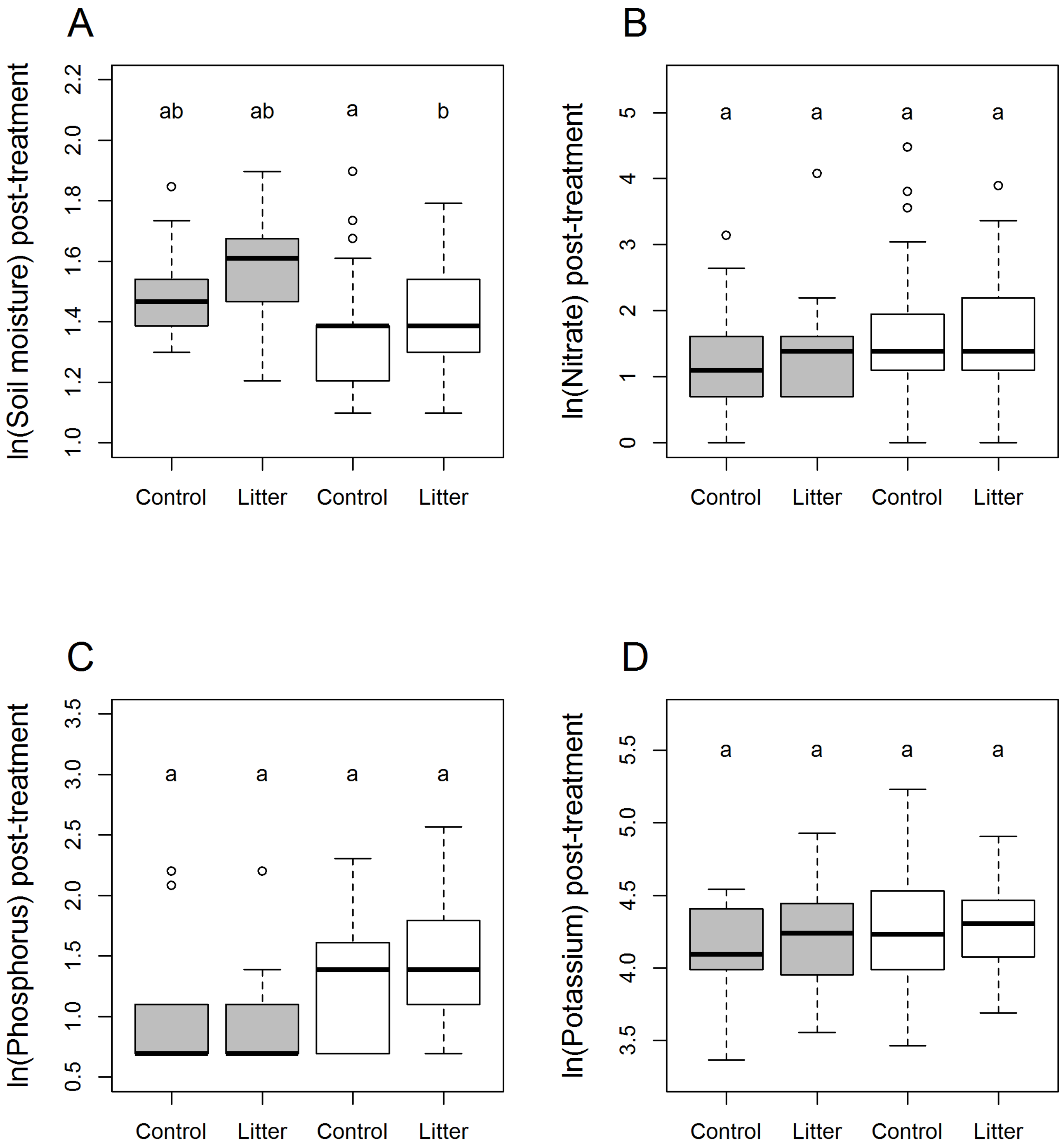

Fig 6.2 Post-treatment abiotic variables measured in control and litter addition plots in the spring of 2013 (grey: *A. acuminata*, white: *E. loxophleba*). Letters denote statistically significant differences among tree-treatment combinations.

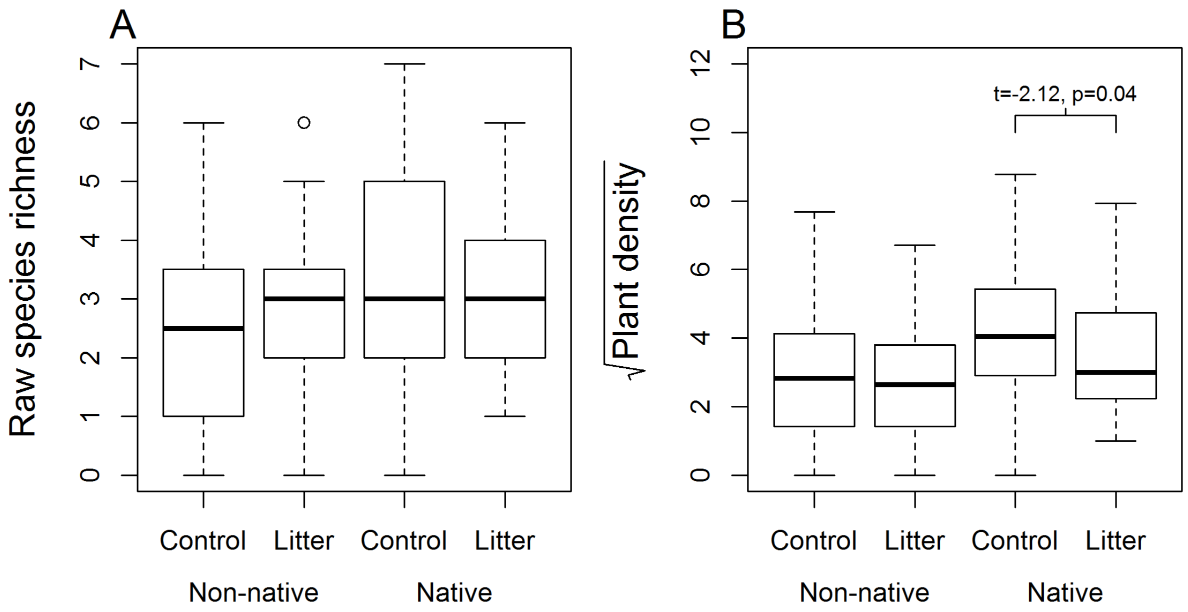

Fig 6.3 (A) Raw species richness and (B) square-root transformed plant densities of native and non-native annuals in control and litter addition treatment plots.

Table 6.1 Coefficients and (SEs) from mixed effects models of plant community responses to litter addition and pre-treatment environmental variables, with transect specified as a random effect. Asterisks denote level of significance (*: p≤0.05, **: p<0.01, ***: p<0.001).

Fixed effects: **Response:**	**Intercept**	**Litter addition**	**Canopy cover**	**Nitrate**	**P**	**K**	**Random effects (variance estimates)**
Rarefied species richness	2.25 (0.95)*	0.04 (0.12)	-0.003 (0.003)	0.09 (0.10)	-0.34 (0.18)	0.27 (0.24)	Among: <0.0001 Within: 0.37
Total plant density	8.33 (2.45)**	-0.65 (0.27)*	-0.02 (0.008)**	-0.12 (0.26)	-0.20 (0.47)	-0.36 (0.61)	Among: 0.66 Within: 2.76
Sqrt(Non-native plant density)	4.91 (2.05)*	-0.25 (0.22)	-0.01 (0.008)	0.14 (0.21)	-0.63 (0.40)	-0.18 (0.50)	Among: 0.72 Within: 3.10
Sqrt(Native plant density)	5.94 (2.53)*	-0.63 (0.30)* Fig 3B	-0.02 (0.007)*	-0.37 (0.27)	0.17 (0.48)	-0.17 (0.64)	Among: 0.42 Within: 2.56

Table 6.2 Coefficients and (SEs) from mixed effects models of focal species responses to litter addition and pre-treatment abiotic variables. Models of abundance used Poisson errors with log link, and plot within transect specified as a random effect. Biomass models were linear models of ln-transformed biomass values with transect specified as a random effect. Asterisks denote level of significance (*: p≤0.05, **: p<0.01, ***: p<0.001).

Fixed effects: **Response:**	**Intercept**	**Litter addition**	**Canopy cover**	**Ln (Nitrate)**	**Ln(P)**	**Ln(K)**	**Random effects (variance estimates)**
A. calendula abundance	-4.99 (4.04)	0.50 (0.49)	-0.02 (0.009)*	0.77 (0.41)	-0.95 (0.77)	0.90 (1.00)	Transect: 0.32 Plot: 1.43
M. myosotidifolia abundance	-1.09 (4.95)	-0.04 (0.55)	0.02 (0.01)	-0.57 (0.46)	1.74 (0.90) *	-0.72 (1.18)	Transect: 6.32 Plot: 2.40
V. myuros abundance	-1.71 (6.38)	0.30 (0.79)	-0.05 (0.02)**	0.64 (0.68)	-0.10 (1.17)	-0.14 (1.59)	Transect: 1.01 Plot: 7.46
W. acuminata abundance	0.68 (1.89)	-0.47 (0.22)*	-0.02 (0.005)* **	0.06 (0.17)	-0.84 (0.33) *	0.29 (0.46)	Transect: 0.32 Plot: 0.23
A. calendula mean biomass/ individual (g)	2.55 (4.32)	0.21 (0.45)	0.02 (0.01)	0.54 (0.39)	0.19 (0.80)	-1.09 (1.09)	Among: 4e-8 Within: 1.99
M. myosotidifolia mean biomass /individual (g)	1.95 (2.25)	0.23 (0.26)	0.002 (0.007)	0.22 (0.24)	0.51 (0.45)	-1.54 (0.57) *	Among: 0.29 Within: 0.48
V. myuros mean biomass/ individual (g)	-4.88 (2.13)*	0.02 (0.26)	<0.0001 (0.006)	0.25 (0.24)	0.35 (0.42)	0.22 (0.24)	Among: 0.22 Within: 0.81
W. acuminata mean biomass/ individual (g)	-4.94 (2.39)*	-0.00007 (0.25)	-0.006 (0.007)	0.18 (0.23)	0.39 (0.43)	0.58 (0.59)	Among: 0.53 Within: 1.32

Chapter 7: General discussion

In this thesis, I explored the role that local-scale biotic interactions play in the formation and maintenance of novel plant communities resulting from recent but extensive invasion and land-use change. Using a diverse winter annual plant system that persists within a fragmented agricultural landscape in southwest Western Australia, I have investigated species interactions in novel communities that differ in composition to original communities due to invasion by non-native species. Throughout, I have demonstrated that outcomes of interactions within and among commonly co-occurring native and invasive non-native species can indeed be negative, aligning with trends often reported in the literature on plant invasions. Interactions within and among native and non-native species, however, were also neutral or even positive. My findings indicate that these communities assemble, in part, as a result of a diverse suite of encounters within and among native and non-native species, the contingencies of which I discuss below.

Summary

In Chapter 3, I demonstrated that a broad range of plant-plant interactions simultaneously operate among native and non-native species in York gum-jam annual plant communities. This variation in interactions was due to focal species' differential sensitivities to the density and the identity of co-occurring individuals. In particular, the relative impacts of intra- versus interspecific interactions on performance (i.e. survival, biomass, and reproductive investment) shifted with density according to species, likely due to differences in species growth habits and growth forms. Specifically, native and non-native forbs (*W. nitida* and *H. glabra* respectively) responded negatively to strong intraspecific competition in terms of survival, yet the non-native grasses (*B. madritensis* and *P. airoides*) were either insensitive to, or responded positively to, intraspecific density. However, in two and three-species mixtures, these non-native grasses had opposite effects on co-occurring species. The robust non-native grass *B. madritensis* consistently excluded interspecific individuals, while the diminutive non-native grass *P. airoides* facilitated the native *W. nitida.* Thus, species identity proved to be a major determinant of interaction outcomes, which ranged from interference competition to facilitation. These results suggest that multispecies coexistence in invaded York gum-jam annual plant communities hinges in part on competitive differences among native and non-native species, and that certain species combinations may not be able to persist, even if highly competitive species are only present at low densities.

In Chapter 4, I explored the potential for facilitation of native by non-native species. In the field, I found that native *W. acuminata* survival was facilitated by the non-native grass *A. cupaniana* across a range of conspecific abundances. *W. acuminata* biomass and flower production in the field were impacted less by neighbouring *A. cupaniana* than conspecifics, suggesting intra- rather than interspecific competition influences *W. acuminata* in mixtures with *A. cupaniana* in the field. In growth chambers, *A. cupaniana* had a neutral effect on *W. acuminata* performance measures across a range of relative abundances and was unaffected by *W. acuminata* and conspecifics. Together, these responses to intra and interspecific competition suggest that coexistence between these two species is likely to be stable under certain conditions. The grasses showed neutral or positive density-dependence, indicative of strategies that may facilitate their post-establishment spread as invaders. In opposition to results obtained in Chapter 3 with congener *W. nitida*, *W. acuminata* survival decreased in communities containing *P. airoides* compared to monocultures or mixtures with *A. cupaniana*, indicating that these interactions perhaps cannot be generalized within functional groups or genera. Overall, this study confirmed the potential importance of facilitative or neutral interactions between native and non-native species in invaded plant communities.

In Chapter 5, I found little evidence of strong competition in a group of commonly co-occurring native and non-native annuals in the field. I also assessed species and community-level responses to growing in original communities (entirely native mixtures) and novel communities (mixtures of natives and non-natives). On average, single-species responses appeared to drive over-yielding trends (via selection and dominance effects) rather than multispecies responses (complementarity) in original communities. Over-yielding of *W. acuminata* only led to significantly positive selection effects in original communities because these effects were cancelled out by negative selection effects incurred by a productive but weakly competitive species, *H. glabra*, in novel communities. The local-scale microenvironment did not affect species yields as much as biotic composition, site-scale environmental differences, or interannual climate variation. My results suggest that factors in addition to interactions may be important for determining the fitness of many species in this system, and thus the stability of original and novel communities.

From a more applied angle, in Chapter 6 I experimentally demonstrated that certain species of non-native annual grass may be detrimental to York gum-jam woodland annual communities simply through deposition of litter, or residual dry biomass. My results showed that even over the relatively short timeframe of one year, the litter of the non-native annual grass *Avena barbata* may cause significant population declines in native species. Importantly, non-native species abundances were not affected by litter in this study, suggesting that the effect of litter may be selectively damaging to native species, especially if compounded over time. This study isolated the aboveground litter effects of invasive non-native annual grass presence from the effects of direct competition from living individuals and the disturbed conditions potentially promoting their establishment. Moreover, I measured litter impacts on plant community structure in conjunction with several important natural local-scale environmental gradients. While native abundances declined, the litter treatments did not affect species richness (native or non-native) once inherent differences in plant abundance related to tree proximity were accounted for. Additionally, focal species productivity was unaffected by litter despite greater soil moisture where litter was present. When combined with regional-scale observations of litter effects on seed size distributions, my results show that the primary direct effect of *A. barbata* litter may be to prevent germination and establishment of native species. If these impacts were to compound over multiple years, it may result in strong reductions in abundance and potentially diversity.

Limitations of this thesis

Throughout my candidature, there were instances of experiments not going exactly to plan due to unforeseen circumstances or insufficient time. For example, in Ch 3, additional native focal species *Goodenia berardiana* and *Rhodanthe spicata* were included in the experimental design to provide a more detailed picture of non-native and native species interactions, but were removed due to insufficient germination. Similarly, in the growth chamber component of Ch 4, the original experimental design called for *W. nitida* as a focal species in addition to *W. acuminata*. Due to insufficient germination of *W. nitida*, however, all replicates that included this species were removed from analyses, which partly limited my ability to compare these results to those found in Ch 3. The different results for the two *Waitzia* species in these chapters did illustrate how species specific these interactions seem to be. In Ch 5, assessing diversity effects in both years was not possible due to changes in the absolute and relative abundances of some focal species between years, though it subsequently highlighted interannual variation as an important determinant of species performance and became an interesting discussion point. Originally, my thesis was to include a study on factors conferring biotic resistance in native communities, but after finding the unexpected evidence of facilitation in the experiment described in Ch 3, the follow-up experiment in Ch 4 was devised and took priority.

Future research needs

While this thesis fills knowledge gaps on how native and non-native species interact in this system, it may also serve as a starting point for a wealth of future research questions.

The research conducted in this thesis provides baseline information on some species' relative sensitivities to intra- versus interspecific competition and associated implications for the stability of woodland annual plant communities. It is now possible to use coexistence models derived by Chesson (2000), parameterized by field data (Levine & HilleRisLambers 2009), for direct calculations of the magnitude of niche and fitness differences among commonly co-occurring native and non-native species in these communities.

In the same vein, I found differences among species in their responses to interannual climate variability and susceptibility to intraspecific competition. These observations suggest that temporal storage effects may be important in these plant communities, possibly operating through seed banks and seed dormancy mechanisms (Pake & Venable 1996; Facelli et al. 2005). This system is well suited to further research on the influence of intra- and interannual environmental heterogeneity on population dynamics and diversity maintenance over long time scales.

Plant-pollinator dynamics for several common annual species have recently been described in intact and invaded York gum-jam annual communities (X. Loy, Hons. thesis). Interspecific differences in pollen-limitation, pollinator assemblages, and flowering phenology may be important insect-mediated determinants of interspecific interactions in this system (X. Loy, Hons. thesis). Other types of inter-trophic interactions almost certainly promote density-dependence and constrain species' relative abundances, such as interactions with soil microbial communities, detritivores, and herbivores, but virtually nothing is known about these interactions at this stage. Filling these knowledge gaps would undoubtedly strengthen our understanding of important niche dimensions promoting coexistence in these diverse plant communities.

Lastly, the conditions required for non-native species to facilitate native species (and the generalities of these conditions) merit further investigation. Although plot-level microenvironmental variables did not explain the positive relationship between *A. cupaniana* and survival of *W. acuminata* in the field, other processes or environmental covariates operating at different scales may contribute to this positive relationship. *A. cupaniana* relationships with other common native annuals across a range of York gum-jam woodlands should also be explored to fully understand the implications of this invasion on community structure and its long-term effects. Similarly, as *A. cupaniana* is a widespread invader in other winter annual plant systems (e.g.

California Floristic Province), it may be worth investigating whether these neutral or facilitative interactions occur with resident annual plant species in *A. cupaniana*'s other invasive ranges, or between functionally similar non-native and native species in a variety of communities.

Conclusion

The experiments composing this thesis contribute baseline empirical support for modern coexistence theory, which is currently lacking despite the general acceptance of the theory in the published literature. Further, my thesis relates the complexities of local-scale interactions to overall community functioning. As a whole, this research not only strengthens the validity of modern theoretical community ecology through experimentation, but contributes valuable knowledge on the ecology of this relatively little-studied yet globally renowned region of floristic diversity.

I have demonstrated in this thesis that while published reports on non-native species impacts are often biased towards those with strong negative effects ("transformers" following the nomenclature of Richardson et al. (2000), or "exploiters" following nomenclature of Lai et al. (2015)), the importance of neutral or positive effects on community structure may often be overlooked. My work provides local-scale empirical support for the growing collection of observations that many areas of high native diversity retain or experience enhanced diversity post-invasion (Stohlgren et al. 1999; Levine 2000; Cleland et al. 2004). These findings challenge historical perceptions of non-native species as predominantly detrimental to resident native communities. Information in this thesis may also be useful for guiding management practices or allocation of management resources in York gum-jam woodlands in the future. Of course, the utility of these results for management may depend on the degree to which the goal of retaining original community function is emphasized compared to returning these communities to pre-invasion species composition (Hobbs et al. 2006).

To conclude, this thesis provides timely contributions to the fields of plant community ecology and biological invasions. A number of important themes emerge from this research. First, interactions that occur among individuals over small spatial and temporal scales have the potential to influence large-scale community dynamics and ecosystem function. Second, interspecific variation in response to competition may, to a degree, underlie overall community structure and coexistence. However, community responses should not be considered in isolation of intraspecific variation and underlying environmental conditions that determine when the impacts of competition are strongest. Last, non-native species fall along a gradient of impact on native species that ranges in direction from negative to positive. Defining the complexities of these impacts is critical to understanding conditions of long-term multispecies coexistence, and the realized functioning of increasingly prevalent novel plant communities worldwide.

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Appendices

Appendix 3.1 Coefficients from mixed effects model of *W. nitida* survival by density and competitor identity. Random effects variance estimates reported in main body of this text.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	1.110	0.548	2.026	0.043
Density	-0.056	0.012	-4.645	3.40E-06
Growing with *H. glabra*	-2.283	0.723	-3.157	0.002
Growing *with H. glabra* and *B. madritensis*	-3.209	0.948	-3.385	0.001
Growing with *P. airoides*	2.395	0.601	3.988	6.67E-05
Growing with *B. madritensis*	-4.273	1.166	-3.663	0.0002

Appendix 3.2 Coefficients from mixed effects model of *H. glabra* survival by density and competitor identity. Random effects variance estimates reported in main body of this text.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.288	0.411	-0.699	0.484
Density	-0.0078	0.007	-1.037	0.300
Growing with *W. nitida*	0.903	0.708	1.275	0.202
Growing with *W. nitida* and *B. madritensis*	3.008	0.957	3.143	0.002
Growing with *B. madritensis*	-0.713	0.865	-0.824	0.410
Density* Growing with *W. nitida*	-0.006	0.012	-0.521	0.603
Density* Growing with *W. nitida* and *B. madritensis*	-0.091	0.022	-4.196	2.72E-05
Density* Growing with *B. madritensis*	-0.027	0.016	-1.701	0.089

Appendix 3.3 Coefficients from mixed effects model of *B. madritensis* survival by density and competitor identity. Random effects variance estimates reported in main body of this text.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	5.387	1.258	4.283	1.85E-05
Density	-0.028	0.017	-1.646	0.100
Growing with *W. nitida* and *H. glabra*	-1.034	0.953	-1.085	0.278
Growing with *W. nitida*	-0.626	0.947	-0.661	0.508
Growing with *H. glabra*	1.140	1.092	1.044	0.296

Appendix 3.4 Coefficients from mixed effects model of *P. airoides* survival by density and competitor identity. Random effects variance estimates reported in main body of this text.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.471	0.421	-1.118	0.264
Density	0.011	0.007	1.565	0.118
Growing with *W. nitida*	1.074	0.667	1.611	0.107
Density* Growing with *W. nitida*	-0.038	0.011	-3.392	0.001

Appendix 3.5 Coefficients from mixed effects model of *W. nitida* biomass per individual by density and competitor identity. Random effects variance estimates reported in main body of this text.

Fixed effects:	Value	Std. Error	DF	t-value	p-value
(Intercept)	-1.805	0.218	16.000	-8.297	0.000
Density	0.001	0.005	16.000	0.144	0.888
Growing with *H. glabra*	-0.410	0.298	16.000	-1.376	0.188
Growing with *H. glabra* and *B. madritensis*	-2.120	0.468	16.000	-4.532	0.000
Growing with *P. airoides*	-0.402	0.223	16.000	-1.802	0.090
Growing with *B. madritensis*	-1.428	0.467	16.000	-3.055	0.008

Appendix 3.6 Coefficients from mixed effects model of *H. glabra* biomass per individual by density and competitor identity. Random effects variance estimates reported in main body of this text.

Fixed effects:	Value	Std. Error	DF	t-value	p-value
(Intercept)	-1.199	0.317	22.000	-3.782	0.001
Density	-0.020	0.005	22.000	-3.988	0.001
Growing with *W. nitida*	0.284	0.285	22.000	0.997	0.330
Growing with *W. nitida* and *B. madritensis*	-1.245	0.316	22.000	-3.945	0.001
Growing with *B. madritensis*	-1.495	0.353	22.000	-4.237	0.000

Appendix 3.7 Coefficients from mixed effects model of *B. madritensis* biomass per individual by density and competitor identity. Random effects variance estimates reported in main body of this text.

Fixed effects:	Value	Std. Error	DF	t-value	p-value
(Intercept)	-2.097	0.087	31.000	-24.234	0.000
Density	-0.014	0.001	31.000	-11.248	0.000
Growing with *W. nitida* and *H. glabra*	0.730	0.082	31.000	8.854	0.000
Growing with *W. nitida*	0.536	0.082	31.000	6.528	0.000
Growing with *H. glabra*	0.490	0.082	31.000	5.969	0.000

Appendix 3.8 Coefficients from mixed effects model of *P. airoides* biomass per individual by density and competitor identity. Random effects variance estimates reported in main body of this text.

Fixed effects:	Value	Std. Error	DF	t-value	p-value
(Intercept)	-3.308	0.439	14.000	-7.536	0.000
Density	-0.003	0.008	14.000	-0.401	0.694
Growing with *W. nitida*	-0.709	0.425	14.000	-1.669	0.117

Appendix 3.9 Coefficients from mixed effects models of the proportion of *W. nitida* individuals investing in reproduction by density and competitor identity. Random effects variance estimates reported in main body of this text.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.38164	0.276835	-1.379	0.168023
Density	-0.03028	0.006056	-5.001	5.71E-07
Growing with *H. glabra*	-1.8698	0.558539	-3.348	0.000815
Growing with *P. airoides*	1.130102	0.278153	4.063	4.85E-05

Appendix 3.10 Coefficients from mixed effects models of the proportion of *H. glabra* individuals investing in reproduction by density and competitor identity. Random effects variance estimates reported in main body of this text.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.351	0.310	-1.130	0.258
Density	-0.021	0.005	-4.178	0.000

Growing with *W. nitida*	0.673	0.257	2.618	0.009
Growing with *W. nitida* and *B. madritensis*	-1.668	0.473	-3.529	0.000
Growing with *B. madritensis*	-2.814	0.628	-4.482	0.000

Appendix 3.11 Coefficients from mixed effects models of the proportion of *B. madritensis* individuals investing in reproduction by density and competitor identity. Random effects variance estimates reported in main body of this text.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.930	0.819	-3.579	0.000
Density	-0.051	0.012	-4.076	0.000
Growing with *H. glabra* and *W. nitida*	2.541	0.877	2.899	0.004
Growing with *W. nitida*	1.650	0.928	1.779	0.075
Growing with *H. glabra*	3.007	0.867	3.470	0.001

Appendix 3.12 Coefficients from mixed effects models of the proportion of *P. airoides* individuals investing in reproduction by density and competitor identity. Random effects variance estimates reported in main body of this text.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.401	0.442	-0.908	0.364
Density	-0.004	0.008	-0.488	0.626
Growing with *W. nitida*	0.728	0.791	0.921	0.357
Density* Growing with *W. nitida*	-0.042	0.015	-2.732	0.006

Appendix 4.1 T-statistic (t), degrees of freedom (df), p-value with Bonferroni correction for multiple comparisons (Adjusted p), sample means, and 95% confidence intervals (CI) from t-tests of environmental variables (transformed to improve normality where appropriate) between *W. acuminata (*monoculture) plots and *W. acuminata* + *A. cupaniana* (mixture) plots at Bendering Reserve in 2013.

Variable	**t**	**df**	**Adjusted p**	**Mean, mixture plots**	**Mean, monoculture plots**	**95% CI**
Soil moisture (%)	-0.13	9.43	1.0	5.60	5.67	-1.25, 1.12
ln (nitrate)	0.94	15.61	1.0	0.94	0.51	-0.54,

						1.40
ln(ammonium)	0.45	15.98	1.0	0.64	0.52	-0.44, 0.67
ln(Colwell phosphorus)	-0.13	15.65	1.0	1.16	1.19	-0.53, 0.47
ln(Colwell potassium)	-1.52	15.41	1.0	4.77	5.00	-0.56, 0.09
ln(overhead tree canopy cover (%))	-2.50	13.81	0.30	3.05	3.77	-1.35, -0.10
A. acuminata litter	1.33	15.61	1.0	40.5	55.63	-8.99, 39.24
Sqrt(*E. loxophleba* litter)	0.62	12.71	1.0	0.71	0.45	-0.65, 1.18
ln(Herbaceous litter)	0.49	13.47	1.0	2.64	2.47	-0.58, 0.93
Nitrate adsorption rate (µg/cm/day)	-1.46	4.0	1.0	0.02	1.38	-3.97, 1.23

Appendix 4.2 Coefficients and (SEs) from mixed effects models of *W. acuminata* performance (proportion of individuals surviving, biomass per individual, proportion flowering, and flower count per flowering individual) in growth chamber experiment by relative frequency when growing in neighbourhoods of *P. airoides* relative to neighbourhoods of *A. cupaniana*. Asterisks denote level of significance (*: p≤0.05, **: p<0.01, ***: p<0.001).

	Response of *W. acuminata*			
Fixed effects:	**Proportion individuals surviving**	**ln(Biomass per individual (g))**	**Proportion of individuals flowering**	**ln(Flower count per flowering individual)**
Intercept (growing with *A. cupaniana*)	1.14 (0.64)	0.42 (0.03) ***	0.68 (0.44)	1.50 (0.28)***
Growing with *P. airoides*	-1.91 (1.10)	-0.19 (0.06)**	0.47 (1.01)	-0.81 (0.78)
Relative frequency	-0.58 (1.12)	-0.21 (0.06)**	-1.15 (0.73)	-0.60 (0.48)
Growing with *P. airoides* x Relative frequency	1.72 (2.10)	0.30 (0.12)*	-2.35 (1.81)	0.79 (1.49)
Random effects (variance estimates):				
Among pot	0.86	0.003	0.18	0.09

Within pot	NA	0.0004	NA	0.61

Appendix 4.3 Coefficients from mixed effects models of *W. acuminata* survival in the field growing with and without *A. cupaniana* along a gradient of conspecific density. Random effects variance estimates are reported in the main body of this text.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.380	0.519	0.732	0.464
Density	0.020	0.031	0.626	0.531
Growing with *A. cupaniana*	0.877	0.341	2.575	0.01

Appendix 4.4 Coefficients from mixed effects models of *W. acuminata* biomass per individual in the field growing with and without *A. cupaniana* along a gradient of conspecific density. Random effects variance estimates are reported in the main body of this text.

Fixed effects:	Value	Std. Error	DF	t-value	p-value
(Intercept)	-0.007	0.344	195	-0.020	0.984
Density	-0.057	0.022	15	-2.58	0.021
Growing with *A. cupaniana*	-0.377	0.253	15	-1.492	0.156

Appendix 4.5 Coefficients from mixed effects models of *W. acuminata* flower count per individual in the field growing with and without *A. cupaniana* along a gradient of conspecific density. Random effects variance estimates are reported in the main body of this text.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	3.408	0.265	12.853	2.00E-16
Density	-0.048	0.017	-2.829	0.005
Growing with *A. cupaniana*	-0.174	0.195	-0.888	0.374

Appendix 4.6 Coefficients from mixed effects models of *W. acuminata* survival in the growth chamber experiment growing with *A. cupaniana* or *P. airoides* at low relative frequency. Random effects variance estimates are reported in the main body of this text.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)

(Intercept)	2.538	0.938	2.705	0.007
With *A. cupaniana*	-1.270	1.075	-1.182	0.237
With *P. airoides*	-3.342	1.228	-2.721	0.007

Appendix 4.7 Coefficients from mixed effects models of *W. acuminata* survival in the growth chamber experiment growing with *A. cupaniana* or *P. airoides* at medium relative frequency. Random effects variance estimates are reported in the main body of this text.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.786	0.266	2.950	0.003
With *A.cupaniana*	-0.204	0.358	-0.568	0.570
With *P.airoides*	-0.694	0.426	-1.630	0.103

Appendix 4.8 Coefficients from mixed effects models of *W. acuminata* survival in the growth chamber experiment growing with *A. cupaniana* or *P. airoides* at high relative frequency. Random effects variance estimates are reported in the main body of this text.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.313	0.760	0.412	0.680
With *A.cupaniana*	0.624	1.027	0.607	0.544
With *P. airoides*	-0.559	1.518	-0.368	0.713

Appendix 4.9 Coefficients from mixed effects models of *W. acuminata* biomass per individual in the growth chamber experiment growing with *A. cupaniana* or *P. airoides* at low relative frequency. Random effects variance estimates are reported in the main body of this text.

Fixed effects:	Value	Std. Error	DF	t-value	p-value
(Intercept)	-2.347	0.190	64.000	-12.325	0.000
With *A.cupaniana*	0.073	0.260	8.000	0.279	0.787
With *P.airoides*	-0.760	0.479	8.000	-1.585	0.152

Appendix 4.10 Coefficients from mixed effects models of *W. acuminata* biomass per individual in the growth chamber experiment growing with *A. cupaniana* or *P. airoides* at medium relative frequency. Random effects variance estimates are reported in the main body of this text.

Fixed effects:	Value	Std. Error	DF	t-value	p-value

(Intercept)	-3.065	0.136	224.000	-22.480	0.000
With *A.cupaniana*	0.050	0.176	11.000	0.284	0.782
With *P.airoides*	-0.042	0.218	11.000	-0.195	0.849

Appendix 4.11 Coefficients from mixed effects models of *W. acuminata* biomass per individual in the growth chamber experiment growing with *A. cupaniana* or *P. airoides* at high relative frequency. Random effects variance estimates are reported in the main body of this text.

Fixed effects:	Value	Std. Error	DF	t-value	p-value
(Intercept)	-3.981	0.203	224.000	-19.585	0.000
With *A.cupaniana*	0.646	0.268	5.000	2.406	0.061
With *P.airoides*	0.886	0.427	5.000	2.076	0.093

Appendix 4.12 Coefficients from mixed effects models of *W. acuminata* proportion of individuals flowering in the growth chamber experiment growing with *A. cupaniana* or *P. airoides* at low relative frequency. Random effects variance estimates are reported in the main body of this text.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.380	0.360	1.054	0.292
With *A.cupaniana*	0.355	0.503	0.705	0.481
With *P.airoides*	-0.380	0.793	-0.478	0.632

Appendix 4.13 Coefficients from mixed effects models of *W. acuminata* proportion of individuals flowering in the growth chamber experiment growing with *A. cupaniana* or *P. airoides* at medium relative frequency. Random effects variance estimates are reported in the main body of this text.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	1.256	0.219	5.746	0.000
With *A.cupaniana*	-0.009	0.290	-0.032	0.974
With *P.airoides*	-0.155	0.376	-0.413	0.680

Appendix 4.14 Coefficients from mixed effects models of *W. acuminata* proportion of individuals flowering in the growth chamber experiment growing with *A. cupaniana* or *P. airoides* at high relative frequency. Random effects variance estimates are reported in the main body of this text.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)

(Intercept)	-0.292	0.274	-1.065	0.287
With *A.cupaniana*	0.115	0.364	0.317	0.752
With *P.airoides*	-2.038	0.841	-2.422	0.015

Appendix 4.15 Coefficients from mixed effects models of *W. acuminata* number of flowers per individual in the growth chamber experiment growing with *A. cupaniana* or *P. airoides* at low relative frequency. Random effects variance estimates are reported in the main body of this text.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	1.547	0.212	7.306	0.000
With *A.cupaniana*	-0.177	0.282	-0.628	0.530
With *P.airoides*	-1.510	0.642	-2.352	0.019

Appendix 4.16 Coefficients from mixed effects models of *W. acuminata* number of flowers per individual in the growth chamber experiment growing with *A. cupaniana* or *P. airoides* at medium relative frequency. Random effects variance estimates are reported in the main body of this text.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	1.256	0.219	5.746	0.000
With *A.cupaniana*	-0.009	0.290	-0.032	0.974
With *P.airoides*	-0.155	0.376	-0.413	0.680

Appendix 4.17 Coefficients from mixed effects models of *W. acuminata* number of flowers per individual in the growth chamber experiment growing with *A. cupaniana* or *P. airoides* at high relative frequency. Random effects variance estimates are reported in the main body of this text.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.805	0.202	3.981	0.000
With *A.cupaniana*	0.227	0.257	0.882	0.378
With *P.airoides*	-0.950	0.747	-1.271	0.204

Appendix 4.18 Coefficients from mixed effects models of focal species survival by their relative frequencies in the growth chamber experiment. Random effects estimates are reported in the main body of this text.

Fixed effects:	Estimate	Std.	z value	Pr(>|z|)

W. acuminata *(+ A. cupaniana)*		Error		
(Intercept)	1.294	0.604	2.143	0.032
Relative frequency	-0.920	0.864	-1.065	0.287
W. acuminata *(+ P. airoides)*				
(Intercept)	-0.565	0.429	-1.317	0.188
Relative frequency	0.789	0.533	1.479	0.139
A. cupaniana *(+ W. acuminata)*				
(Intercept)	1.840	1.075	1.712	0.087
Relative frequency	1.484	1.550	0.957	0.338
P. airoides *(+W. acuminata)*				
(Intercept)	1.397	2.652	0.527	0.598
Relative frequency	1.366	3.312	0.413	0.680

Appendix 4.19 Coefficients from mixed effects models of focal species biomass per individual by their relative frequencies in the growth chamber experiment. Random effects estimates are reported in the main body of this text.

Fixed effects: ***W. acuminata*** *(+A. cupaniana)*	Value	Std. Error	DF	t-value	p-value
(Intercept)	0.401	0.020	17.000	20.273	0.000
Relative frequency	-0.162	0.030	17.000	-5.439	0.000
W. acuminata *(+ P. airoides)*					
(Intercept)	0.255	0.049	9.000	5.199	0.001
Relative frequency	0.018	0.069	9.000	0.255	0.804
A. cupaniana *(+ W. acuminata)*					
(Intercept)	0.171	0.016	16.000	10.668	0.000
Relative frequency	-0.042	0.024	16.000	-1.740	0.101
P. airoides *(+W.acuminata)*					
(Intercept)	0.110	0.049	9.000	2.248	0.051
Relative frequency	0.104	0.064	9.000	1.626	0.138

Appendix 4.20 Coefficients from mixed effects models of focal species proportion of surviving individuals flowering by their relative frequencies in the growth chamber experiment. Random effects estimates are reported in the main body of this text.

Fixed effects: ***W. acuminata*** *(+A. cupaniana)*	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.658	0.387	1.700	0.089
Relative frequency	-1.097	0.524	-2.095	0.036
W. acuminata *(+P. airoides)*				
(Intercept)	1.022	1.030	0.993	0.321
Relative frequency	-3.418	1.931	-1.770	0.077

A. cupaniana *(+W. acuminata)*				
(Intercept)	0.238	0.428	0.556	0.578
Relative frequency	-0.042	0.588	-0.072	0.943
P. airoides (+*W. acuminata*)				
(Intercept)	-2.872	1.099	-2.613	0.009
Relative frequency	2.980	1.301	2.290	0.022

Appendix 4.21 Coefficients from mixed effects models of *W. acuminata* flower count per individual by relative frequency in the growth chamber experiment growing with either *A. cupaniana* or *P. airoides*. Random effects estimates are reported in the main body of this text.

Fixed effects: ***W. acuminata*** (+*A. cupaniana*)	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	1.666	0.212	7.865	0.000
Relative frequency	-0.934	0.298	-3.139	0.002
W. acuminata (+*P.airoides*)				
(Intercept)	0.979	0.452	2.165	0.030
Relative frequency	-0.345	0.549	-0.628	0.530

Appendix 5.1 Description of focal species in each mixture at Bendering Reserve and number of replicates of each mixture type in both years. Asterisks denote non-native species.

Mixture type	**Component species**	$\mathbf{n_{2012}}$	$\mathbf{n_{2013}}$
Monoculture	*A. cupaniana* (Poaceae)*	9	10
	G. nodulosus (Haloragaceae)	10	10
	H. glabra (Asteraceae)*	10	10
	R. manglesii (Asteraceae)	11	10
	Trachymene sp. (Araliaceae)	12 (7 *T. ornata* + 5 *T. pilosa*)	10 (2 *T. cyanopetala* + 5 *T. ornata* + 3 *T. pilosa*)
	W. acuminata (Asteraceae)	14	10
Original mixture	*G. nodulosus* *W. acuminata* *R. manglesii* *Trachymene* sp.	11 (1 *T. cyanopetata* + 3 *T. ornata* + 7 *T. pilosa*)	10 (4 *T. cyanopetala* + 2 *T. ornata* + 4 *T. pilosa*)
Novel mixture	*G. nodulosus* *W. acuminata*	10	10

	*A. cupaniana** *H. glabra **		

Appendix 5.2 Coefficients from mixed effects models of individual plant biomass by mixture type, soil moisture, and soil P in 2012. A dash denotes instances where focal species was not present in a given mixture type. Asterisks denote level of significance (*: p≤0.05, **: p<0.01, ***: p<0.001).

A. cupaniana	Value	Std.Error	DF	t-value	p-value
(Intercept)	-5.905	0.357	213.000	-16.536	0.000
Novel mixture	0.194	0.184	12.000	1.051	0.314
Soil moisture	0.120	0.121	12.000	0.992	0.341
Colwell P	0.013	0.007	12.000	1.855	0.088
Random effects (variance estimates)	Block: 0.008 Quadrat: 0.078 Residual:0.436				
H. glabra					
(Intercept)	-3.056	0.463	190.000	-6.606	0.000
Novel mixture	-0.529	0.231	13.000	-2.285	0.040
Soil moisture	0.081	0.148	13.000	0.545	0.595
Colwell P	0.036	0.035	13.000	1.042	0.316
Random effects (variance estimates)	Block: 9.31e-9 Quadrat: 0.168 Residual: 0.608				
G. nodulosus					
(Intercept)	-4.965	0.540	259.000	-9.193	0.000
Novel mixture	-0.049	0.227	21.000	-0.214	0.832
Original mixture	-0.461	0.228	21.000	-2.020	0.056
Soil moisture	0.259	0.164	21.000	1.575	0.130
Colwell P	-0.049	0.081	21.000	-0.603	0.553
Random effects (variance estimates)	Block: 0.012 Quadrat: 0.213 Residual: 0.217				
R. manglesii					
(Intercept)	-4.181	0.582	218.000	-7.185	0.000
Original mixture	-0.230	0.152	12.000	-1.513	0.156
Soil moisture	0.104	0.164	12.000	0.636	0.537
Colwell P	-0.020	0.071	12.000	-0.282	0.783
Random effects (variance estimates)	Block: 9.5511e-9				

	Quadrat: 0.095 Residual: 0.180				
T. pilosa					
(Intercept)	-4.383	1.470	117.000	-2.982	0.004
Original mixture	-1.179	0.409	6.000	-2.885	0.028
Soil moisture	1.073	0.457	6.000	2.349	0.057
Colwell P	-0.422	0.246	6.000	-1.715	0.137
Random effects (variance estimates)	Block: 0.462 Quadrat:0.194 Residual: 0.212				
W. acuminata					
(Intercept)	-2.586	0.487	363.000	-5.306	0.000
Novel mixture	0.207	0.206	25.000	1.001	0.327
Original mixture	0.092	0.204	25.000	0.449	0.657
Soil moisture	-0.013	0.141	25.000	-0.091	0.928
Colwell P	-0.087	0.074	25.000	-1.181	0.249
Random effects (variance estimates)	Block: 0.012 Quadrat: 0.174 Residual: 0.476				

Appendix 5.3 Coefficients from mixed effects models of individual plant biomass by mixture type, soil moisture, and soil P in 2013. A dash denotes instances where focal species was not present in a given mixture type. Asterisks denote level of significance (*: p≤0.05, **: p<0.01, ***: p<0.001).

A. cupaniana	Value	Std.Error	DF	t-value	p-value
(Intercept)	-5.072	0.481	252.000	-10.541	0.000
Novel mixture	-0.523	0.272	10.000	-1.919	0.084
Soil moisture	0.029	0.097	10.000	0.295	0.774
Colwell P	0.042	0.064	10.000	0.659	0.525
Random effects (variance estimates)	Block: 0.06 Quadrat: 0.17 Residual:0.57				
G. nodulosus					
(Intercept)	-3.931	0.463	279.000	-8.490	0.000
(Intercept)	-0.392	0.217	15.000	-1.808	0.091
Novel mixture	-0.025	0.258	15.000	-0.095	0.925
Original mixture	0.087	0.093	15.000	0.929	0.367

Soil moisture	0.038	0.036	15.000	1.073	0.300
Random effects (variance estimates)	Block: 3.67e-9 Quadrat: 0.152 Residual: 0.476				
H. glabra					
(Intercept)	-2.064	0.465	152.000	-4.441	0.000
Novel mixture	-0.453	0.197	11.000	-2.297	0.042
Soil moisture	0.030	0.084	11.000	0.356	0.728
Colwell P	0.037	0.038	11.000	0.988	0.344
Random effects (variance estimates)	Block: 0.03 Quadrat: 0.08 Residual: 0.70				
R. manglesii					
(Intercept)	-3.438	0.536	219.000	-6.409	0.000
Original mixture	0.282	0.317	8.000	0.890	0.400
Soil moisture	-0.063	0.086	8.000	-0.731	0.486
Colwell P	-0.045	0.063	8.000	-0.720	0.492
Random effects (variance estimates)	Block: 0.023 Quadrat: 0.23 Residual: 0.355				
T. pilosa					
(Intercept)	-3.301	1.296	95.000	-2.548	0.012
Original mixture	-0.812	0.702	2.000	-1.157	0.367
Soil moisture	0.140	0.245	2.000	0.570	0.626
Colwell P	-0.082	0.114	2.000	-0.715	0.549
Random effects (variance estimates)	Block: 4.0e-8 Quadrat: 0.462 Residual: 0.336				
W. acuminata					
(Intercept)	-1.111	0.576	194.000	-1.929	0.055
Novel mixture	0.052	0.324	15.000	0.159	0.876
Original mixture	0.141	0.351	15.000	0.402	0.693
Soil moisture	0.049	0.103	15.000	0.477	0.641
Colwell P	-0.018	0.061	15.000	-0.290	0.776
Random effects (variance estimates)	Block: 1.4e-8 Quadrat: 0.36 Residual: 0.581				

Appendix 5.4 Means and 95% confidence intervals of observed plot-level biomass deviations from expected yields and constituent diversity effects in novel and original species mixtures in 2012. Asterisks denote level of significance (H_o: $\mu=0$; *: $p \leq 0.05$, **: $p<0.01$, ***: $p<0.001$).

	Mixture type	
Response:	**Novel (n=10)**	**Original (n=11)**
Deviation from expected yield	-0.21 (-0.50-0.07)	0.83* (0.002 – 1.65)
Complementarity	-0.06 (-0.14 – 0.02)	0.38 (-0.45 – 1.21)
Selection	0.04 (-0.08 – 0.16)	0.48*** (0.30 – 0.65)
Dominance	0.08 (-0.02 – 0.17)	0.46*** (0.25 – 0.67)
Trait-dependent complementarity	-0.03 (-0.08 – 0.01)	0.01 (-0.10 – 0.13)

Appendix 5.5 Coefficients and (SEs) from mixed effects models of species deviations from expected relative yields when grown in either community type compared to monoculture in 2012. A dash corresponds to instances where a focal species was not present in a community type. Asterisks denote level of significance (*: $p \leq 0.05$, **: $p<0.01$, ***: $p<0.001$).

	Mixture type	
Species:	**Novel (n=10)**	**Original (n=11)**
A. cupaniana	0.03 (0.05)	-
G. nodulosus	0.03 (0.06)	0.008 (0.07)
H. glabra	-0.23 (0.06)***	-
R. manglesii	-	-0.005 (0.06)
Trachymene sp.	-	0.04 (0.08)
W. acuminata	0.12 (0.05)*	0.19 (0.07)**
Random effects (variance estimates):		
Among block	0.003	0.005
Within block	0.01	0.05

Appendix 5.6 Coefficients from mixed effects models of *A. cupaniana* seed production in interaction neighbourhoods within quadrats in 2013 by neighbourhood identity (relative to single individual plants), neighbour abundance, and overhead woody canopy cover (%). Random effects variance estimates are reported in the main text of the chapter.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)

(Intercept)	4.639	0.383	12.120	<2e-16
Non-native neighbourhood	-0.160	0.398	-0.401	0.688
Native neighbourhood	-0.433	0.393	-1.102	0.271
Neighbour abundance	-0.013	0.020	-0.647	0.518
Canopy cover (%)	-0.031	0.013	-2.475	0.013

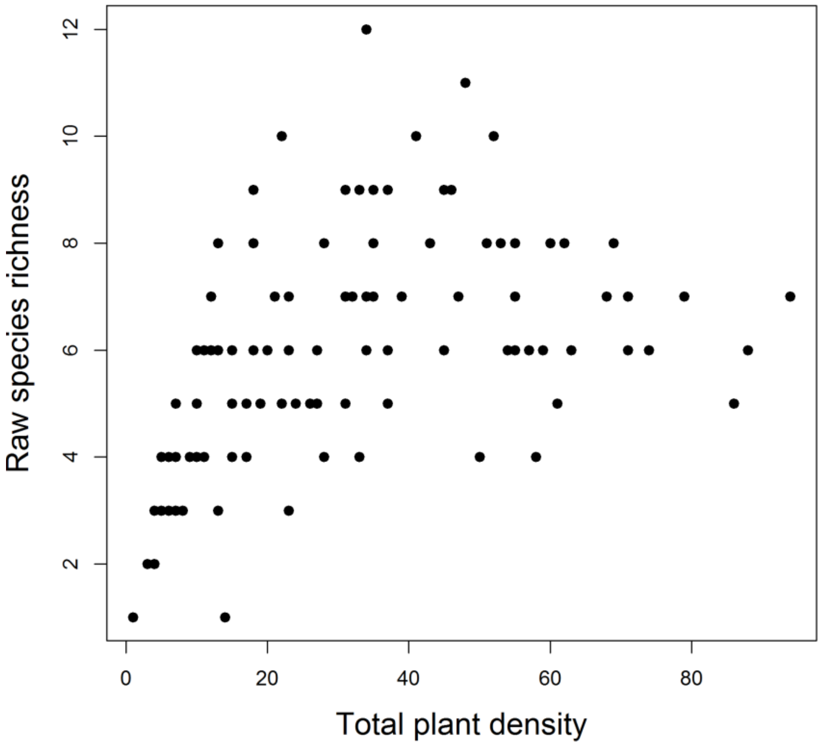
Appendix 5.7 Coefficients from mixed effects models of *T. cyanopetala* seed production in interaction neighbourhoods within quadrats in 2013 by neighbourhood identity (relative to single individual plants), neighbour abundance, reserve (Kunjin relative to Bendering), and overhead woody canopy cover (%). Random effects variance estimates are reported in the main text of the chapter.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	4.096	0.316	12.952	<2e-16
Non-native neighbourhood	0.145	0.251	0.577	0.564
Native neighbourhood	-0.279	0.235	-1.186	0.236
Neighbour abundance	-0.027	0.021	-1.295	0.195
Kunjin Reserve	-0.270	0.211	-1.278	0.201
Canopy cover (%)	0.005	0.008	0.591	0.554

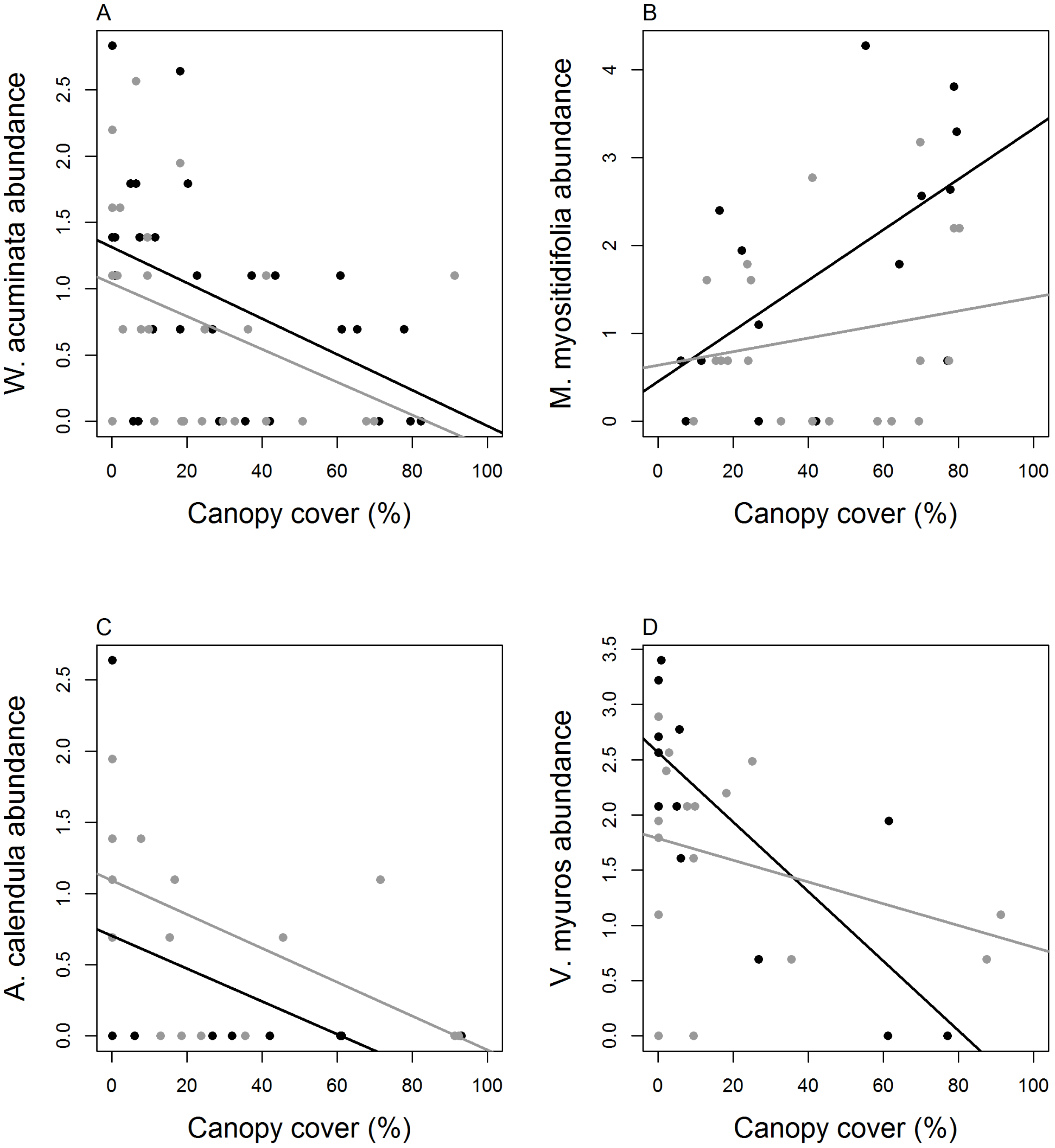
Appendix 5.8 Coefficients from mixed effects models of *T. cyanopetala* seed production in interaction neighbourhoods within quadrats in 2013 by neighbourhood identity (relative to single individual plants), neighbour abundance, reserve (Kunjin relative to Bendering), and overhead woody canopy cover (%). Random effects variance estimates are reported in the main text of the chapter.

Fixed effects:	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	7.196	0.278	25.850	0.000
Non-native neighbourhood	-0.520	0.240	-2.170	0.030
Native neighbourhood	-0.487	0.253	-1.923	0.055
Neighbour abundance	-0.078	0.024	-3.172	0.002
Kunjin Reserve	-0.158	0.162	-0.981	0.327
Canopy cover (%)	0.008	0.008	1.033	0.302

Appendix 6.1 Raw species richness by total plant density in experimental plots (n=110).



Appendix 6.2 Abundances of (A) *W. acuminata*, native, (B) *M. myositidifolia*, native, (C) *A. calendula*, non-native, and (D) *V. myuros*, non-native, by percent canopy cover and presence of *A. barbata* litter (grey) compared to control (black).



Appendix 6.3 Coefficients from mixed effects models of plant community responses to litter addition and pre-treatment environmental variables, with transect specified as a random effect (variance estimates reported in main text of chapter).

Rarefied species richness	Value	Std.Error	DF	t-value	p-value
(Intercept)	2.249	0.953	99.000	2.361	0.020
Litter addition	0.039	0.117	99.000	0.329	0.743
Percent canopy cover	-0.003	0.003	99.000	-1.099	0.275
Ln(nitrate)	0.094	0.103	99.000	0.919	0.360
Ln(P)	-0.339	0.178	99.000	-1.900	0.060
Ln(K)	0.273	0.243	99.000	1.121	0.265
Total plant density					
(Intercept)	8.326	2.450	99.000	3.398	0.001
Litter addition	-0.649	0.275	99.000	-2.363	0.020
Percent canopy cover	-0.023	0.008	99.000	-2.940	0.004
Ln(nitrate)	-0.116	0.256	99.000	-0.453	0.652
Ln(P)	-0.198	0.473	99.000	-0.418	0.677
Ln(K)	-0.356	0.612	99.000	-0.581	0.562
Sqrt(Non-native plant density)					
(Intercept)	4.910	2.046	99.000	2.399	0.018
Litter addition	-0.250	0.216	99.000	-1.158	0.250
Percent canopy cover	-0.012	0.008	99.000	-1.569	0.120
Ln(nitrate)	0.143	0.210	99.000	0.678	0.500
Ln(P)	-0.633	0.400	99.000	-1.581	0.117
Ln(K)	-0.178	0.502	99.000	-0.354	0.725
Sqrt(Native plant density)					
(Intercept)	5.943	2.525	99.000	2.354	0.021
Litter addition	-0.630	0.297	99.000	-2.122	0.036
Percent canopy cover	-0.017	0.007	99.000	-2.435	0.017
Ln(nitrate)	-0.367	0.265	99.000	-1.385	0.169
Ln(P)	0.168	0.481	99.000	0.350	0.727
Ln(K)	-0.168	0.637	99.000	-0.264	0.793

Appendix 6.4 Coefficients from mixed effects models of focal species' abundances in responses to litter addition and pre-treatment abiotic variables. Random effects variance estimates reported in main text of chapter.

A. calendula	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-4.989	4.043	-1.234	0.217
Litter addition	0.497	0.486	1.023	0.306
Canopy cover (%)	-0.018	0.009	-2.075	0.038
Ln(nitrate)	0.771	0.406	1.898	0.058

Ln(P)	-0.945	0.772	-1.224	0.221
Ln(K)	0.896	0.995	0.901	0.368
M. myositidifolia				
(Intercept)	-1.086	4.950	-0.219	0.826
Litter addition	-0.037	0.546	-0.068	0.946
Canopy cover (%)	0.024	0.014	1.753	0.080
Ln(nitrate)	-0.567	0.457	-1.240	0.215
Ln(P)	1.737	0.901	1.927	0.054
Ln(K)	-0.718	1.178	-0.610	0.542
V. myuros				
(Intercept)	-1.705	6.381	-0.267	0.789
Litter addition	0.300	0.793	0.378	0.705
Canopy cover (%)	-0.047	0.016	-2.985	0.003
Ln(nitrate)	0.644	0.678	0.949	0.343
Ln(P)	-0.100	1.173	-0.085	0.932
Ln(K)	-0.142	1.586	-0.090	0.929
W. acuminata				
(Intercept)	0.679	1.894	0.359	0.720
Litter addition	-0.469	0.217	-2.159	0.031
Canopy cover (%)	-0.023	0.005	-4.517	0.000
Ln(nitrate)	0.060	0.169	0.353	0.724
Ln(P)	-0.844	0.332	-2.540	0.011
Ln(K)	0.287	0.464	0.619	0.536

Appendix 6.5 Coefficients from mixed effects models of focal species' biomass (mean per individual) responses to litter addition and pre-treatment abiotic variables. Random effects variance estimates reported in main text of chapter.

A. calendula	Value	Std.Error	DF	t-value	p-value
(Intercept)	2.546	4.320	18.000	0.589	0.563
Litter addition	0.210	0.446	18.000	0.472	0.643
Canopy cover (%)	0.018	0.009	18.000	1.963	0.065
Ln(nitrate)	0.540	0.388	18.000	1.390	0.181
Ln(P)	0.185	0.796	18.000	0.232	0.819
Ln(K)	-1.094	1.093	18.000	-1.001	0.330
M. myositidifolia					
(Intercept)	1.954	2.246	29.000	0.870	0.391
Litter addition	0.231	0.260	29.000	0.889	0.381
Canopy cover (%)	0.002	0.007	29.000	0.243	0.810
Ln(nitrate)	0.221	0.242	29.000	0.910	0.370
Ln(P)	0.513	0.448	29.000	1.144	0.262
Ln(K)	-1.544	0.566	29.000	-2.728	0.011
V. myuros					
(Intercept)	-4.884	2.134	36.000	-2.289	0.028
Litter addition	0.022	0.265	36.000	0.082	0.935
Canopy cover (%)	0.000	0.006	36.000	0.016	0.987

Ln(nitrate)	0.248	0.235	36.000	1.054	0.299
Ln(P)	0.354	0.425	36.000	0.835	0.410
Ln(K)	0.226	0.516	36.000	0.438	0.664
W. acuminata					
(Intercept)	-4.945	2.387	52.000	-2.071	0.043
Litter addition	0.000	0.247	52.000	0.000	1.000
Canopy cover (%)	-0.006	0.007	52.000	-0.873	0.387
Ln(nitrate)	0.181	0.233	52.000	0.775	0.442
Ln(P)	0.392	0.432	52.000	0.909	0.367
Ln(K)	0.585	0.586	52.000	0.998	0.323