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Diversity and ecosystem consequences of multispecies invasion in a dry forest plant community

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Abstract

A key component of ecological change is the invasion of natural systems by alien plant species. As species introductions continue to rise, there is an ongoing need for research to understand the impacts of multiple alien species on communities and ecosystems. Traditionally, studies of plant invasion impacts have largely focussed on single, usually dominant invaders. While this evidence is important and insightful, it does not account for the majority of invaded habitats that contain many co-occurring invaders. Collectively, alien species may exhibit certain attributes or functions that differ from native species. Multispecies invasion could impact community phylogeny, functional structure and ecosystem properties more severely than the impacts of any single invader. In this thesis I investigate the consequences of multispecies invasion for understorey communities, and how they function, in a dry forest system. This system contains many understorey alien species that are well-integrated into the local plant communities. Using a combination of field sampling at multiple spatial scales, literature evidence and a trait-based approach, I examine how multispecies invasion impacts community phylogenetic and functional structure, as well as community productivity. First, using metrics of phylogenetic diversity I show that, collectively, aliens do not detectably impact phylogenetic patterns in the understorey across spatial scales, despite obvious phylogenetic differences between aliens and natives. This implies that understorey communities currently retain their phylogenetic integrity in the wake of multispecies invasion. Second, I investigate differences in life strategies between aliens and natives, and whether functional composition relates to resource availability and stress. Aliens represent a subset of the life strategies already existing in natural communities, but unlike natives, they are not limited by environmental conditions. Third, traits linked to invasion success, and patterns of trait-convergence and –divergence, were related to a gradient of multispecies invasion. Functional diversity increased but stabilised at intermediate and high levels of invasion, demonstrating that multispecies invasion is changing the functional structure of understorey communities. Finally, I determine the relative contribution of functional identity, functional diversity and environment to productivity, and how alien species alter these contributions. Functional identity explained more variation in productivity than functional diversity, and alien traits mimicked the native relationship between functional identity and productivity. In summary, multispecies invasion had little impact on the overall phylogenetic structure of recipient communities, and did not significantly alter aboveground community productivity. The results of this research show how examining multispecies invasion as a continuum or gradient provides both support for existing evidence

on invasion success, as well as novel insights into how multispecies invasion alters functional structure. For the dry forest understorey, the increased abundance of aliens with traits promoting rapid life cycle completion, and the subsequent change to functional structure, is the most immediate and detectable impact of multispecies invasion. As the number of species introductions increase, a shift in focus from single-species invasions to multispecies invasions is needed to expand our knowledge on the consequences of invasion for recipient communities, ecosystems and the services they provide.

Publications during enrolment

Published

McGeoch, M.A., Lythe, M.J., Henriksen, M.V., and McGrannachan, C.M. 2015. Environmental impact classification for alien insects: a review of mechanisms and their biodiversity outcomes. Current Opinion in Insect Science 12:46-53.

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Latombe, G., Pyšek, P., Jeschke, J.M., Blackburn, T.M., Bacher, S., Capinha, C., Costello, M.J., Fernández, M., Gregory, R.D., Hobern, D., Hui, C., Jetz, W., Kumschick, S., McGrannachan, C., Pergl, J., Roy, H.E., Scalera, R., Squires, Z.E., Wilson, J.R.U., Winter, M., Genovesi, P., and McGeoch, M.A. 2016. A vision for global monitoring of biological invasions. Biological Conservation 213:295-308.

Submitted

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Thesis including published works declaration

I hereby declare that this thesis contains no material which has been accepted for the award of any other degree or diploma at any university or equivalent institution and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

This thesis includes one submitted publication and three unpublished data chapters. The core theme of the thesis is invasion ecology. The ideas, development and writing up of all the papers in the thesis were the principal responsibility of myself, the student, working within the School of Biological Sciences under the supervision of Prof Melodie McGeoch and Prof Roslyn Gleadow.

(The inclusion of co-authors reflects the fact that the work came from active collaboration between researchers and acknowledges input into team-based research.)

In the case of Chapters 1, 2, 3 and 4 my contribution to the work involved the following:

Thesis Chapter	Publication Title	Status *(published, in press, accepted or returned for revision, submitted)*	Nature and % of student contribution	Co-author name(s) Nature and % of Co-author's contribution	Co-author(s), Monash student Y/N*
1	Scale-dependent patterns in the phylogenetic relatedness of alien and native taxa	Submitted	Design, data collection, data analysis, manuscript write-up 85%	1) Gillis Horner, data collection, input to manuscript 10% 2) Melodie McGeoch, design, input to manuscript	No
2	Life strategies of alien and native floras in response to environment	Not submitted	Design, data collection, data analysis, manuscript write-up 95%	1) Ros Gleadow, input to manuscript 1% 2) Melodie McGeoch, input to manuscript 4%	No
3	Multispecies invasion increases and homogenizes function in an understorey plant metacommunity	Not submitted	Design, data collection, data analysis, manuscript write-up 90%	1) Melodie McGeoch, design, input to manuscript 10%	No
4	The impact of traits, environment and invasion on productivity	Not submitted	Design, data collection, data analysis, manuscript write-up 90%	1) Ros Gleadow, input to manuscript, 1% 2) Melodie McGeoch, design, input to manuscript 9%	No

I have not renumbered sections of submitted or published papers in order to generate a consistent presentation within the thesis.
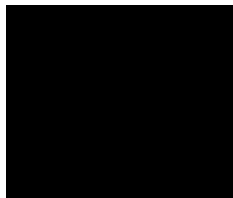
Student signature: **Date:** 4 December 2017

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the student's and co-authors' contributions to this work. In instances where I am not the responsible author I have consulted with the responsible author to agree on the respective contributions of the authors.

Main Supervisor signature: **Date:** 4 December 2017

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General Introduction

Environmental and ecological change is occurring at an unprecedented rate and is largely caused by anthropogenic activities and disturbance (Sala et al. 2000; Tylianakis et al. 2008). A key component of change is the invasion of natural environments by alien plant species (Vilá et al. 2011). Invading plant species can reach high abundances in recipient ecosystems, leading to environmental deterioration and diversity loss (Mack et al. 2000; Vilá et al. 2011; Tekiela & Barney 2015). The severity of plant invasion impacts has propelled efforts to understand the drivers and consequences of alien species introductions (Gurevitch et al. 2011; Lai et al. 2015). However, the lack of a robust framework for understanding alien impacts, coupled with limited empirical data, has impeded efforts to understand and manage plant invasions (Parker et al. 1999; Pyšek et al. 2012; Pearson et al. 2016). Because invader impacts are focal for guiding management and prioritization efforts, it is important to understand how alien invasions affect recipient communities and ecosystems (Lockwood et al. 2013; Ricciardi et al. 2013). Furthermore, as the number of species introductions continues to rise, there is a need to focus studies on the impacts that multiple alien species have on natural systems (Hellmann et al. 2008; Perrings et al. 2010; Kuebbing et al. 2013).

The impact of invasion

Invasion impact can be quantified in many ways. Often, an anthropogenic perspective is applied, so that impact is defined in terms of economic and social health costs and gains (Garcia-Llorente et al. 2008). Here, the focus is on ecological impact, defined by Ricciardi et al. (2013) as measureable changes to ecosystem properties by non-native (alien) species. There are four implications of this definition. First, all introduced species have some impact on the ecosystem they establish in, whether minimal or large. Second, impacts can be positive or negative (increase or decrease the process or property of interest), and vary in strength. Third, impacts can be compared across space, and through time (Ricciardi et al. 2013). Finally, measurements of impact can be taken across different levels of organisation, including the organism, population, community, ecosystem or region (Ricciardi et al. 2013). Impact is often viewed as the final, discrete stage of the invasion process, and is arguably the most important stage, as this is where alien species are likely to severely and negatively affect ecosystem properties such as biodiversity and ecosystem functioning (Richardson et al. 2000; Lockwood et al. 2013). However, once introduced, an alien species may have ecological impacts at any

stage of invasion (Ricciardi et al. 2013). Here, I focus on impact as a discrete and final stage of invasion, where alien species have already passed through earlier stages of invasion (i.e. arrival, establishment and spread) and have integrated into native communities.

There are many ways that alien plant species are known to impact natural ecosystems. Native species richness, abundance and diversity can be reduced by invasive plants, causing the loss of distinct native communities (Winter et al. 2009; Pyšek et al. 2012). Hybridization between invasive and native species can cause the loss of genetic variation in native populations (Vilá et al. 2000). Impacts to mutualistic networks, such as plant-pollinator interactions, can occur through disruptions to pollinator visits or the creation of habitats unfavourable for pollinators (Brown et al. 2002; McKinney & Goodell 2010; Schweiger et al. 2010). Invasive plants can change the chemical and structural quality of litter, in turn affecting soil nutrient cycles and arthropod communities (Liao et al. 2008; Ehrenfeld 2010; Litt et al. 2014). The timing and intensity of fire regimes may be altered by alien species increasing fuel loads (Rossiter et al. 2003; Brooks et al. 2004). Changes to habitat structure induced by alien plants can have flow-on effects to other trophic levels, by altering resource availability, predation rates and nesting patterns (Schmidt & Whelan 1999; Remes 2003; Simberloff 2011). These, and other impacts associated with invasion by alien plants, can affect ecosystem services necessary for human activities and well-being (Pejchar & Mooney 2009; Pyšek et al. 2012).

Not all impacts of alien plants are detrimental to local diversity. Once integrated into a recipient environment, aliens may create new mutualistic relationships, for instance with pollinators, or benefit nutrient cycling by increasing soil organic matter (Ehrenfeld 2003; Schweiger et al. 2010). This in turn can increase native species abundances and overall ecosystem productivity (Pyšek et al. 2012). For example, some invasive species, such as blackberry, may provide shelter for native fauna, reducing predation from natural and introduced predators (Rodriguez 2006). Regardless of the direction of impact (i.e. positive or negative), it is the magnitude of ecosystem change between pre- and post-invasion that is fundamentally important (Pyšek et al. 2012).

Plant invasion impact studies to date have largely focussed on single, usually dominant species (Pyšek et al. 2008; Pearson et al. 2016; Warvek et al. 2017). While this evidence is important and insightful, there is a need to shift focus to impacts of multiple alien species, as invaded habitats regularly contain many co-occurring invaders (Kuebbing et al. 2013). The combined impact of any number of plant invaders can be either additive or non-additive. Additive impacts are simply the sum of the impacts of each individual invader (Kuebbing et al. 2013). The "invasional meltdown" hypothesis represents an extreme case of an additive

impact, where an invader facilitates invasion by subsequent species, leading to further degradation of the ecosystem (Simberloff & Von Holle 1999; Green et al. 2011). When impacts are additive, it may be possible to predict co-occurring alien impacts by extrapolating evidence from single-invader impact studies (Kuebbing et al. 2013). Non-additive impacts are harder to detect, as subsequent invaders may amplify or alleviate impacts experienced by a community (Kuebbing et al 2013; Schuster & Dukes 2014). Although every new alien species added and incorporated into an ecosystem could arguably cause measureable ecological impact, this is not always the case (Rejmánek 2000; Meffin et al. 2010; Pyšek et al. 2012).

Species' traits and measuring functional structure

The recent focus on trait-based approaches to plant community ecology has sought to provide generality and predictability to ecological processes (McGill et al. 2006). Traits are defined as the morphological, physiological and phenological properties of organisms, measurable at an individual scale, without allusion to the environment or higher levels of organisation (Violle et al. 2007). These properties impact upon the three components of individual performance - growth, reproduction and survival - thereby indirectly affecting fitness (Violle et al., 2007). Traits may be specific functions of an organism or a property related to that function ('functional marker', *sensu*. Garnier et al., 2004). For example, traits related to vegetative growth include soil nitrogen (N) uptake (a function) or root density (a functional marker) (Garnier & Navas, 2012). A trait-based approach provides a mechanistic link between species' functions and their environment (abiotic and biotic), identifies community assembly and structure rules, and provides understanding of how species' functions affect ecosystem functions (Chapin et al., 1993; Shipley, 2010; Garnier & Navas, 2012).

Several developed techniques link traits to plant community assembly and ecosystem functioning. The earliest classification scheme involving traits and their functions was developed by Raunkiaer (1934). This involved the classification of plant species into groups represented by similar life forms and environmental responses (Raunkiaer, 1934; Schellberg & Pontes, 2012). The classification of species sharing similar morphological or physiological traits into 'plant functional groups' (PFGs) has been used to explain ecosystem functioning (Wright et al., 2006). A common example of PFGs used is the grass-forb-legume classification (Tilman et al., 1997; Wright et al., 2006). The use of *a priori* PFGs, however, has been criticized for being necessarily subjective, which results in considerable loss of trait variation and explanatory power within datasets (Wright et al., 2006; Shipley, 2010). Dealing directly

with specific traits avoids these problems (Shipley, 2010; Helsen et al., 2012). Interacting plant traits should be investigated in combination, rather than in isolation, because interpreting single-trait responses to abiotic or biotic factors is limited (Schellberg & Pontes, 2012). Furthermore, some traits, such as leaf N concentration and leaf lifespan, often co-vary and should be assessed together (Reich et al., 2003; Díaz et al., 2004; Garnier & Navas, 2012). Some studies, however, have found that single trait measures outperform multi-trait measures (Butterfield & Suding, 2013; Fu et al., 2014). Additionally, traits may act as substitutes for other traits, or may represent overall plant performance, such as vegetative height (Lavorel et al., 2011). This thesis incorporates both single and multi-trait analyses to better understand trait-ecological relationships.

Traits are often used to measure the functional structure of communities (Cadotte et al. 2011). Functional structure is defined as the distribution of trait values measured in a particular community (Díaz et al., 2007, Garnier et al. 2016). Two components of traits – trait value and trait range – are used in quantifying functional structure (Díaz et al., 2007). Trait value is calculated as a community-weighted mean (CWM), and gives the average value of a particular trait in a community, weighted by the relative abundance of each species (Garnier et al. 2004). The CWM represents the most probable trait value expressed by an individual if drawn at random from the community (Garnier et al. 2016). Trait range describes the functional dissimilarity between species and gives an estimation of the functional diversity of traits within a community (Petchey & Gaston 2006). Functional diversity can be measured through multiple indices (Schleuter et al. 2010; Pavoine & Bonsall 2011). One commonly-used metric is Rao's quadratic entropy (FD_Q), which calculates the sum of trait distances between species pairs, weighted by species' relative abundances (Rao 1982; Botta-Dukát 2005). Using CWM and FD_Q to jointly quantify functional structure is recommended, as these two indices are complementary, simple to use and can be applied to numerous traits (Lepš et al. 2006). Furthermore, these indices have low sensitivity to the absence of intraspecific variation measurements, and their sensitivities to the choice of calculation and experimental methods are well-understood (Lavorel et al. 2008; Pakeman 2014; Garnier et al. 2016). Recently, the use of CWMs to link trait-environment relationships to plant survival probabilities has been called into question (Laughlin et al. 2018). In this study, I do not specifically test correlations between CWM traits and environmental conditions, and instead focus on how CWM traits are related to invasion and ecosystem functioning.

It should be noted that the term 'functional diversity' has been used to take into account indices of both trait value and trait range (i.e. functional structure), or to solely take into account

indices measuring functional dissimilarity (i.e. FD_Q). Throughout this thesis, I specifically use the term 'functional diversity' to refer to the range of trait values in a community and its' associated metrics (i.e. FD_Q). I use the term 'functional structure' (*sensu*. Garnier et al. 2016) to describe the distribution (i.e. mean, range and relative abundance) of measured community trait values.

A conceptual model for multispecies invasion

Multispecies invasion can impact different components of recipient communities and ecosystems (Rejmánek et al. 2005). In Figure 1, I present a conceptual model outlining how multispecies invasion influences particular properties of invaded communities and ecosystems, and how invasion interacts with other mechanisms to potentially drive changes in these systems. The conceptual model also serves as an overall guide for the structure of my thesis, with each chapter addressing particular components of the model.

The top centre and centre are comprised of two different community components - phylogenetic diversity and functional structure - that can interact and affect each other (Figure 1). Functional structure can also affect ecosystem functioning through mechanisms proposed by the biomass ratio hypothesis and the complementarity hypothesis. The biomass ratio hypothesis proposes that the trait values of the dominant species in a community will strongly influence ecosystem functioning (Grime 1998), while the complementarity hypothesis states that the range of trait values will have a greater impact (Tilman 1997).

Multispecies invasion can impact these community and ecosystem properties, through their phylogenetic relationships with native species and by differing in their traits and functional niches (van Kleunen et al. 2010). In addition, other mechanisms or factors, such as the physical environment or interactions between organisms, can directly affect functional structure and ecosystem functioning, or indirectly, by influencing alien species themselves (Díaz et al. 2007; Shipley 2010).

Although I link possible mechanisms to community and ecosystem patterns in this conceptual model the ultimate concern and interest of each chapter and the thesis overall lies with the resulting impact of the observed patterns. Thus Figure 1 acts as a framework to reveal the interconnectedness of invasion, environment and hypothesis-driven mechanisms, and how these connections may impact on the phylogenetic and functional structure of native communities, and on ecosystem functioning.

Rationale and thesis aim

Alien species have invaded almost every terrestrial habitat in all areas of the world, and these invaded habitats regularly contain many co-occurring aliens (Mooney & Hobbs 2000: Hobbs et al. 2006). Invasion by multiple alien species is a given: humans must live with, manage and attempt to conserve natural systems that contain many well-integrated invaders (Simberloff 2009; Kuebbing et al. 2013). Because of their permanent presence in these systems, it is important to understand what the implications of these multispecies invasions are. Focusing on how invasion by multiple alien species affects native communities and systems will help us to understand these implications. However, the prevalence of single-invader studies has limited the ability to test how invasive assemblages of species affect recipient communities (Kuebbing et al. 2013; Pearson et al. 2016). If alien species differ in their traits, or function differently, to native species, then the cumulative impact of these differences may be more severe than the impacts of any one alien species.

This thesis aims to examine how multispecies invasion drives changes in community diversity and ecosystem functioning. For this purpose, understorey communities with different levels of multispecies invasion were studied in a dry forest ecosystem of south east Australia. Alien species are well-integrated into these communities, having already passed through the invasion stages of arrival, establishment and spread (Richardson et al. 2000). This means that ecological impact can be investigated in these communities as a discrete and final stage of the invasion process. I use a predominantly trait-based approach to examine the impact of multispecies invasion. This provides insight into how alien and native species differ functionally, which rules of community assembly and structure drive or impede alien impacts, and how alien species traits affect ecosystem functioning (Webb et al. 2002; van Kleunen et al. 2010; Hejda and de Bello 2013).

Study system

Chiltern-Mt. Pilot National Park is a 21 560 ha protected area in north-eastern Victoria, Australia (Figure 2a). It consists of two main areas - the 'Chiltern section' (4 320 ha) and the 'Mt. Pilot section' (14 123 ha) – and numerous smaller sections (3 117 ha; Parks Victoria 2008). Many sections of the park have been afforded protection since 1980 under the *National Parks (Amendment) Act 1978*, but its' current extent was established in 2002 (Parks Victoria 2008). The park contains several ecological vegetation classes, including granitic hills woodlands, box-ironbark forests, and grassy dry and valley grassy woodlands. These systems

are largely open canopies of multiple eucalypt (*Eucalyptus*) species and a single native cypress pine species (*Callitris*).

Historical and ongoing land use in and around Chiltern-Mt. Pilot has created many disturbances that affect the region's ecological integrity. Extensive gold mining practices between 1850 and 1950 has changed the landscape considerably (Parks Victoria 2008). Timber removal for commercial purposes occurred as late as the 1990s and the loss of large old box and ironbark trees has affected the survival of native fauna. Land adjacent to the park was cleared for stock grazing, and this has impacted on the environment through soil compaction and the spread of alien weeds (Parks Victoria 2008). Although there is an absence of alien tree species within Chiltern-Mt. Pilot National Park, the understorey has been invaded by multiple, predominantly herbaceous (i.e. grasses and forbs) species. Natural disturbances such as fire have also considerably impacted the landscape. The most recent (2003 Eldorado) fire resulted in the burning of 33 % (7 156 ha) of the park (Parks Victoria 2008). This resulted in the establishment of a thick understorey of regrowth in the affected areas (Parks Victoria 2008). Despite the impact of these disturbances, Chiltern-Mt. Pilot protects a variety of threatened wildlife and habitats.

Overview of sampling method

Site selection

Fifteen sites (communities) were chosen for *in situ* measurements of plant traits in Chiltern-Mt. Pilot National Park (Figure 2b, 3). These communities were situated in the Mt. Pilot section of the park, spanning a distance of ~ 22 km (between 36°22'00S - 36°32'75S and 146°54'72E - 146°77'25E). The communities were selected from 45 sites thoroughly surveyed for vegetation composition and structure in the austral spring of 2013 and 2014. Each community was 22.4 x 22.4 m (500 m^2) and were further divided into 25, 20 m^2 subplots. Distances between communities were 1 to 22 km, and were located $\geq$ 100 m from vehicle tracks and riparian edges. Areas of low species richness (< 10 vascular plant species) or uninhabitable substrate of > 10 % (e.g. rocky ground) were avoided. Community elevations ranged from 213 − 572 m a.s.l. These communities collectively represent a metacommunity in this system, which is influenced by both local interactions (e.g. competition) and regional processes (e.g. habitat filtering; Logue et al. 2011).

Species pool

The Chiltern-Mt. Pilot understorey species pool was compiled of species recorded in the park. Sources used included the Victorian Biodiversity Atlas (https://vba.dse.vic.gov.au/vba/, accessed 29 Jan 2015), the Atlas of Living Australia (http://www.ala.org.au, accessed 29 Jan 2015), the Chiltern-Mt. Pilot National Park Management Plan (Parks Victoria 2008), the Friends of Chiltern-Mt. Pilot National Park's flora species list (http://www.friendsofchiltern.org.au, accessed on 30 Jan 2015), research publications and data from quantitative observational field surveys of the 45 sites. The final species pool contained 720 understorey plant species, representing 292 genera and 67 families. The alien component of the species pool was 185 (25.69 %) species and the native component 535 (74.31 %).

Quantifying levels of invasion

Encompassing a range of invasion levels across communities was the main criterion for site selection. This was crucial for the establishment of an invasion gradient across communities. Initially, invasion level was determined using species occupancy data from the subplots of the 45 surveyed sites, and the chosen sites ranged from 21.6 – 75.6 % alien species occupancy. Once chosen, communities were sampled for species abundance data from 50, 1 x 1 m^2 quadrats (two per subplot). Tree species and epiphytes on trees were excluded. The abundance data were used to calculate the relative alien cover (%) of each community, and this replaced the occupancy data as the quantified level of multispecies invasion. The updated range of relative alien cover across communities was 3.92 % - 61.08 %.

Trait and environment data collection

In-field data were collected for six traits during the austral spring of 2014 and 2015. The most common species in each community (i.e. 85-95 % of total community cover) were sampled (Table 1). Eighty percent of total community cover is the suggested minimum for sampling of trait data, as this best captures effects on ecosystem properties and ensures adequate sampling (Garnier et al. 2004; Pakeman and Quested 2007). Sampled number of species ranged from 8 to 23 per community. In addition, data for seven traits were obtained from the TRY database (Kattge et al. 2011), Walsh and Entwisle (1992-1996), and existing literature sources. A list of all traits used is provided in Table 2. It should be noted that each trait was selected based on its' relevance to particular chapters, and therefore, are chapter-specific. Aboveground biomass and ten environmental characteristics were quantified at each site. Full detail on biomass

sampling is given in Chapter 4. Methods for environment measurements are detailed in Chapters 2 and 4.

Thesis outline

This thesis contains four data chapters that quantify the impact of multispecies invasion on understorey communities within the dry forest system, using metrics from community and functional ecology. Figure 5 demonstrates how each chapter is incorporated into the thesis conceptual model. Each chapter has a focus independent of other chapters, and each chapter is written as a stand-alone publication. As such, there is some repetition of the description of the study system and basic methods across chapters.

Chapter 1 examines the phylogenetic relatedness of alien and native species across spatial scales (Figure 5a). Darwin's naturalization hypothesis proposes successfully-established alien species are distantly related to native species due to differences in ecological niches, but studies have provided support both for and against this hypothesis (Daehler 2001). Spatial scale can influence phylogenetic patterns, with phylogenetic clustering predicted to occur at coarse spatial scales and phylogenetic overdispersion at finer scales (Cavender-Bares et al. 2006; Procheş et al. 2008). Determining whether alien and native sub-communities are closely or distantly related across spatial scales is important in understanding patterns of invasion (Diez et al. 2008). Furthermore, identifying whether invaded communities exhibit similar phylogenetic patterns to their alien or native components across spatial scales can provide insight on how invasion impacts community phylogenetic structure. It will also help to identify at what spatial scale this impact is likely to occur.

In Chapter 2, differences in life strategies between alien and native herbaceous species are quantified using Grime's C-S-R theory (Figure 5b). I use traits found to be the best predictors of C-S-R strategies in combination to reveal which life strategies are dominant in this system, and how these life strategies may differ between aliens and natives. Relationships between C-S-R composition and the environment are also investigated. Successful invasion by alien plants is predicted to increase when resources become more abundant, either through disturbance or a decrease in resource uptake by natives (Davis et al. 2000). Given this prediction, aliens would exhibit life strategies and traits that help them to outcompete natives and thrive in disturbed environments (Grime 2001). Determining how alien life strategies differ from local native species will provide insight into how aliens collectively shift the trait structure and functioning of communities. Environmental factors related to resource availability and stress may influence

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the functional responses of both aliens and natives (Radford 2013). Testing life strategy-environment relationships may reveal what aspects of the environment are limiting or benefitting alien integration into recipient communities.

Chapter 3 investigates how increases in multispecies invasion are related to changes in community-wide traits and patterns of trait convergence and divergence across an invasion gradient (Figure 5c). Several traits that enhance performance, such as high specific leaf area, have been linked to invasion success (van Kleunen et al. 2010; Leishman et al. 2014; Marx et al. 2016). Often, the traits possessed by alien species are shaped by mechanisms such as habitat filtering and niche differentiation, and their influence may determine whether aliens have similar or different traits to natives (Thompson et al. 1995; Lake and Leishman 2004). These mechanisms are also known to operate at a metacommunity scale, and drive patterns of trait convergence and divergence along ecological gradients (Stubbs and Wilson 2004; Cornwell and Ackerly 2009; Logue et al. 2011). However, trait convergence and divergence have not been related to gradients of multispecies invasion. Furthermore, studies linking traits to invasion success have focussed on pairwise comparisons of aliens and natives, or invaded and uninvaded communities (Pyšek and Richardson 2007; Kuebbing et al. 2013). The few studies involving invasion gradients have considered only single-species invasions (Robertson and Hickman 2012; Bansal and Sheley 2016). Examining traits and patterns of convergence and divergence along a multispecies invasion gradient could identify what components of community trait structure are altered by multispecies invasion.

In Chapter 4 the importance of traits and environment for community productivity, and how multispecies invasion affects trait-productivity relationships, is quantified (Figure 5d). Plant communities and their traits are believed to impact ecosystem functioning, including productivity, either through the trait values of dominant species (i.e. functional identity; Grime 1998) or through the range of trait values in a community (i.e. functional diversity; Tilman 1997). In addition, local environmental conditions can strongly impact community productivity (Díaz et al. 2007). Jointly examining the relative importance of trait values, trait range and environment for productivity provides an understanding of how these mechanisms combine to impact ecosystem functioning (Díaz et al. 2007). In addition, aliens may have trait values that amplify or decrease the importance of particular community traits linked to productivity (Hejda and de Bello 2013). Determining if aliens collectively impact productivity more strongly through functional identity or functional diversity provides insight into the consequences of multispecies invasion for ecosystem functioning.

Finally, in the general discussion, the findings from each chapter are discussed together, in the context of the study system, and how these results contribute to our general understanding of the impacts of multispecies invasion for invaded communities and ecosystems.

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Tables

Table 1. List of understorey species sampled for trait measurements across the 15 communities.

Family	Species	Author	Status
Apiaceae	*Daucus glochidiatus*	(Labill.) Fischer, C. Meyer & Ave Lall.	Native
	Hydrocotyle laxiflora	DC.	Native
Asparagaceae	*Lomandra filiformis*	(Thunb.) Britten	Native
	Lomandra longifolia	Labill.	Native
	Lomandra multiflora	(R. Br.) Britten	Native
Asteraceae	*Carduus pycnocephalus*	Spreng.	Alien
	Cirsium vulgare	(Savi) Petr.	Alien
	Euchiton japonicus	(Thunb.) Anderb.	Native
	Hypochaeris spp.	L.	Alien
	Xerochrysum viscosum	(Sieber ex DC.) R.J. Bayer	Native
Campanulaceae	*Wahlenbergia spp.*	Schrad. ex Roth	Native
Caryophyllaceae	*Cerastium glomeratum*	Thuill.	Alien
	Stellaria media	(L.) Vill.	Alien
Celastraceae	*Stackhousia monogyna*	Labill.	Native
Colchicaceae	*Burchardia umbellata*	R. Br.	Native
Convolvulaceae	*Dichondra repens*	J.R. Forster & G. Forster	Native
Dilleniaceae	*Hibbertia obtusifolia*	DC.	Native
	Hibbertia riparia	(R. Br. ex DC.) Hoogland	Native
Droseraceae	*Drosera peltata*	Thunb.	Native
Ericaceae	*Acrotriche serrulata*	(Labill.) R. Br.	Native
	Brachyloma daphnoides	(Sm.) Benth	Native
	Leucopogon virgatus	(Labill.) R.Br.	Native
Fabaceae	*Desmodium varians*	(Labill.) G. Don	Native
	Platylobium formosum	Sm.	Native
	Trifolium arvense	L.	Alien
	Trifolium campestre	Schreb.	Alien
	Trifolium dubium	Sibth.	Alien
Gentianaceae	*Centaurium erythraea*	Rafn	Alien
Geraniaceae	*Geranium sp. 2*	L.	Native
Haloragaceae	*Gonocarpus tetragynus*	Labill.	Native
Hypericaceae	*Hypericum gramineum*	G. Forst.	Native
	Hypericum perforatum	L.	Alien
Juncaceae	*Juncus aridicola*	L.A.S. Johnson	Native
	Luzula densiflora	(H.Nordensk.) Edgar	Native
	Luzula flaccida	(Buchenau) Edgar	Native
Lamiaceae	*Ajuga australis*	R. Br.	Native
Oxalidaceae	*Oxalis perennans*	Haw.	Native
Phyllanthaceae	*Poranthera microphylla*	Brongn.	Native
Poaceae	*Aira elegantissima*	Schur	Alien
	Anthoxanthum aristatum	Boiss.	Alien
	Briza maxima	L.	Alien
	Briza minor	L.	Alien

Family	Species	Author	Status
	Bromus diandrus	Roth	Alien
	Bromus madritensis	L.	Alien
	Dichelachne hirtella	N.G. Walsh	Native
	Holcus lanatus	L.	Alien
	Microlaena stipoides	(Labill.) R.Br.	Native
	Pentapogon quadrifidus	(Labill.) Baill.	Native
	Poa sieberiana	Spreng.	Native
	Rytidosperma pallidum	(R.Br.) A.M. Humphreys & H.P. Linder	Native
	Rytidosperma spp.	Steud.	Native
	Vulpia bromoides	(L.) Gray	Alien
	Vulpia spp.	C. Gmel.	Alien
Primulaceae	*Lysimachia arvensis*	(L.) U. Manns & Anderb.	Alien
Pteridaceae	*Cheilanthes austrotenuifolia*	H.M. Quirk & T.C. Chambers	Native
Ranunculaceae	*Ranunculus pumilio*	R. Br. ex DC.	Native
Rubiaceae	*Sherardia arvensis*	L.	Alien
Violaceae	*Viola hederacea*	Labill.	Native
Xanthorrhoeaceae	*Stypandra glauca*	R.Br.	Native

Table 2. List of field-based and literature-sourced traits, and their associated chapters.

Trait	Unit of measurement	Relevant Chapter(s)
In-field		
Leaf area	mm^2	Chapter 3, 4
Leaf dry matter content	%	Chapter 2
Leaf dry mass	mg	Chapter 2, 3, 4
Leaf thickness	mm	Chapter 3, 4
Specific leaf area	mm^2 mg^{-1}	Chapter 2, 3, 4
Maximum vegetative height	mm	Chapter 2, 3, 4
Literature-sourced		
Clonal	clonal/non-clonal	Chapter 3, 4
Flowering duration	months	Chapter 2, 3
Flowering start	six point classification	Chapter 2
Lateral spread	six point classification	Chapter 2
Leaf dry matter content	%	Chapter 2
Life history	annual/perennial	Chapter 3
Seed mass	mg	Chapter 3

Figures
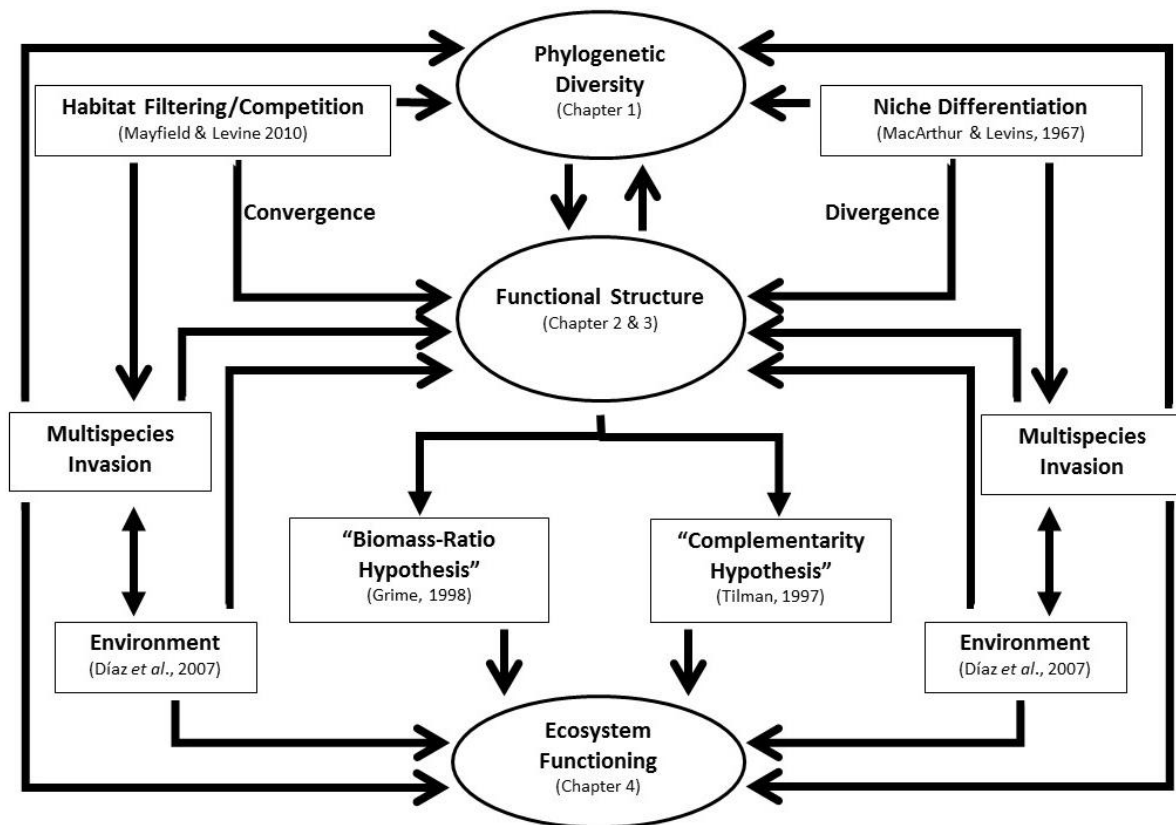
Figure 1. Thesis conceptual model. The model outlines how multispecies invasion influences community and ecosystem properties, and how it interacts with other mechanisms to potentially drive changes in these systems.
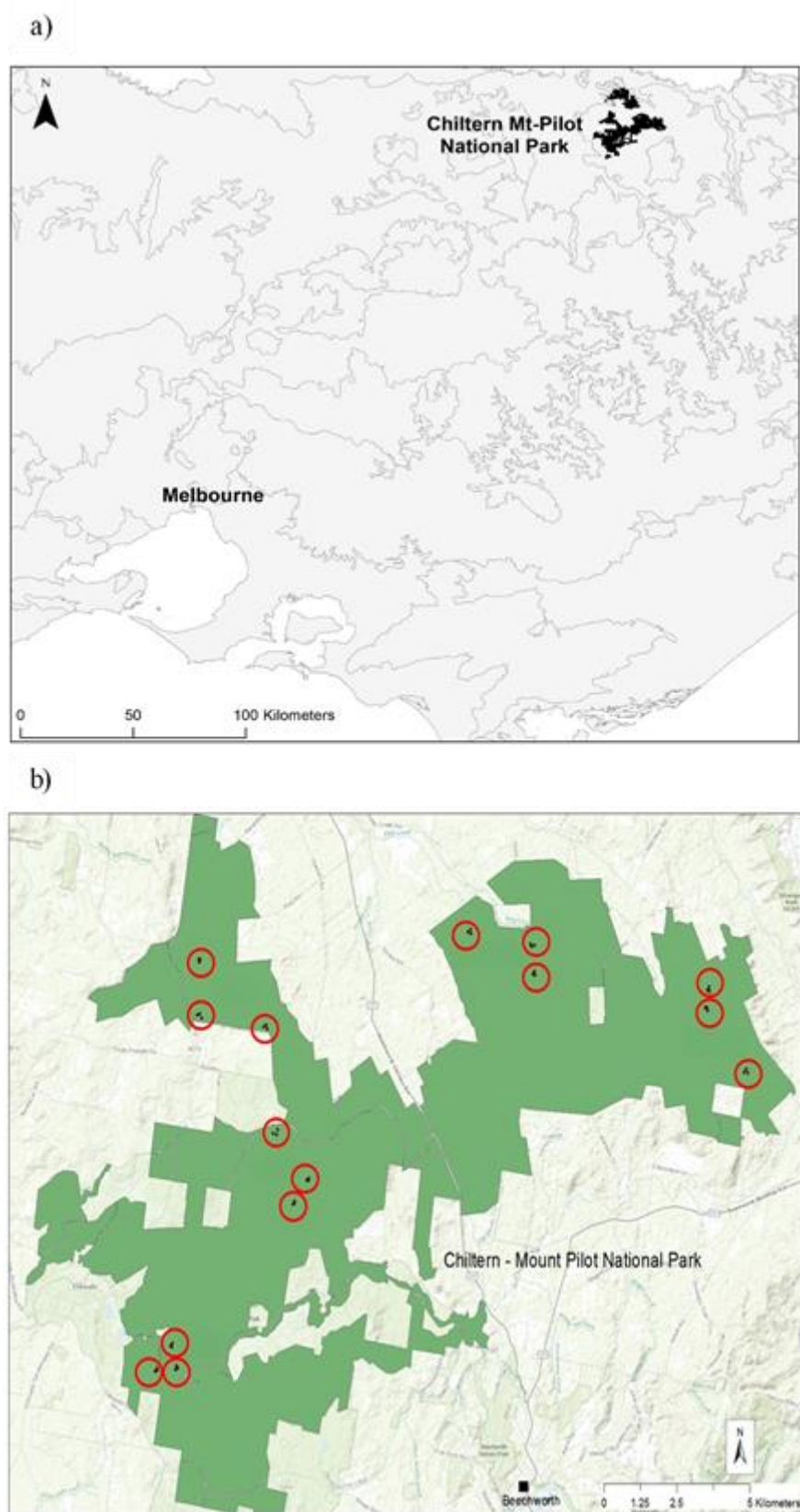
Figure 2. a) Location of Chiltern-Mt. Pilot National Park in north-east Victoria, Australia. b) Position of the 15 communities in the Mt. Pilot section.

Figure 3. Sites of four of the sampled communities.
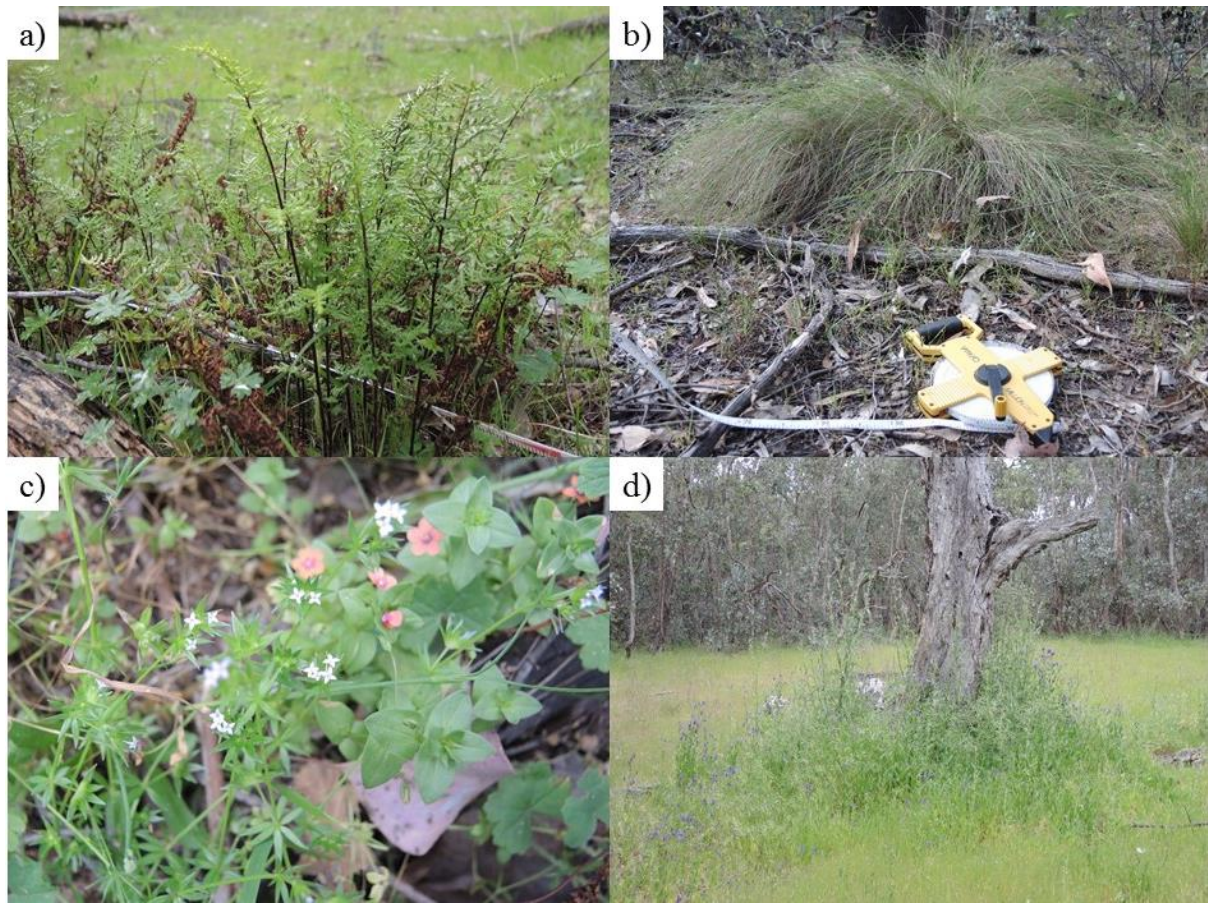
Figure 4. Selected species from the understorey communities. a) The fern *Cheilanthes austrotenuifolia*, flanked by *Geranium sp. 2* (both native). b) The tussock grass *Rytidosperma pallidum* (native). c) *Sherardia arvensis* (left) and *Lysimachia arvensis* (right; both alien). d) *Carduus pycnocephalus* (alien) growing around the base of a dead eucalypt.
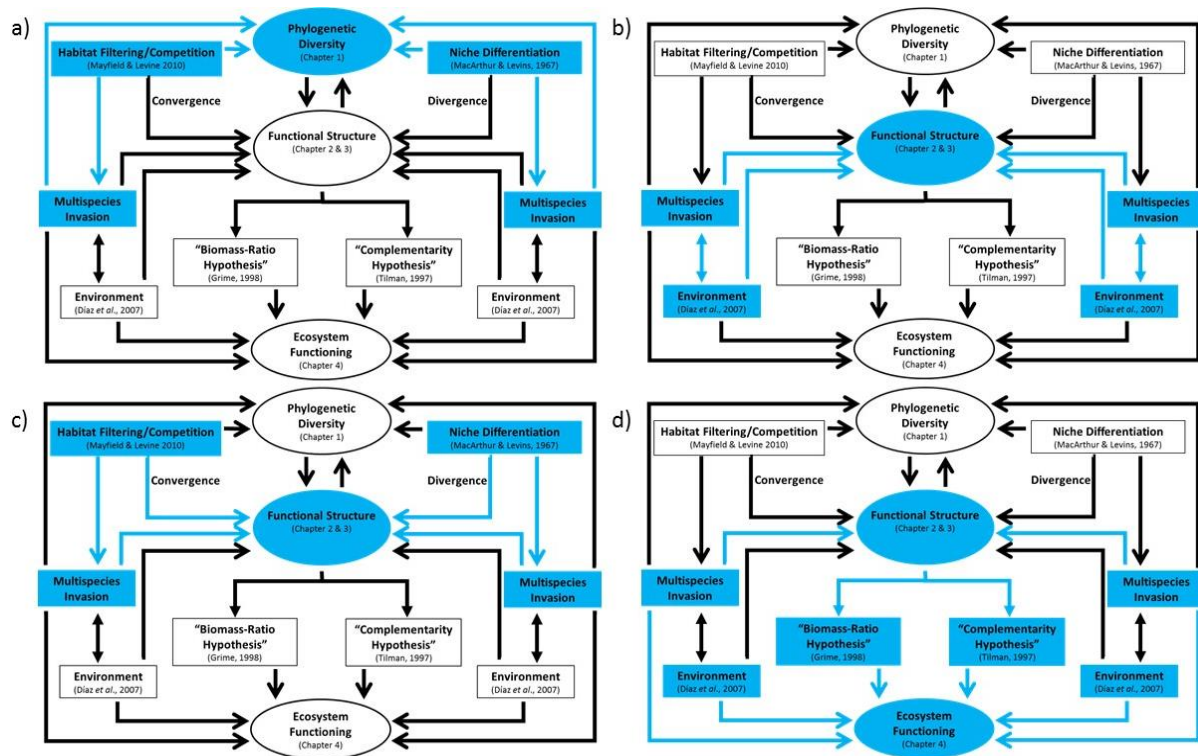
Figure 5. Chapter integration into the thesis conceptual model. The highlighted (blue) sections are the components relevant to a) Chapter 1, b) Chapter 2, c) Chapter 3, and d) Chapter 4.

Chapter 1

Scale-dependent patterns in the phylogenetic relatedness of alien and native taxa

Introduction

Assimilation of alien species into resident communities is driven by mechanisms such as interactions with extant species, regional-scale environmental filters, dispersal constraints and stochastic events such as disturbance (Levine 2000). Environmental filters and dispersal constraints reduce the pool of potential alien colonists to species with traits that enable their transport, arrival and establishment (Keddy 1992; Diez et al. 2008). However, persistence and expansion in the new environment is considered to be largely determined by interactions with resident native species and the degree of niche overlap shared by alien and native species (Mitchell et al. 2006). Once successfully established, alien species can impact the diversity patterns (e.g. biodiversity; functional and phylogenetic diversity) of native communities (Winter et al. 2009; Vilá et al. 2011).

Phylogenetic methods are useful for testing hypotheses about the assembly mechanisms that influence community diversity, including invaded communities (Webb et al 2002; Cavender-Bares et al. 2006). Specifically, the phylogenetic relatedness of alien species to recipient native communities can be used as a metric of niche overlap, and has also been used to predict the likelihood of invasion success of alien species (Diez et al. 2008). The idea that alien and native species relatedness influences the success of alien establishment was originally proposed by Darwin (1859). 'Darwin's naturalization hypothesis' (Daehler 2001) proposes that aliens introduced into new ecosystems are less likely to invade successfully if they are closely related to the natives in the recipient community. This implies that closely-related species are more likely to share similar ecological niches as a result of common ancestry, leading to resource competition, and a priority effect where established native species outcompete their closely-related alien counterparts (Tan et al. 2012). Conversely, species distantly related to each other (i.e. phylogenetic overdispersion) are expected to differentiate resource use, resulting in decreased competition and increased success at invading the resident community. Darwin also proposed a contradictory hypothesis, that aliens may establish more successfully in novel locations if they are closely related to natives (i.e. phylogenetically clustered), because they share similar environmental preferences. These two hypotheses have given rise to 'Darwin's naturalization conundrum' (Diez et al. 2008): success of alien establishment is more feasible when they are either closely or distantly related to natives in the invaded community.

Both hypotheses have garnered support, exacerbating the conflict that Darwin's naturalization conundrum presents (Lososová et al. 2015; Park & Potter 2015). Reasons for mixed support may be caused by factors other than environmental conditions or competition:

1) First, facilitation and plant-pollinator interactions can lead to phylogenetic clustering independently of environmental filtering (Sargent & Ackerly 2008). 2) Competition can also drive phylogenetic clustering when certain phenotypes are correlated with competitive dominance, such as when tall, closely-related species competitively exclude shorter taxa in light-limited environments (Mayfield & Levine 2010; Godoy et al. 2014). 3) Aliens may be less inclined to experience herbivory when they are distantly related to natives, increasing their chance of success in the new environment (i.e. the 'enemy release' hypothesis; Keane & Crawley 2002). 4) Processes determining invasion success can differ among invasion stages (i.e. colonisation, establishment and spread of aliens; Theoharides & Dukes 2007) and affects the direction and importance of phylogenetic relationships between alien and native taxa (Diez et al. 2008; Schaefer et al. 2011). For example, abiotic conditions may have greatest influence at establishment, whereas interactions with resident species may dominate when aliens begin to spread (Diez et al. 2008; Schaefer et al. 2011). 5) Finally, human-mediated introductions of aliens may impact community phylogeny by shaping the structure of the species pool. Aliens introduced for ornamental or agricultural purposes are often closely related, possessing traits which make them appealing for human use, while being phylogenetically distinct from natives (Cadotte et al. 2009).

Importantly, differences in the spatial extent of phylogenetic studies may also play a role (Thuiller et al. 2010; Cadotte & Davies 2016; Ma et al. 2016). Ecological patterns and the processes that generate them, including the process of invasion, are well known to be scale-dependent, (Lambdon & Hulme 2006; Proches et al. 2008). Species moving through the different stages of invasion (colonization to establishment to spread) pass through filters that operate at different scales (abiotic, biotic, dispersal; Theoharides & Dukes 2007). At fine spatial scales (i.e. within habitats) where competition between individuals occurs, niche dissimilarity between alien and native species is expected, resulting in aliens and natives being less related than expected by chance. As the spatial resolution increases, the influence of environmental filtering in shaping communities tends to increase. Thus, at coarser spatial scales it is expected that the phylogenetic relatedness of alien and native species may increase, compared to finer scales, as closely-related species tend be sorted along environmental gradients (Carboni et al. 2013). These closely-related species are expected to share traits derived from a common evolutionary history, allowing them to survive under the prevailing abiotic conditions (Pearson et al. 2012). Given these assumptions, Darwin's naturalization hypothesis should be supported more strongly and more consistently at fine than course spatial extents (Pearson et al. 2012; Carboni et al. 2013).

Identifying phylogenetic patterns for communities of interest, in particular invaded communities, is informative. If the alien species sub-community (i.e. the alien component of the community) is phylogenetically clustered, this provides insight into both the history of invasion at a regional scale and which species could be involved in future invasions. Similarity between the phylogenetic patterns of the entire community and the alien sub-community at a specific spatial scale could indicate at what spatial scale invasion is likely to impact community phylogenetic structure. This impact may have consequences on the functional and biological diversity of resident communities. Most research involving the phylogenetic consequences of invasion for native communities focus on the phylogenetic differences between native and alien taxa (Duncan & Williams 2002; Schaefer et al. 2011). Other studies report on how the phylogenetic structure of native communities influences susceptibility to invasion and how ensuing invasion changes phylogenetic structure at a particular spatial scale (Gerhold et al. 2011; Lososová et al. 2015). Less attention has been given to determining the extent to which 1) alien sub-communities drive the phylogenetic structure of whole communities and 2) whether these patterns change with spatial scale (although see Carboni et al. 2013; Ma et al. 2016).

Here I examine the phylogenetic relatedness of alien and native plant species across spatial scales within a species-rich invaded dry forest understorey ecosystem in south east Australia. I first test at the species pool (landscape) scale (i) if the understorey plant community and its native and alien sub-communities are phylogenetically clustered or overdispersed, and (ii) if the patterns of phylogenetic relatedness of the entire community more closely resemble those of the alien or native sub-communities (as one indicator of community novelty). I then examine iii) how these phylogenetic patterns change with spatial scale, including if alien plant species are more or less related to native plant species than expected at random at each scale. I predict Darwin's naturalization hypothesis will hold at the finest spatial scales and not at coarser scales, and therefore that phylogenetic relatedness will decline with increasing spatial scale. Furthermore, based on previous findings I predict that alien plant species will be more phylogenetically clustered across spatial scales than native species (Cadotte et al. 2010a; Carvallo et al. 2014).

Methods

Study location and sampling resolutions

Chiltern-Mt. Pilot National Park (north-east Victoria, Australia) was established in 1980, and encompasses 21 560 ha of granitic hills woodlands and box-ironbark forest of predominantly open canopies of multiple eucalypt (*Eucalyptus*) taxa and a single native cypress pine (*Callitris*). The regional landscape was extensively used for gold mining, forestry and agriculture by European settlers, resulting in more than 80 % loss of native vegetation (Parks Victoria 2008). Since European settlement the surviving ecosystems have been under pressure from disturbances such as alien species invasion and soil erosion from changing land use (Parks Victoria 2008). Nevertheless, the park protects a number of flora with high conservation value, including several orchid species (Parks Victoria 2008).

Within the park, five spatial scales were used to investigate changing phylogenetic patterns in the understorey plant community: park (referred to as the landscape scale; 215 km^2, $n = 1$), array (4.5 km^2; $n = 5$), subarray (1.5 km^2; $n = 15$), plot (500 m^2; $n = 45$) and subplot (20 m^2; $n = 132$; Figure 1). For simplicity, the study sites across all spatial scales are collectively or individually referred to as 'sample units'. Five arrays were independently positioned across the extent of the park between 1 and 18 km apart. Subplots represent the finest spatial resolution (Figure 1), and three subplots from each plot were randomly selected for use in the study (one plot included only one subplot and another only two subplots, due to a lack of alien species present in these plots).

Species pool

A plant species list was compiled for Chiltern-Mt. Pilot, which represents the species pool for the study. This included presence records from the Victorian Biodiversity Atlas (https://vba.dse.vic.gov.au/vba/, accessed 29 Jan 2015) and the Atlas of Living Australia (http://www.ala.org.au, accessed 29 Jan 2015), the Chiltern-Mt. Pilot National Park Management Plan (Parks Victoria 2008), the Friends of Chiltern-Mt. Pilot National Park's Flora species list (http://www.friendsofchiltern.org.au, accessed on 30 January 2015), research publications and our own quantitative observational field survey. Because the community of interest was the species-rich herbaceous understorey, purely aquatic species, tree species, epiphytic species on trees, and ferns were excluded. Ferns were excluded because, being

distantly related to angiosperms, they can often overwhelm phylogenetic patterns with long phylogenetic branches (Kembel & Hubbell 2006).

Species composition was determined in field surveys for sample units at each spatial resolution below the landscape scale. In the Austral spring of 2013 and 2014, 45 (22 x 22 m) plots were sampled for plant species, with composition determined at the subplot scale. Plot matrices were combined to create presence-absence matrices for the subarrays and arrays. The resulting species lists were subsets of the species pool list generated at the landscape scale. All species across all matrices were categorised as either alien or native, using information from Walsh & Entwisle (1992-1996) and the Victorian Biodiversity Atlas (https://vba.dse.vic.gov.au/vba/, accessed 29 Jan 2015).

Phylogenetic analyses

A supertree for the species pool was created using the APG III phylogeny (version 13, http://www.mobot.org/MOBOT/research/APweb/) and Phylomatic (Webb & Donoghue 2005). Branch lengths were assigned to the phylogenetic tree using the branch length adjustment algorithm (BLADJ) in Phylocom (Webb et al. 2008). This algorithm fixes known molecular and fossil dates to the nodes of the phylogenetic tree, giving rise to branch lengths on the phylogeny calibrated in millions of years (Wikstrom et al. 2001). The resulting supertree contained polytomies (unresolved relationships) within a number of genera, which can influence measures of phylogenetic diversity (Kuhn et al. 2011). The polytomies were resolved using the method of Pagel (1992) in Phylocom (Webb et al. 2008).

Four measures of phylogenetic diversity were calculated for each sample unit: (1) alien and native species combined (the whole-community), (2) the alien and (3) native sub-communities and (4) one calculation for the phylogenetic difference between alien and native sub-communities. These measures were obtained using two metrics of phylogenetic diversity. The mean pairwise distance (MPD) provides the mean of all pairwise phylogenetic distances between the taxa within a local assemblage (Webb et al. 2002). This metric expresses phylogenetic diversity at a tree-wide (basal) level. The mean nearest taxon distance (MNTD) represents the mean phylogenetic distance of each taxon to its closest relative within the local assemblage (Webb et al. 2002), is considered a branch tip (terminal) metric and tends to be less sensitive to phylogenetic resolution than MPD (Swenson 2009). Both MPD and MNTD are expressed in millions of years (Ma).

Indices of phylogenetic diversity are often highly correlated with species richness, making comparisons across sites and spatial scales with different numbers of species difficult (Pavoine & Bonsall 2010). To rectify this, null models were used to calculate standardised effect sizes of MPD and MNTD (Swenson 2014). An independent swap algorithm was implemented to generate 999 randomly-assembled local assemblages for each sample unit (Gotelli & Entsminger 2003). This algorithm conserves both species richness and frequency of occurrence across samples while randomising species co-occurrence. Because I am interested in the phylogenetic relatedness of species that co-occur within assemblages, the independent swap algorithm was most relevant for use in null models (Gotelli & Entsminger 2003).

To effectively implement the independent swap algorithm for the whole community at the landscape scale (i.e. the species pool) it was necessary to include species located outside of Chiltern-Mt. Pilot. This was achieved by creating a 20 km radius buffer (comparable to the extent of the array placement within the park) from the centre point of the park. Using the Atlas of Living Australia (http://www.ala.org.au, accessed 29 January 2015) all plant species located within the buffer zone that were not already present within the boundaries of the park were recorded.

The net relatedness index (NRI, from MPD) and nearest taxon index (NTI, from MNTD) were calculated as the standardised effect sizes of phylogenetic relatedness (Webb 2000):

$$NRI = -1 * \frac{MPD_{obs} - MPD_{rnd}}{sd(MPD_{rnd})}$$

$$NTI = -1 * \frac{MNTD_{obs} - MNTD_{rnd}}{sd(MNTD_{rnd})}$$

Here, MPD_{obs} represents the observed MPD of each sample unit, MPD_{rnd} represents the mean MPD obtained from the 999 randomisations and sd(MPD_{rnd}) is the standard deviation of MPD_{rnd}. NRI and NTI reveal patterns of relatedness among species at different phylogenetic resolutions and were therefore both used (Webb et al. 2002; Swenson 2014). Positive NRI values suggest co-occurring species within a sampling unit are more likely to be related to each other than expected by chance, due to *tree-wide* (i.e. species pool level) phylogenetic clustering. Negative NRI values indicate co-occurring species are less related to each other than expected at random due to *tree-wide* phylogenetic overdispersion of co-occurring species (Webb et al. 2000; Kembel & Hubbell 2006). Phylogenetic clustering at the *terminal branches* results in positive NTI values, indicating closely-related species (e.g. congeners) are more likely to occur together within sampling units. When closely-related species occur less frequently together within sampling units NTI values will be negative as a result of

phylogenetic overdispersion at the *terminal branches* (Kembel & Hubbell 2006). Whole community, alien and native NRI and NTI were obtained using the COMSTRUCT algorithm in Phylocom (Webb et al. 2008) and the NRI and NTI for relationships between aliens and natives obtained using Phylocom's COMDIST and COMDISTNT algorithms, respectively.

Two-tailed t-tests were used to test if the mean observed NRI and NTI at each spatial scale (excluding landscape, which had only one value) were significantly different from the null expectation of zero (i.e. significantly different from a random phylogenetic pattern). Two-tailed tests were appropriate as NRI and NTI are used to detect both phylogenetic clustering and overdispersion that drive both metrics in opposing directions (Webb 2000). A two-way fixed effects ANOVA was implemented to test whether mean NRI and mean NTI differed significantly between alien and native sub-communities and across spatial scales, including an interaction term. A one-way ANOVA was used to test if mean NRI and mean NTI for the phylogenetic relatedness of aliens and natives differed across spatial scales.

Results

Phylogenetic patterns across spatial scales

The Chiltern-Mt. Pilot understorey species pool included 720 plant species, 292 genera and 67 families. Aliens accounted for 185 (25.69 %) and natives 535 (74.31 %) species (Appendix A; Figure A1). Mean pairwise distance ranged from 479 Ma to 516 Ma across all community groups and spatial scales (Table A1). The alien sub-community consistently had the lowest MPD at all spatial scales (Table A1). The whole community and native sub-community MPD were similar at each spatial scale. Mean nearest taxon distance ranged from 112 Ma to 297 Ma (Table A1). The whole community had the lowest MNTD while the alien sub-community had the highest MNTD across all spatial scales. MNTD declined with spatial scale for all community groups.

At the landscape scale, the understorey plant community was phylogenetically clustered (both net relatedness index and nearest taxon index) (Figure 2). Alien and native sub-communities were also clustered (Figure 2). At the tree-wide level (NRI), the whole community and alien and native sub-communities were similarly clustered to each other (Figure 2). However, at the terminal level (NTI), aliens were more clustered than natives, with values for natives similar to the whole community (Figure 2).

Across spatial scales finer than the landscape, whole community and native sub-community NRI differed from the alien sub-community, and were overdispersed rather than clustered

(Figure 2). The NTI of all three groups were clustered (Figure 2). At the tree-wide level (NRI), overdispersion increased with spatial scale. Phylogenetic clustering at the terminal level (NTI) also increased with spatial scale for the whole community. The native sub-community did not change in NTI across spatial scales (Figure 2). Mean NRI was significantly different to random at all spatial scales except at the subplot scale for the whole community and at the array scale for the native sub-community. This was despite the mean NRI for the array being further from zero (i.e. a random phylogenetic pattern) than the means of the finer spatial scales (Table 1). Mean NTI was not significantly different from random across all spatial resolutions for both community and native sub-community (Table 1).

The alien sub-community was strongly and significantly clustered (both NRI and NTI; Figure 2a, b). This clustering increased with spatial scale and different from null expectations across all spatial scales (Table 2). The phylogenetic pattern of the whole community was more similar to the native than the alien sub-community. This was particularly evident for NRI (Figure 2a). However, at the landscape scale, NRI of all three groups was similarly clustered (Figure 2a).

There were significant differences in NRI and NTI between the two sub-communities (NRI ~ community group + spatial scale + community group * spatial scale; $F(1, 386) = 570.92$, $p = < 0.001$), (NTI ~ community group + spatial scale + community group * spatial scale; $F(1, 386) = 198.9$, $p < 0.001$). Significant differences were found across spatial scales for NRI ($F(3, 386) = 11.62$, $p = < 0.001$), but not for NTI ($F(3, 386) = 2.03$, $p = 0.108$). However, there were significant interactions between sub-community and spatial scale for both metrics (NRI $= F(3, 386) = 31.55$, $p = < 0.001$; NTI $= F(3, 386) = 5.43$, $p = 0.001$).

Phylogenetic distance between alien and native species assemblages

Alien and native sub-communities were distantly related to each other as indicated by high overdispersion at the landscape scale (both NRI and NTI; Table A1). Overdispersion was particularly apparent for NTI, (NTI = -18.3 versus NRI = -4.17; Table A1). At all spatial scales finer than the landscape both NRI and NTI were overdispersed (Figure 3). Again, this was particularly pronounced for NTI. In both cases, overdispersion increased with spatial scale.

Patterns of relatedness were significantly different from null expectations at all spatial scales, except at the array scale for NRI (Table 2). This was despite the array-NRI value being further from 0 (i.e. a random phylogenetic pattern) than the NRI values at finer spatial scales (Table 2a). The phylogenetic distance between alien and native sub-communities was

significant at all spatial scales (NRI (F (3, 193) = 4.65, $p = < 0.001$); NTI (F (3, 193) = 55.77, $p = < 0.001$)).

Discussion

Ecological processes are well understood to operate at characteristic spatial scales, and scale-dependent processes may therefore be expected to play a role in shaping the phylogenetic patterns of invasion (Procheş et al. 2008). At coarse spatial scales (continental, islands, bioregional), phylogenetic clustering of alien species is common (Duncan & Williams 2002; Lososová et al. 2015; Park & Potter 2015). In contrast, studies comparing phylogenetic relatedness of native and alien species within habitats and at finer scales (< 100 m²) have most often found phylogenetic overdispersion (Swenson et al. 2007; Jiang et al. 2010; Carboni et al. 2013). Differences across studies may therefore be a consequence of the scale of the study rather than being inherently contradictory (Cavender-Bares et al. 2006; Cadotte & Davies 2016). Nonetheless, phylogenetic patterns contrary to what might be expected for a particular scale have also been found, making it difficult to associate particular ecological processes to phylogenetic patterns across spatial scales (Pavoine & Bonsall 2011; Schaefer et al. 2011; Marx et al. 2016). Here I shed light on this variation in outcomes by jointly considering scale and species origin (alien or native) in an alien-rich plant community.

Phylogenetic pattern at the landscape scale

Across the landscape, the community was phylogenetically clustered, providing support for the hypothesis that phylogenetic clustering is more evident at coarse spatial scales because species exhibit similar environmental preferences as a result of common ancestry (Carboni et al. 2013). Nearly half (49 %) of all species belonged to only four of the 67 families (Poaceae, Asteraceae, Orchidaceae and Fabaceae) represented in the community. This dominance by a few families at the landscape scale explains the phylogenetic clustering detected by the net relatedness metric (NRI), which captures phylogenetic patterns at a tree-wide scale. However, clustering was also apparent at lower taxonomic levels, as 27.67 % of all species were represented by just 5.48 % of the 292 genera. This dominance by a small number of genera is reflected in the nearest taxon metric (NTI), in which the influence of terminal branches plays a stronger role (i.e. within/among genera) than deeper phylogenetic relationships.

The clustering in the community as well as its alien and native components at this landscape scale (~ 215 km²) is similar to patterns observed elsewhere at regional (e.g. ≥ 35 km²) and

continental scales (Duncan and Williams 2002; Cadotte et al. 2009; Carboni et al. 2013). Strong relatedness at this scale in this dry forest ecosystem may be a result of the high species richness of native Orchidaceae, constituting 16 % of native and 12.41 % of total species richness. Relatively few orchid species were recorded at scales finer than the landscape, but their high representation in the species pool means that the Orchidaceae are likely to have more weighting and impact on phylogenetic patterns at the landscape scale, and this would result in increased clustering. The species pool is also clustered because alien- and native-exclusive genera make up 27.4 % and 61.99 % of the total genera, indicating these two sub-communities form two largely distinct floras. Within aliens, 33 % of species belong to the 15 % most species-rich genera, and for natives this was as high as 47 %, driving the strong phylogenetic clustering in both groups.

There are two possible explanations for the phylogenetic clustering of both native and alien components at the landscape scale: 1) coarse-scale environmental conditions similarly restrict the phylogenetic diversity of the community and both sub-communities, despite the alien and native sub-communities being distantly related to each other. Variation in environmental conditions at finer spatial scales and different tolerances to disturbance (i.e. aliens being more disturbance-adapted; D'Antonio et al. 1999) may then account for the different phylogenetic patterns exhibited between the native and alien sub-communities at spatial scales finer than the landscape. (2) The landscape scale examined in this protected area is too large to distinguish phylogenetic patterns of, and between, community groups. Protected areas are convenient for examining community patterns because their borders are predefined, as well as for quantifying species pools of aliens that have successfully established in otherwise largely-intact native communities. Lack of phylogenetic structure has been found in other protected areas, both smaller and larger than the one I examined (for aliens in an Australian park (15 068 ha) and for natives in Cameroon (526 000 ha); Cadotte et al. 2009; Manel et al. 2014)), suggesting that factors other than phylogenetic relatedness, such as dispersal limitation and historical events, drive community composition at landscape scales.

Alien and native sub-communities

Although the native sub-community was overdispersed (NRI) or no different from random (NTI), the alien sub-community was strongly phylogenetically clustered. Indeed, as predicted, this pattern held across all spatial scales. The strong phylogenetic clustering of the alien sub-community suggests that habitat filtering may be restricting invading species to those with

traits that allow them to persist under prevailing environmental conditions (Cornwell & Ackerly 2009; Tecco et al. 2010). Closely-related taxa are assumed to have similar functional traits, and this implies that closely-related species will pass through the same environmental filters to establish in a new environment (Cadotte et al. 2009; Weiher & Keddy 1995; Kraft et al. 2007). However, other studies across multiple landscapes (coastal forest, urban, foothills) and spatial scales (1 m², 1600 m², city-scale) have shown that aliens are more phylogenetically clustered than natives, and have proposed that this is a result of non-random selection of plant species in the human-mediated dispersal process (Ricotta et al. 2009; Cadotte et al. 2010a, Carvallo et al. 2014). The land in and around Chiltern-Mt. Pilot has been extensively used for agricultural and grazing activities since the 1830s and these activities have increased the risk of invasion into the park by agricultural weeds, which make up ~ 86% of aliens in the understorey (Randall 2002; Parks Victoria 2008).

Aliens and natives were more distantly related to each other than expected at random across all spatial scales, providing support for Darwin's naturalization hypothesis. This is not unexpected given the different geographic origins and evolutionary histories of the native and alien sub-communities. Darwin's naturalization hypothesis is one of the oldest hypotheses in invasion ecology, with evidence both for and against. Our results support previous findings from a number of landscapes, including Mediterranean coastal dunes and Californian grasslands, which conclude that aliens and natives tend to be distantly related to each other (Strauss et al. 2006; Davies et al. 2010; Carboni et al. 2013). Biotic interactions such as competition may drive community assembly, with biotic resistance by resident natives excluding phylogenetically-similar invaders (Davies et al. 2010). Frequency of occurrence data from the surveyed plots show that aliens are well-integrated between natives across frequency classes in the occupancy distribution (unpubl.). The majority of these aliens are from alien-exclusive genera such as *Hypochaeris*, *Trifolium* and *Bromus*. Interactions with resident natives may therefore be restricting the spread of closely-related (congener) aliens, while distantly-related aliens are able to spread and become abundant. However, human-mediated introductions of aliens can favour species with desirable or economically-useful traits (Chrobock et al. 2011) and these species are likely to be closely related while being distinct from natives in their traits and phylogenies (Cadotte et al. 2009). If this is the case, different traits may allow aliens to overcome biotic resistance from and outcompete natives, exacerbating phylogenetic differences between the two sub-communities (Diez et al. 2008; Gross et al. 2013). Many species from alien-exclusive genera (e.g. *Bromus*, *Hypochaeris*, *Vulpia*) were common across sample units, increasing differences across spatial scales.

Phylogenetic differences were most evident at the landscape scale, particularly for NTI, where overdispersion increased from -5.69 to -18.3 between the array and landscape (Table A1).

Although aliens were more strongly related to each other than natives, and over 25% of the species in the community were alien, patterns of phylogenetic relatedness in the full community remained statistically indistinguishable from the native sub-community. This suggests that invading aliens have to date had little impact on phylogenetic patterns in the understorey community, which - in a phylogenetic sense - has retained its integrity. This is somewhat surprising, given that the alien sub-community is very different to the native sub-community and that it is comparatively species rich. The proportion of alien species to natives across spatial scales, even at 25%, may still be too low to alter community phylogeny. Alternatively, because aliens do not disproportionately dominate the native community in this system, it remains rich with native species that retain its phylogenetic integrity (Carvallo et al. 2014). Furthermore, phylogenetic redundancy (high species richness within certain lineages; Shade & Handelsman 2012) within the native sub-community may provide stability and resistance to any phylogenetic change (Ricotta et al. 2018). Despite natives being overdispersed for NRI, the high number of native species in families such as Poaceae, Orchidaceae and Asteraceae may provide some phylogenetic resilience in the wake of invasion by alien species. Although aliens are currently not having a detectable impact on the phylogenetic relatedness signature of the community, life history and functional trait differences between aliens and natives may nonetheless have important consequences for the ecosystem.

Phylogenetic patterns across spatial scales

Regardless of phylogenetic relatedness being clustered or overdispersed, relatedness tended towards random with scale in the full and both sub-communities. In contrast to the expected outcome (Cavender-Bares et al. 2006; Diez et al. 2008; Procheş et al. 2008; Carboni et al. 2013), phylogenetic overdispersion increased rather than decreased with spatial scale. This held true even for aliens, despite being significantly clustered at even the finest (20m²) spatial scale. Yang et al. (2014) also found overdispersion (quantified as net relatedness) increased with spatial scale (ranging from 25m² to 10 000m²), for trees in different size classes in tropical forest in China. This provides support for the argument that habitat filtering and competition do not exclusively dominate phylogenetic patterns at coarse and fine spatial scales, respectively (Davies et al. 2010). Rather, other processes such as facilitation and stochastic events may be more important determinants of phylogenetic community structure, particularly at the fine

scales at which plant communities have traditionally been considered to compete (Mayfield & Levine 2010; Kraft et al. 2015; Cadotte & Davies 2016).

It is not clear why overdispersion increased with spatial scale in this dry forest understorey. Coarse-scale overdispersion may be the result of convergent evolution among dissimilar lineages or due to past speciation events (Cadotte & Davies 2016). Overdispersion could be driven by local stochastic events, for example where disturbances such as fire create available niches that are then filled by alien and disturbance-adapted natives (Ding et al. 2012). Additionally, post-fire facilitation has been linked to overdispersion during intermediate phases of succession in Mediterranean plant communities (Verdu et al. 2009). This is the result of nurse plants and facilitated plants having different regeneration niches which increases overdispersion (Verdu et al. 2009). This region of Victoria in Australia is prone to summer fires, the last major fire in the park occurred in 2003 and smaller, localised fires occur regularly (Parks Victoria 2008). Another possible explanation is that propagule dispersal by animals, wind and stormwater can disperse species substantial distances away from source populations (Cousens et al. 2008). Most understorey species (~60–65%) within the park are wind-dispersed or have no specialised method of dispersal. If these largely generalist species establish successfully, patterns of phylogenetic relatedness may tend towards random. The inclusion of species abundance data may in future provide insight into mechanisms, such as competition, that influence community assembly and determine patterns of phylogenetic relatedness across spatial scales (Cadotte et al. 2010b).

Conclusions

By jointly considering scale and species origin, I have shown that the existing variation in empirical evidence associated with Darwin's naturalization conundrum may be a result of the differences in spatial scale used, as well as the influence of human-mediated introductions. The alien sub-community has little influence on the phylogenetic structure of the whole community across spatial scales, despite being species rich and phylogenetically different to the native sub-community. Species in the alien sub-community were phylogenetically clustered, which may be a relic of human-mediated introductions favouring closely-related aliens with similar traits and pathways of introduction (Cadotte et al. 2009). Aliens and natives were more distantly related to each other than expected at random across all spatial scales, providing further support for Darwin's naturalization hypothesis. Phylogenetic patterns were consistent across spatial scales but weakened toward random with decreasing spatial scale. This contradicts the expected outcome that overdispersion increases at fine spatial scales and

clustering at larger scales. The results highlight that phylogenetic differences between alien and native sub-communities do not necessarily translate into phylogenetic impacts on invaded communities. Our results also suggest that phylogenetic patterns across spatial scales can contradict expected patterns, and that the ecological processes believed to drive these expected patterns are not always reliable or obvious predictors.

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Tables

Table 1. Differences between phylogenetic relatedness and a null expectation of zero in the understorey community at each spatial scale, measured as mean net relatedness index (NRI) and mean nearest taxon index (NTI). Community = all plant species (i.e. aliens and natives); Alien = alien sub-community; Native = native sub-community. Between = phylogenetic relatedness of alien and native sub-communities. Significant p values ($p \leq 0.05$) are in bold.

Spatial Scale	Group	df	Net Relatedness Index (NRI)			Nearest Taxon Index (NTI)		
			t	sd	*p*	*t*	sd	*p*
Array	Community	4	-2.85	0.94	**0.047**	1.45	1.17	0.222
	Alien	4	8.17	1.12	**0.001**	8.54	0.75	**0.001**
	Native	4	-2.75	0.74	0.051	0.23	0.52	0.828
	Between	4	-2.17	1.69	0.1	-11.38	1.12	**< 0.001**
Subarray	Community	14	-3.58	0.88	**0.003**	1.9	1.01	0.079
	Alien	14	9.3	1.30	**< 0.001**	9.2	0.97	**< 0.001**
	Native	14	-5.06	0.74	**< 0.001**	3.03	0.57	**0.009**
	Between	14	-2.65	1.66	**0.02**	-11.16	1.49	**< 0.001**
Plot	Community	44	-5.3	0.8	**<0.001**	0.46	0.93	0.65
	Alien	44	12.29	1.43	**<0.001**	12.68	0.98	**< 0.001**
	Native	44	-5.81	0.94	**<0.001**	3.82	0.8	**< 0.001**
	Between	44	-3.97	1.6	**< 0.001**	-13.92	1.52	**< 0.001**
Subplot	Community	131	-0.80	0.89	0.423	1.24	0.99	0.216
	Alien	131	16.07	0.91	**< 0.001**	19.90	0.90	**< 0.001**
	Native	131	-5.87	0.87	**< 0.001**	7.28	0.83	**< 0.001**
	Between	131	-4.91	0.94	**< 0.001**	-16.56	1.02	**< 0.001**

Figures
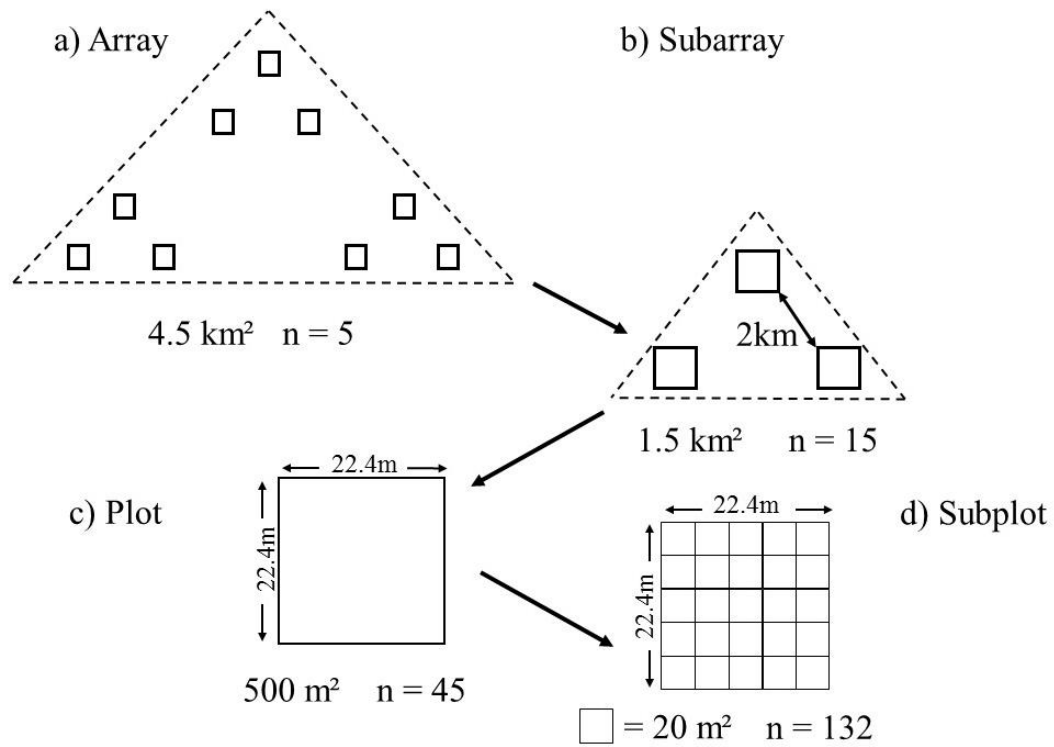
Figure 1. Arrangement of spatial scales used in the study. Spatial scales from coarsest (encompassing the entire understorey flora in the park) to finest resolution as follows: a) array, b) subarray, c) plot and d) subplot scales. Areas shown represent total area sampled (area of occupancy) at that scale.
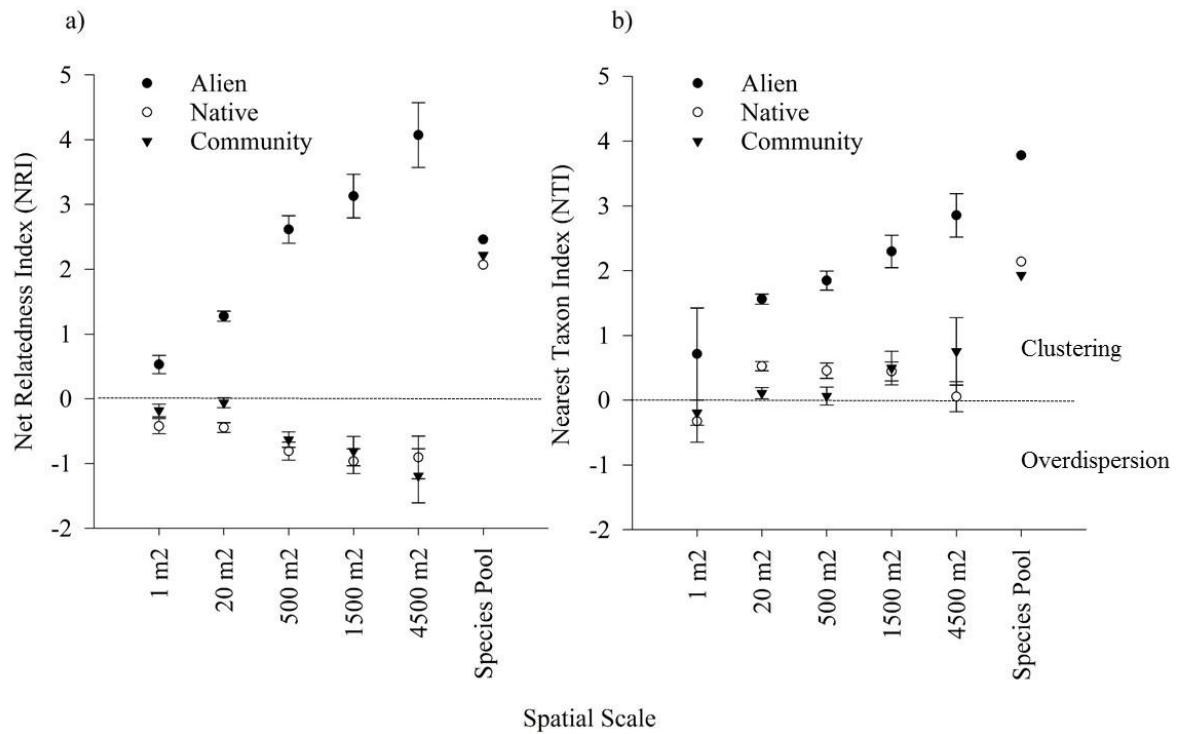
Figure 2. Scale dependent phylogenetic patterns in the understorey plant community, and, the native and alien sub-communities. a) Mean (± s.e.) net relatedness index (NRI) and b) mean (± s.e.) nearest taxon index (NTI). Positive values indicate phylogenetic clustering and negative values indicate phylogenetic overdispersion. Spatial scales on x-axis move from finest (subplot) to coarsest (landscape) spatial scale.
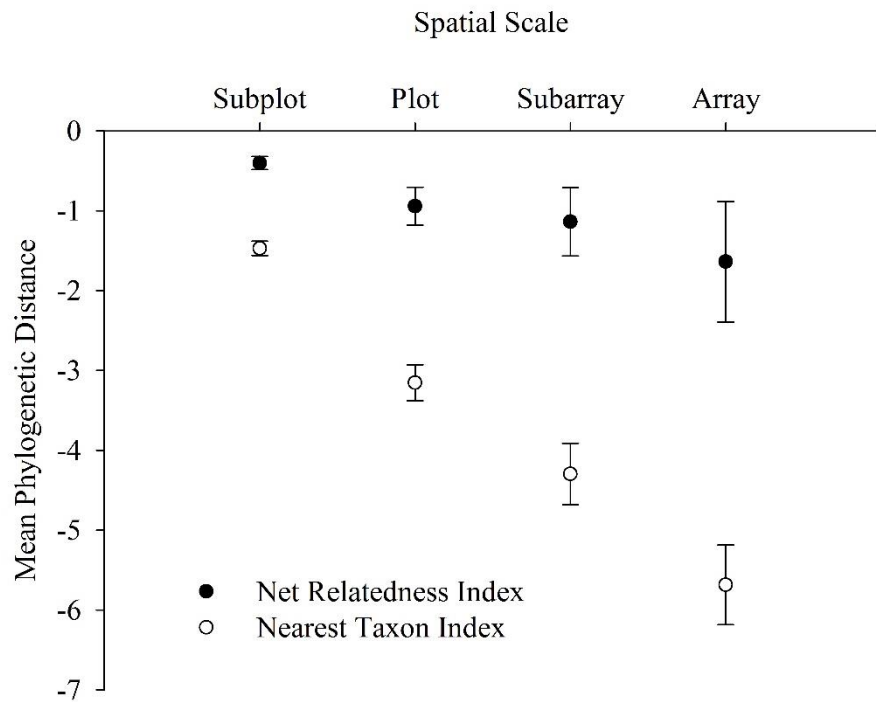
Figure 3. Differences in phylogenetic relatedness between alien and native species across spatial scales, from finest (subplot) to coarsest (array) scale. Mean (± s.e.) net relatedness index (NRI) and mean (± s.e.) nearest taxon index (NTI). All values are negative, indicating phylogenetic overdispersion.

Appendix A

Description of the species pool of Chiltern-Mt. Pilot National Park.

The most species-rich families overall were Poaceae (107), Asteraceae (98), Orchidaceae (87) and Fabaceae (52; Figure A1). For alien species, the most species-rich families included Poaceae (45), Asteraceae (26), Fabaceae (17) and Caryophyllaceae (12; Figure A1). The families with the highest native species richness were Orchidaceae (87), Asteraceae (72), Poaceae (62) and Fabaceae (35; Figure A1).

A total of 292 genera were present in the species pool. Of these genera, 143 (48.97 %) were represented by only one species. At least one alien species was present in 113 genera (38.7 % of total genera) and at least one native species was present in 212 genera (72.6 % of total genera). The number of alien-exclusive genera was 80 (27.4 % of total genera) and the number of native-exclusive genera was 181 (61.99 % of total genera). This gives a total of 261 (89.38 %) genera consisting exclusively of either alien or native species. The genera containing the richest alien flora included *Trifolium* (10) and *Bromus* (5) (Figure A1). The most species-rich genera for native species were *Pterostylis* (25), *Rytidosperma* (18) and *Juncus* (17) (Figure A1). *Pterostylis* (25), *Juncus* (21), *Rytidosperma* (18) and *Caladenia* (16) were the most species-rich genera overall (Figure A1)

Table A1. Metrics of phylogenetic diversity across spatial scales from landscape to subplot. Positive mean net relatedness index (NRI) and mean nearest taxon index (NTI) represent phylogenetic clustering and negative values represent phylogenetic overdispersion. Groups are as follows: Community = species pool at landscape scale (i.e. aliens and natives); Alien = alien sub-community; Native = native sub-community; Between = phylogenetic relatedness of alien and native sub-communities.

Spatial Scale	Group	Mean Pairwise Distance (millions of years)	Net Relatedness Index (NRI)	Mean Nearest Taxon Distance (millions of years)	Nearest Taxon Index (NTI)
Landscape (n = 1)	Community	513.64	+2.22	112.05	+1.93
	Alien	508.5	+2.46	130.76	+3.78
	Native	512.12	+2.07	115.76	+2.14
	Between	516.41	-4.17	214.75	-18.3
Array (n = 5)	Community	513.97	-1.19	167.84	+0.75
	Alien	494.29	+4.07	186.66	+2.85
	Native	515.48	-0.91	188.98	+0.05
	Between	516.03	-1.64	295.13	-5.69
Subarray (n = 15)	Community	513.34	-0.81	192.61	+0.49
	Alien	491.74	+3.13	218.35	+2.3
	Native	515.67	-0.96	214.82	+0.44
	Between	515.33	-1.14	324.89	-4.3
Plot (n = 45)	Community	513.14	-0.63	220.59	+0.06
	Alien	481.62	+2.61	250.31	+1.85
	Native	516	-0.81	242.90	+0.46
	Between	516.24	-0.94	349.68	-3.15
Subplot (n = 132)	Community	509.52	-0.06	272.02	+0.11
	Alien	478.99	+1.28	297.16	+1.56
	Native	512.45	-0.45	289.02	+0.52
	Between	513.01	-0.40	379.9	-1.47

Figure A1. The Chiltern-Mt. Pilot National Park alien and native species richness for a) the 28 most species-rich understorey plant families and b) the 25 most species-rich understorey plant genera.

a)
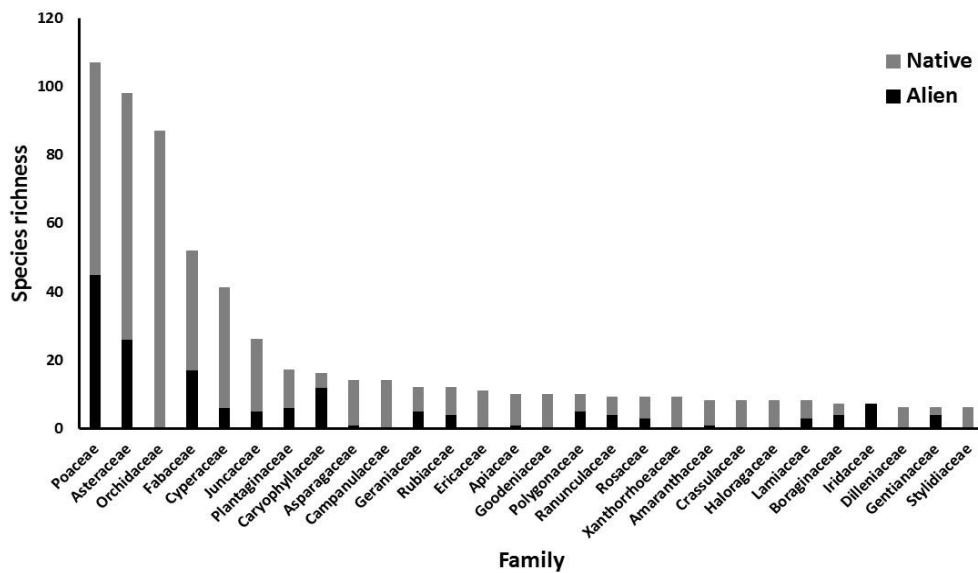
b)
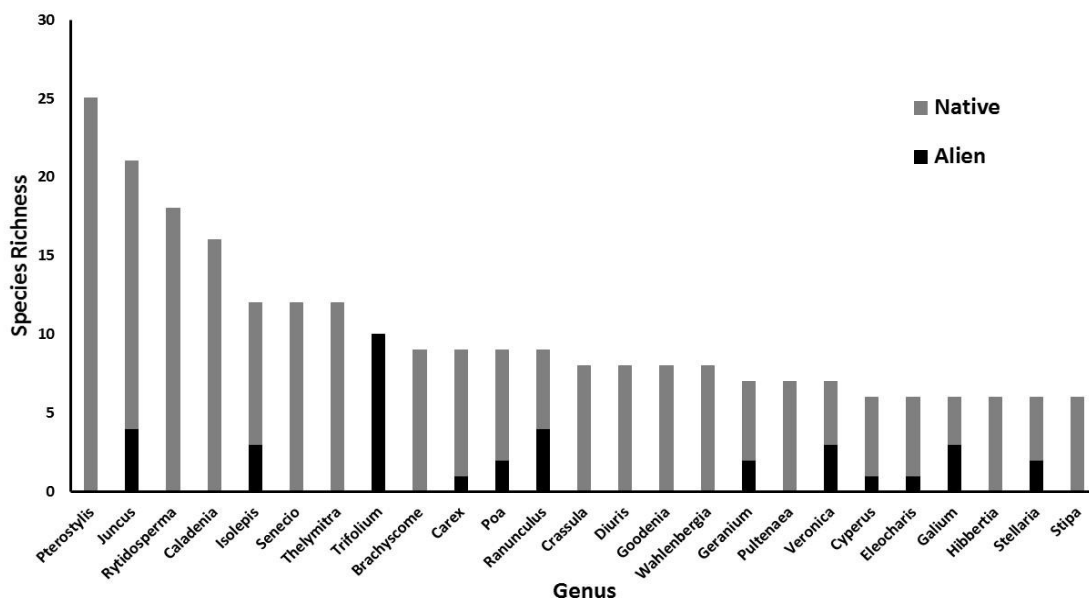
Chapter 2

Life strategies and composition of alien and native floras in response to environment

Introduction

Biological traits are commonly used to classify plant species based on their ecological strategies (Weiher et al. 1999; Hunt et al. 2004). Ecological strategies represent responses to environmental conditions, interactions with other organisms and stochastic events such as disturbance (Westoby et al. 2002). The different strategies used by plant species are characterized by differences in trait syndromes (i.e. combinations of traits). For example, a resource-rich habitat may favour competitive species with traits that rapidly acquire resources, while resource-poor habitats promote the survival of species with traits that conserve resources (Grime et al. 1997; Wright et al. 2004). Different environmental responses may cause resident and invading alien species to exhibit contrasting trait syndromes and strategies (Funk and Vitousek 2007; Tecco et al. 2010). Using a scheme which classifies species into life strategies based on their traits is therefore useful for determining how native communities respond to changes in resource availability, environmental stress and disturbance, and whether invading alien species respond in similar or different ways to the same set of environmental conditions.

The most well-known and best developed theory that categorises species based on their life strategies is Grime's competitor-stress-tolerator-ruderal (C-S-R) scheme (Grime 1974; 1977; 2001). According to the scheme, gradients of stress (conditions restricting production) and disturbance (destruction of biomass) partition species into three primary survival strategies, depending on the level of stress and disturbance a species experiences in its habitat (Figure 1; Grime 1977). Plant species are categorised into strategies based on particular trait syndromes representing trade-offs between a species' ability to compete with neighbouring species (C), persist under stress (S) or tolerate disturbance (R) (Grime 1977). Competitors (C-strategists) thrive in productive environments of low disturbance and exhibit traits allowing rapid growth and increased competitive ability. These include high SLA, increased height and clonal ability, long life-span and high root:shoot ratio (Grime et al. 1997). Stress-tolerant (S-strategist) species dominate in low-resource environments with little disturbance, and are typically slow-growing perennials with durable structures suitable for resource conservation and defence (Grime et al. 1997; Grime & Pierce 2012). Ruderal (R-strategist) species are characteristic of low-stress, high-disturbance environments and are short-lived, short-statured species with high reproductive outputs (Grime et al. 1997; Negreiros et al. 2014). Under high-stress, high-disturbance conditions, few to no species are able to survive (Grime 1977).

These three strategies form a spectrum, and each strategy (C, S and R) represents the extreme coordinates of C-S-R space (Figure 1). Sixteen intermediate strategies (e.g. SR, CR,

CSR) are recognized within C-S-R space and represent different levels of stress and disturbance (Grime 2001). Although Grime's C-S-R scheme was first developed 40 years ago it is still relevant, as it allows the comparison of life strategies across species, communities and regions, it is applicable to a wide range of habitats, and has even been used to identify life strategies in other organisms, such as soil bacteria (Negreiros et al. 2014; Fierer 2017). Since its initial development and corroboration in temperate biomes in the United Kingdom, the C-S-R scheme has been successfully validated in plant communities across multiple biomes, including glacier foreland communities in Italy, mountain grasslands in Brazil and remnant grassy woodlands of Australia (Caccianiga et al. 2006; Negreiros et al. 2014; Cross et al. 2015).

The C-S-R scheme has also been used to investigate whether invading alien species differ from native species in their ecological strategies. An underlying assumption of invasion is that few alien species will successfully colonize a novel habitat until environmental conditions change to become suitable for alien establishment ('fluctuating resource hypothesis'; Davis et al. 2000; Moles et al. 2008). Specifically, increases in resource availability (e.g. soil nutrients) and disturbance have been shown to increase the probability of successful invasion, particularly if exacerbated by other factors, such as the release of aliens from herbivory or soil pathogens (Davis et al. 2000; Lake & Leishman 2004; Hierro et al. 2006; Moles et al. 2008). Under high increases in resource availability and disturbance conditions, invading alien species are therefore predicted to be successful if they are either C- or R-strategists, or intermediate between these (i.e. CR-strategists; Grime 1979; Pyšek et al. 1995; Pyšek et al. 2009).

There are two main outcomes from studies investigating life strategy differences between aliens and natives. The first conclusion is that aliens differ from natives by being predominantly competitive-ruderal strategists, while natives tend to use strategies incorporating stress-tolerance. Aliens are more likely than natives to be C-, CR- or R-strategists in several habitats, including grasslands, forests, agricultural land, and human settlements (Pyšek et al. 1995; Pyšek et al. 2009; Jansen et al. 2011; Dainese & Bragazza 2012). In some cases, these outcomes were the result of altered resource (e.g. nitrogen and water) or disturbance (e.g. fire and grazing) conditions (King & Wilson 2006; Radford 2013). The tendency of native species to have stress-tolerant strategies has been suggested as a predisposition to resource limitation (King & Wilson 2006; Lambdon et al. 2008b; Radford 2013). However, in specific habitats, such as freshwater communities and wet meadows, natives have exhibited rapid growth (C) strategies and aliens conservative (S) strategies (Dainese & Bragazza 2012). The second conclusion suggests that, overall, alien and native species do not differ greatly in their life strategies. In these cases, both alien and native floras are either generalists (i.e. CSR-strategists)

or CR-dominated with little representation from stress-tolerators (Thompson et al. 1995; Pyšek & Richardson 2007; Cross et al. 2015).

Although there are exceptions, most evidence suggests that aliens are preferentially C-CR-R-strategists. The question then becomes whether natives have similar strategies to aliens, or if they are predominantly S-strategists. The answer to this is likely to be contingent on the resource availability of the environment in question. If aliens and natives share similar strategies, then these similarities may be driven by similar responses to resource availability and stress. Contrasting strategies between aliens and natives could indicate that their C-S-R compositions are influenced by different environmental factors. Many studies have investigated differences in alien and native C-S-R strategies but few have considered whether different environmental factors may be driving patterns found.

Here, I use a trait-based approach to determine which C-S-R strategies dominate herbaceous (forbs and graminoids) communities in a dry forest ecosystem, and how alien and native floras differ in their C-S-R composition. I also test whether resource availability and stress are driving these differences by examining CSR-environment relationships separately for alien and native species. Specifically I ask three questions: 1) What is the distribution of C-S-R strategies in herbaceous communities? 2) How do alien and native floras differ in their C-S-R strategies? 3) Are differences in C-S-R composition between aliens and natives explained by different responses to resource availability and stress? I predict that alien species will have competitive-ruderal dominant strategies. If native species differ in their strategies from alien species, I predict that different environmental factors will influence the C-S-R composition of both groups.

Methods

Study location

Chiltern-Mt. Pilot National Park is a protected area of 21 560 ha in north-east Victoria, Australia. It contains granitic hills woodlands and box-ironbark forest of native cypress pine (*Callitris*) and eucalypt (*Eucalyptus*) trees. Forestry, agriculture and gold mining in and around the park before 1980 have resulted in more than 80 % loss of these ecosystems (Parks Victoria 2008). Ongoing disturbance in the region continues to increase, and includes invasion by multiple alien species (Parks Victoria 2008). While few alien tree species exist within the park, the understorey community has been invaded by numerous, predominantly herbaceous alien

species. Despite this, Chiltern-Mt. Pilot protects several significant flora and fauna (Parks Victoria 2008).

Fifteen 500 m² plots (communities) were sampled within Chiltern-Mt. Pilot National Park. These communities were distanced at 1 to 22 km apart and each was divided into 25, 20 m² subplots. Total herbaceous species richness was recorded for each community and species were categorised as alien or native using information from the Victorian Biodiversity Atlas (https://vba.dse.vic.gov.au/vba/, accessed 29 Jan 2015) and Walsh & Entwisle (1992-1996). Two 1 m x 1 m quadrats (50 per community) were randomly placed within subplots to record percent cover for each herbaceous species present. Percent cover was estimated using the categories 0 %, 0.5 %, 1 %, 2 %, 5 % and subsequent intervals of 5 % from 10 to 100 (Daubenmire, 1959). The total percent cover for each species in a community was obtained by combining the measurements from each quadrat. All species' cover measurements were combined to obtain a total percent cover for each community.

Collection of trait data

Data were collected on seven plant traits (3 in-field, 3 from existing literature sources, 1 a combination of both), which were used to allocate C-S-R strategies to species, as outlined by Hodgson et al. (1999). The traits include: 1) maximum vegetative height (mm), 2) leaf dry mass (mg), 3) leaf dry matter content (LDMC, %), 4) specific leaf area (SLA; mm² mg⁻¹), 5) lateral spread, 6) flowering start and 7) flowering duration (months).

Trait data were collected for species that cumulatively made up 80-95 % of total herbaceous cover in each community. A minimum cumulative relative abundance of 80 % (cover is used here as a proxy for abundance) is required for species selection for trait sampling, as this best captures any impacts of traits on functional structure (Garnier et al., 2004; Pakeman & Quested, 2007). As a result, trait data were collected for the 52 most-dominant herbaceous species across all 15 communities.

Field trait data were collected from late September to early December in both 2014 and 2015. Maximum vegetative height of each species in each community was recorded *in-situ* from the tallest individual. Forty leaf samples (ten individuals; four leaves per individual) were collected per species in each community (Pérez-Harguindeguy et al. 2013). From these samples, leaf dry mass, LDMC and SLA were measured. Fresh leaves were weighed to obtain fresh leaf mass then scanned using a Canon LiDE210 flatbed scanner. ImageJ software was used to obtain the one-sided area of each leaf (Schneider et al. 2012). Samples were then oven-

dried for 72 hours at 70°C. Leaf dry mass was recorded from dried samples. Leaf dry matter content was calculated as the percent of dry mass (mg) to fresh mass (mg) of each sample. Specific leaf area (mm² mg⁻¹) was calculated by dividing the leaf area of each sample by its leaf dry mass. Information on lateral spread, flowering start and flowering duration was sourced from Walsh & Entwisle (1996) and several literature-based sources. Data on leaf dry matter content for those species for which field measurements were not collected (s = 24, 46 %) were obtained from the TRY database (Kattge et al. 2011), the La Trobe University Plant Trait Database, and Venn et al. (2014; 2016).

Environmental measurements

Ten environmental variables were measured in each community. These variables are related to resource availability or stress that either promote or hinder plant growth and photosynthesis (Cartorci et al. 2011, Brady & Weil 2016). The variables included 1) slope (degrees), 2) altitude (m a.s.l.), 3) soil magnesium (Mg) content (mg/kg), 4) total soil carbon (%), 5) total soil nitrogen (%), 6) soil C:N ratio, 7) canopy openness (mean %), 8) live basal area (m² ha), 9) soil pH and 10) soil phosphorous (P) content (mg/kg).

Five soil samples (0-5 cm of upper mineral horizon) were collected from each community from the four corner subplots and the centre subplot and pooled into one mixed composite sample. Chemical analyses were conducted on 40 °C oven-dried samples. Soil Mg was equilibrated with 1M ammonium acetate at pH 7.0 for 30 minutes by mechanical shaking at a soil:solution ratio of 1:10 (Rayment & Lyons 2011). Total soil C and N concentrations were measured using catalytic combustion and thermal conductivity using a LECO IR Analyser (Rayment & Lyons 2011) and the C:N ratio for each community was calculated using the resulting measurements. Soil pH was determined using a conductivity meter in a 1:5 soil-water suspension. Soil P concentrations were measured using the Bray 1 method (Rayment & Lyons 2010). To determine canopy openness, three hemispherical photographs were taken at dawn or dusk in the centre of the south-west, centre and north-east subplots of each community. These photos were analysed using Winscanopy Pro 2014a software to produce a measure of canopy openness from each photograph. Mean canopy openness was then calculated for each community. Live basal area was determined from circumference measurements of all live tree stems with a diameter breast height > 10 cm.

Allocation of C-S-R strategies

I used the methods outlined in Hodgson et al. (1999) and Hunt et al. (2004) to allocate C-S-R strategies to species and communities, involving the trait data from the seven measured traits. Maximum height, lateral spread and flowering start each use a six-point classification of species' traits (Table B1). Because the flowering start classification outlined in Hodgson et al. (1999) was developed in the northern hemisphere, a correction of six months was made to the classification scheme, as has been used in previous studies (Weiher et al. 1999; Negreiros et al. 2014; Cross et al. 2015). The method outlined in Hodgson et al. (1999) involves the use of the seven traits in predictor regressions. The seven traits are used as predictor variables, and the range of trait values representing pre-defined, calibrated ("gold standard") indices of C- S- and R- dimensions were used as the response variables (Hodgson et al. 1999; Cerabolini et al. 2010). The outputs from regression models were then transformed into raw coordinates of C- S- and R- dimensions. Outliers were truncated so that all coordinates lie within C-S-R space (i.e. Figure 1). Coordinate values ranged from -2.5 to 2.5 (Caccianiga et al. 2006). The coordinates were compared to all of the 19 recognised strategy combinations. To ensure there was adequate representation across strategies, I used the seven major strategies (C, S, R, CS, CR, SR, CSR) originally outlined in Grime (1979) rather than the 19 subsequently proposed in (Grime 2001). The result of this analysis allocated a C-S-R strategy to each of the 52 species.

To scale up the C-S-R strategies from the species to community level, I used the method of Hunt et al. (2004). For each community, all species are listed with their corresponding C-S-R strategy and relative abundance (%). The percent abundance (P_i) of each C-S-R type is calculated as

$$P_i = \sum_{j=1}^{n} P_j$$

Where P_j is the relative abundance of the n species occurring both within the community and the specific C-S-R type (Hunt et al. 2004). The net position of each community in C-S-R space is then plotted on a ternary diagram and provides an indication of which strategy or strategies dominate each community.

Comparison of alien and native C-S-R strategies

C-S-R strategies of alien and native species were plotted on a ternary diagram to show their representation in C-S-R space. To examine differences between alien and native species of

different growth forms, I further divided aliens and natives into the following four groups: alien graminoids, native graminoids, alien forbs and native forbs. The positions of these four groups in C-S-R space was plotted on an additional ternary diagram. ANOVA models were used to compare differences in the use of primary C-S-R strategies between aliens and natives and between graminoids and forbs. The percentage of primary (C, S and R) strategies used by each species was obtained by translating the coordinates (ranging from -2.5 to 2.5) of C, S and R dimensions onto a positive axis (i.e. adding 2.5 to each coordinate value, so that the minimum possible value = 0), then calculating the percentages (Caccianiga et al. 2006; Pierce et al. 2007). Significant differences were tested for each primary strategy separately. An interaction term between species status and growth form was included to test for combined effects on C-S-R strategies.

Relating environmental factors to C-S-R composition

Redundancy analysis (RDA) was used to assess the variation in C-S-R strategies explained by environmental factors. This was done separately for 1) all species, 2) alien species, 3) native species, 4) graminoids and 5) forbs. C-S-R composition of communities was arranged in site-by-strategy matrices, summing the relative abundance of each species in each community belonging to a particular strategy. All matrices were Hellinger-transformed to resolve double absences being treated as similarities between sites (Legendre & Gallagher 2001). Due to the high number of environmental variables considered, a Pearson's cross correlation was run to reduce the number of predictors and to remove highly-correlated variables (Table B3). Four environmental predictors were retained for analysis: 1) soil P content, 2) total soil N, 3) canopy openness and 4) soil pH. Partial RDA was used to calculate the contribution of each environmental predictor to total variability in C-S-R strategy (Borcard et al. 1992). To assess if each independent environmental predictor significantly influenced C-S-R composition, the adjusted R^2 values were subjected to permutation tests (1000 permutations; Legendre & Legendre 1998). All analyses were performed using the *vegan* package in R Studio 3.3.1 (Oksanen et al. 2017; R Core Team, 2016).

Results

Dominant C-S-R strategies in understorey communities

The 15 communities exhibited overall either competitor-stress tolerator-ruderal (CSR, n = 6) or stress-tolerator-competitor (SC, n = 7) strategies (Figure 2). One community had a dominant

stress-tolerator-ruderal (SR) and one a dominant stress-tolerator (S) strategy. Communities therefore tended to be either generalist (i.e. "CSR" strategists) or have a strategy that incorporated a stress-tolerator component.

Differences in CSR strategies between alien and native taxa

A total of 21 alien and 31 native species (together making up 85-95 % cover) were assessed across the 15 communities. The most common strategy among aliens was stress-tolerator (S, 11.5 % of all species), followed by ruderals (R, 9.6 %) (Table 1). Both competitor (C) and SR strategies were represented by only one alien species (Table B2). The dominant strategy for natives was competitor-ruderal (CR, 21.2 %), followed by S (13.5 %, Table 1). No native species had an SR strategy.

Aliens and natives exhibited a range of C-S-R strategies, although aliens lacked species with a C-strategy (Figure 3a). When aliens and natives were divided into graminoids and forbs, a distinct aggregation of alien and native graminoids emerged, centred in the S-SC portion of C-S-R space (Figure 3b). No clear pattern emerged for either alien or native forbs (Figure 3b).

The percentage of C-dimension space occupied by natives was significantly higher than aliens (Table 3, Figure 4a). Differences between aliens and natives in the percentage of R- and S-strategies used were not significant (Table 1, Figure 4a). Forbs had significantly higher percentages of C- and R-strategies, and grasses were significantly higher in percentage of S-strategy used (Figure 4b-d). No significant interaction between species status (alien or native) and growth form (graminoid or forb) was apparent (Table2).

Influence of environmental factors

For all species, the total variation in C-S-R composition explained by environmental variables was 18.6 % (adjusted R^2, Table 3). Stress-tolerators dominated high pH and low N soils, while SC-strategists were associated with low pH and high N soils (Figure 5a, Table B4). For alien species, there were no strong links to the considered environmental variables for any of the C-S-R strategies, and the environmental variables explained none of the variation in C-S-R composition (Table 3, Figure 5b, Table B4). Total explained variation for C-S-R composition of native species was 25 % (adjusted R^2; Table 3). Native SC-strategists were strongly associated with soils high in N content and low in pH (Figure 5c). Native S-strategists were moderately linked to low phosphorous soils (Figure 5c). Graminoids had the highest total variation explained by environmental predictors (39.9 %, adjusted R^2). Stress-tolerator

graminoids were abundant in low N soils, while SC-strategists were less abundant (Figure 5d). For forbs, 26.9 % of total variation was explained, but C-S-R strategies were weakly associated with the environmental variables (Figure 5e, Table 3; A3).

Soil N content significantly explained the most variation in the C-S-R composition of all species ($R^2 = 0.113$, $p = 0.007$), followed by soil pH ($R^2 = 0.021$, $p = 0.04$, Table 3). Neither soil phosphorous nor canopy openness independently explained any of the variation in C-S-R composition across any of the species groups (Table 3). None of the environmental predictors significantly explained alien or forb C-S-R composition (Table 3). For native species, pH exclusively explained 17.6 % of variation in C-S-R composition ($p = 0.013$, Table 3). Variation in graminoid C-S-R composition was significantly explained by soil N content ($R^2 = 0.399$, $p = 0.002$).

Discussion

Alien species are predicted to successfully invade natural habitats when resources become more abundant, either through disturbance that reduces the ability of native species to use available resources, or through direct increases in particular resources, such as water or soil nutrients (Davis et al. 2000; Grime 2001). Given this prediction, alien species are assumed to exhibit life strategies incorporating a combination of high competitiveness and adaptation to disturbance (i.e. C-, CR-, or R-strategies; Grime 2001). My results do not support this prediction, and alien species were rather most commonly stress-tolerant, and occupied a portion of C-S-R space already filled by natives. The significant difference between alien and native C-strategists reveals competitiveness is more prevalent amongst natives. These results therefore do not support the fluctuating resource hypothesis (Davis et al. 2000). The C-S-R composition of aliens was unaffected by environmental factors relating to resource availability and stress, while native C-S-R composition was significantly influenced by soil N. This decoupling of alien C-S-R composition from environmental stress and resource availability may allow aliens to more readily tolerate prevailing environmental conditions and become integrated into the communities they have invaded.

Distribution of C-S-R strategies in understorey communities

Almost all herbaceous communities in this dry forest understorey exhibited one of two strategies: a generalist (CSR) or a stress-tolerator-competitor (SC) strategy. These communities can be regarded as generalist because species use a diverse range of strategies, rather than

through the dominance of generalist (CSR) species. Few species had a CSR-strategy, and were represented in only two communities. Therefore, generalist communities are the result of species collectively having a diverse range of life strategies. This suggests that in these communities, effects of stress, disturbance and resource availability are either moderate, or are temporally or spatially confined, allowing species of all life strategies to exist at similar abundances (Grime 2001).

In contrast, the SC-dominated communities are a result of the high relative abundance of two stress-tolerator-competitor species: *Microlaena stipoides* and *Rytidosperma pallidum*. Both species are native grasses and reached high relative abundance (from 28 – 95 % relative cover, though usually not together) in SC-dominated communities. Stress-tolerator-competitor graminoids are typical of habitats with moderate productivity and low disturbance, and have a high capacity for lateral vegetative spread and long-lived leaves (Grime 2001). The high relative abundance of these two species may be due to higher soil N (Chivers & Aldous 2005). The combined relative cover of *M. stipoides* and *R. pallidum* significantly increased as the level of soil N increased, with the SC-dominated communities predominantly having both higher cover and higher total N (Figure B1). This relationship between soil N and these dominant-SC species is further supported by the ordination analysis. Soil N was significantly related to C-S-R composition for all species and for graminoids, and among the strongest relationships from the ordinations was a decrease in SC-strategy with a decrease in soil N. Together, these results suggest that soil N is driving the dominance and SC-strategy of *M. stipoides* and *R. pallidum*, in the communities where the SC-strategy dominates.

Differences in alien and native C-S-R strategies

Aliens differed to natives in their use of C-strategy, but not in use of S- or R-strategy. Most alien species, when weighted by relative cover, had an S-strategy (42.85 %), while the most common strategy among native species was CR (38.71 %). This outcome contradicts the idea that alien species will predominantly exhibit C-CR-R strategies, due to increased competitiveness and adaptation to disturbance (Davis et al. 2000). Combinations of competitor and ruderal strategies have previously been found to dominate alien species assemblages (Pyšek et al. 1995; Dainese & Bragazza 2012; Vukovic et al. 2014). In this system, R- and CR-strategies were each represented by 19.05 % of alien relative cover, and C-strategy by only one alien species – *Hypericum perforatum*. Natives had higher proportions of species using all strategies with a competitor component (i.e. C, SC, CR, CSR). The significant difference

between aliens and natives in C-strategy use suggests that natives are more readily able to use available resources, giving them a competitive advantage over the alien species in this system (Grime 2001). Because natives have evolved under prevailing environmental conditions in this region, they may be better-adapted to temporal or spatial resource fluctuations, such as water availability and soil nutrients, than the more recent aliens. Most of these aliens are of European or Eurasian origin, and have evolved in more temperate ecosystems (Randall 2002). Alternatively, natives may be exhibiting some level of biotic resistance or competitive dominance over aliens by monopolising resources (Grime 2001; Seabloom et al. 2003; Levine et al. 2004). Aliens may more successfully integrate into native communities if they are R- or S-strategists, because they can establish after disturbance or stressful conditions that reduce native competitiveness (Keane & Crawley 2002; Corbin & D'Antonio 2004).

Overall, differences in the use of C-, S- and R-strategies were greater between graminoids and forbs than between aliens and natives. Graminoids – regardless of alien or native status – were distinctly aggregated within the S-strategy component of C-S-R space, while forbs were more evenly-distributed throughout C-S-R space (Figure 3b). These results are similar to the occupancy of C-S-R space by graminoids and forbs analysed across many different biomes at a global scale (Pierce et al. 2017). Forb species had a greater range than graminoids in the percentage of strategies used (Figure 4b-d). This greater range of strategy-use and the spread across C-S-R space reveals that forbs are likely using a variety of life strategies, compared to graminoids. Furthermore, the C-S-R composition of forbs was unaffected by environmental factors of resource availability and stress. This suggests that collectively, herbaceous species in this system can tolerate a wide range of environmental conditions, and this tolerance is evident in the divergence in life strategies. In contrast, graminoids are largely restricted to stress-tolerant strategies and are strongly influenced by total soil N (Table 3). Australian dry forest soils are typically low fertile habitats and are often characteristic of species that are stress-tolerant, including native perennial grasses (Hill et al. 2005; Grime 2001). The ordination analysis for graminoids revealed that there was a strong relationship between soil N and S-strategy along the first axis, where the abundance of stress-tolerator species increased as the level of N decreased (Figure 5d).

Interestingly, all alien graminoids except one were annuals, while all native graminoids were perennial. This difference in life history (annual/perennial) between alien and native graminoids, coupled with their aggregation in C-S-R space, suggests that alien and native graminoids are using different mechanisms to tolerate stress. Grubb (1998) divided Grime's (1977, 1979) S-strategy into three sub-strategies, on account of nutrient-poor habitats

containing a high variety of plant species. First, the 'low-flexibility' strategy corresponds to Grime's S-strategy, represented by species with long leaf life spans and slower growth rates in both juvenile and adult phases of the life cycle (Eckstein & Karlsson 2001). Second, the 'gearing-down' strategy is typical of species with short-lived leaves, which can tolerate resource limitation, but exhibit a rapid growth response when disturbance or resource addition relieves resource limitations. Finally, the 'switching' strategy allows stress-tolerator seedlings to change their strategy as adults, and this change between the two stages of the life cycle is signalled by an increase in growth rate (van der Maarel 2005). Leaf life span is implicated in the first two strategies, and SLA is highly correlated with leaf life span (high SLA = low leaf life span; low SLA = high leaf life span; Eckstein & Karlsson 2001; Westoby et al. 1998; Wright et al. 2004). In the system examined here, alien annual graminoid species consistently had higher SLA values than native perennial graminoids. This suggests that native perennial graminoids are using the 'low-flexibility' strategy by being perennials with long-lived leaves and low SLA. In contrast, alien annual graminoids may follow the 'gearing-down' strategy with fast (annual) growth rates and higher SLA, providing an advantage when resource limitation is relieved. Increased proportions of annual species and high SLA has been linked to increases in invasion level within this system (see Chapter 3). Thus, invading alien graminoids are adapted to survive in the stressful conditions of this system, but they come equipped to take advantage of increases in resources when they arise.

Environment and C-S-R composition

The C-S-R composition of communities was significantly related to soil characteristics. Total soil N and soil pH changed as abundances in S-strategists and SC-strategists changed (Figure 5a). Therefore, community life strategies are being affected by environmental factors relating to resource availability and stress. High soil acidity, as well as low N levels are known to limit plant growth and favour stress-tolerant species such as perennial tussock grasses (Grime 1979; Stevens et al. 2010). The sampled communities are mostly situated on acidic soils, ranging from neutral (soil pH = 6.6 − 7.3) to strongly acidic (pH = < 5.5), and are predominantly low (n=11) in total soil N (% N = 0.05 − 0.15), with three communities with moderate soil N (% N = 0.15 − 0.25) and one high soil N (% N = 0.25 − 0.5; Hazelton & Murphy 2007). Although soil N and pH were not significantly related to each other, S-strategists reached higher abundances in soils that were less acidic with low N. As soils became more acidic and generally had higher N levels, S-strategists declined in prevalence, to be replaced with SC-strategists that

are better adapted to exploit the higher N conditions. Stress-tolerator strategies have been associated with high acidity, and SC-strategies with high N levels in abandoned fields in China (Wang 2002). In addition, declines in S-strategy and increases in C-strategy have been linked to N deposition in broad-leaved woodlands in Belgium (Verstraeten et al. 2013). My results provide further evidence that soil characteristics play a key role in driving the C-S-R composition of herbaceous communities.

When communities were divided into the four species groups (aliens, natives, graminoids, forbs) there were obvious differences in how C-S-R composition responded to the environment. Similar to all species, natives with an SC-strategy, such as *Microlaena stipoides*, were more prevalent in soils with higher acidity. Furthermore, graminoids with an S-strategy increased in prevalence in low-N soils, while SC-strategists became less-prevalent. Therefore, the life strategies of species in these communities are influenced by different environmental factors, dependent on their status (alien/native) or growth form. The combination of these influences are then driving the life strategies identifiable at a community scale. However, the lack of environmental effects on alien and forb C-S-R composition suggests that these species can tolerate multiple environments, and may indicate higher plasticity than their native and graminoid counterparts (Davidson et al. 2011). Increased plasticity and tolerance to a wide range of habitat conditions may allow aliens to more readily integrate into dry forest understorey communities. *Hypochaeris radicata*, a common alien in this system, is known for its variability in morphology, such as leaf shape and root form (Turkington & Aarssen 1983; Mitchell & Bakker 2014). It is also known to tolerate a wide range of moisture conditions and nutrient deficiencies (Lambert 1963; Turkington & Aarssen 1983). Alternatively, other environmental factors that were not measured, such as soil moisture or fire disturbance, may be driving the C-S-R composition of aliens (Fisher et al. 2009; Radford 2013; Paudel et al. 2017). While alien graminoids, such as *Briza minor* and *Aira elegantissima*, may be somewhat restricted by low soil N levels, their status as annuals with high SLA ensures they are able to increase their competitive advantage once N availability rises (Grubb 1998). Alien forbs are spread across C-S-R space (Figure 3b) and, collectively, these species may have integrated into this system using a variety of life strategies, and have done so regardless of the environmental conditions. It also supports previous studies of Mediterranean islands and Australian tropical savannas which showed that aliens use a wide range of life strategies to thrive in communities they have invaded (Lambdon et al. 2008a; Radford 2013). The use of several life strategies may allow aliens to occupy the same niches as natives (Lambdon et al. 2008a; Cross et al. 2015).

Conclusions

Aliens occupied a portion of C-S-R space already filled by natives, thereby reinforcing the C-S-R signals that exist in this system. Despite this, aliens are not limited in their life strategies by environmental factors such as soil pH, suggesting greater opportunities to invade and integrate into the dry forest understorey. Native communities, such as those found in protected areas, may be susceptible to invasion regardless of variation in local environmental conditions, but the functional consequences of invasion may be minimal when aliens exhibit similar life strategies and growth forms to natives. However, when aliens and natives differ in their growth forms, the impact to the distribution of community life strategies upon alien integration may be more severe.

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Tables

Table 1: Representation of C-S-R strategies across total (s = 52), alien (s = 21) and native (s = 31) plant species in the 15 communities. C = competitors, CR = competitive-ruderals, SC = stress-tolerant competitors, CSR = competitive stress-tolerant ruderals, R = ruderals, SR = stress-tolerant ruderals, S = stress-tolerators.

C-S-R Strategy	Total No. species	Total species (%)	No. Aliens	Aliens (% all species)	No. Natives	Natives (% all species)
C	5	9.62	1	1.92	4	7.69
CR	14	26.92	3	5.77	11	21.15
SC	9	17.31	3	5.77	6	11.54
CSR	4	7.69	2	3.85	2	3.85
R	6	11.54	5	9.62	1	1.92
SR	1	1.92	1	1.92	0	0
S	13	25	6	11.54	7	13.46

Table 2: Differences in Grime's CSR strategies between species (s = 52) of different status (alien or native) and growth form (graminoid or forb). ANOVA models indicate differences in **a)** % competitive (C) strategy, **b)** % stress-tolerator (S) strategy, and **c)** % ruderal (R) strategy. Significant p values are in bold.

	ANOVA Model				
a)	Competitor strategy	Sum sq	df	F	p
	alien/native	2264	1	8.648	**0.005**
	graminoid/forb	1419	1	5.421	**0.024**
	alien/native * graminoid/forb	435	1	1.663	0.203
b)	Stress-tolerator strategy				
	alien/native	382	1	0.648	0.425
	graminoid/forb	14597	1	24.798	**< 0.001**
	alien/native * graminoid/forb	127	1	0.216	0.644
c)	Ruderal strategy				
	alien/native	786	1	1.324	0.256
	graminoid/forb	6914	1	11.645	**0.001**
	alien/native * graminoid/forb	92	1	0.155	0.696

Table 3: Variation partitioning (adjusted R²) in C-S-R strategy composition for taxa of different status (alien/native) or growth form (graminoid/forb). Significance of single environmental variables. The p values are derived from permutation tests (1000 permutations) using adjusted R² values. Joint effects could not be tested for significance. Significant p values ($p \leq 0.05$) are shown in bold. Negative adjusted R² values can be treated as zero (Legendre 2008). P = soil phosphorous, N = soil nitrogen, Ope = canopy openness, pH = soil pH.

Variables	All species		Aliens		Natives		Graminoids		Forbs	
Fractions	Adj R²	p	Adj R²	p	Adj R²	p	Adj R²	p	Adj R²	p
P	-0.007	0.317	-0.02	0.774	0.02	0.227	-0.054	0.492	0.042	0.528
N	0.113	**0.007**	-0.026	0.447	0.054	0.06	0.399	**0.002**	0.07	0.393
Ope	-0.012	0.711	-0.061	0.866	-0.044	0.804	-0.003	0.751	-0.016	0.643
pH	0.021	**0.04**	0.026	0.195	0.176	**0.013**	-0.018	0.137	0.157	0.201
Total Adj R²	0.134		0.026		0.25		0.399		0.269	
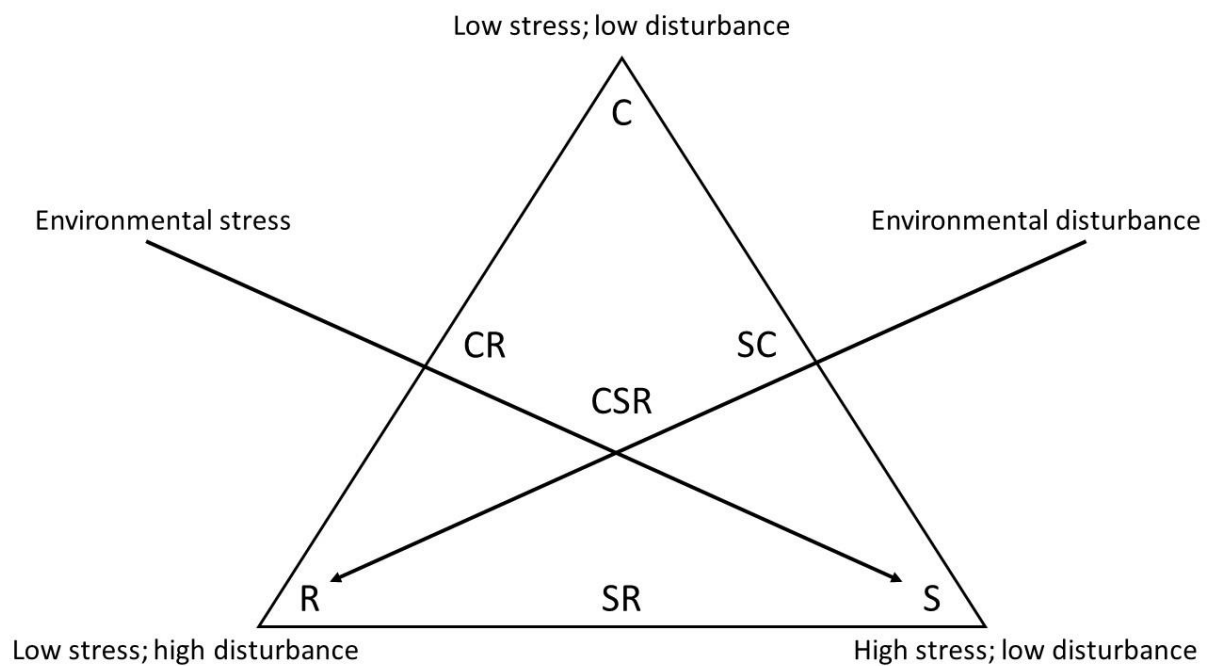
Figure 1: Representation of C-S-R space, showing the position of the three main strategies and their intermediate strategies. Arrows represent dimensions of stress and disturbance. Competitor (C), stress-tolerator (S) and ruderal (R) represent the locations of the three primary strategies. CR, SC, SR and CSR represent intermediate strategies. CSR space is bounded by units C = 0 to 1, S = 0 to 1, R = 0 to 1. Adapted from Hunt et al. (2004).
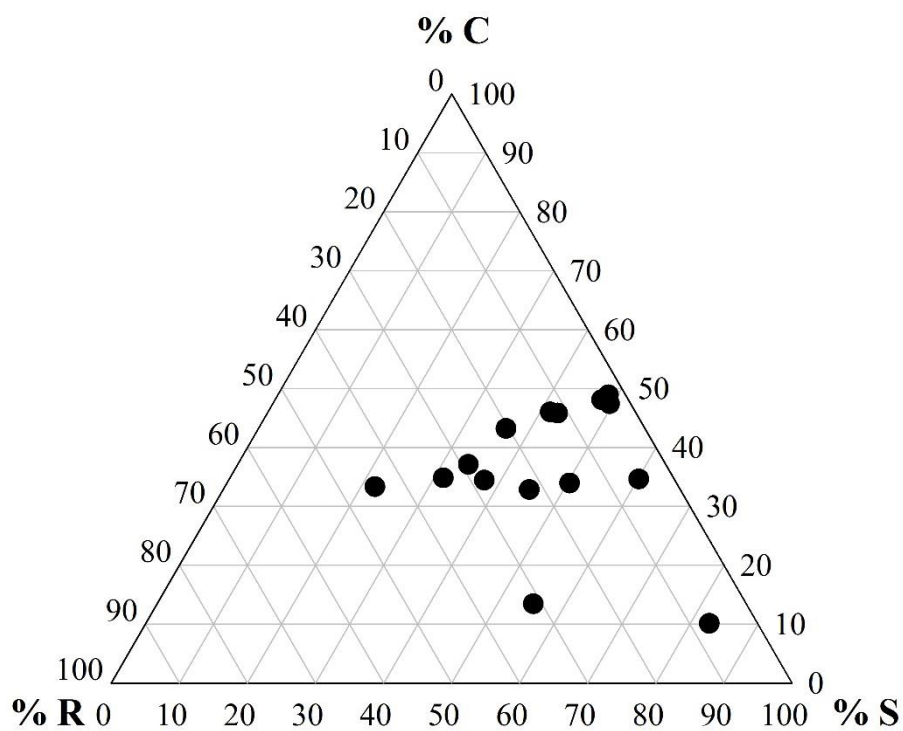
Figure 2: Position of herbaceous communities in C-S-R space. C = competitors, S = stress-tolerators, R = ruderals. Percentages along axes show the relative importance of C, S and R dimensions to the overall C-S-R strategy of each community.
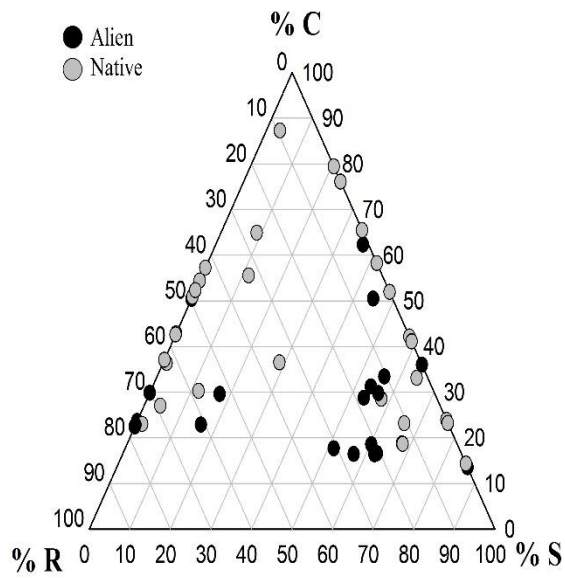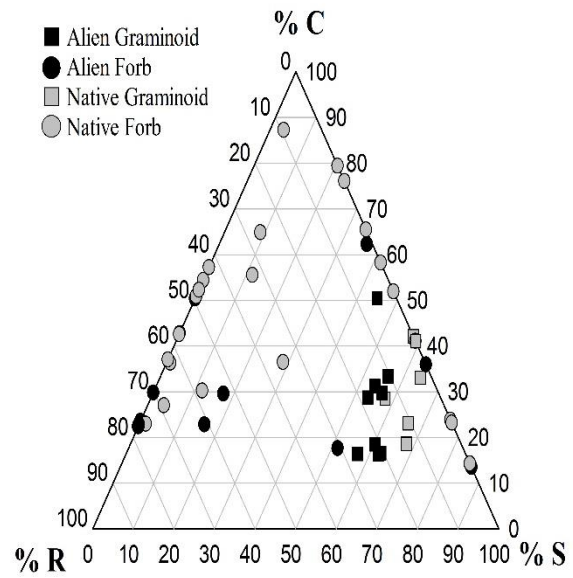
Figure 3: Position in C-S-R space of species in the understorey, grouped by a) alien or native status and b) alien or native status and growth form. C = competitors, S = stress-tolerators, R = ruderals. Percentages along axes show the relative importance of C, S and R dimensions to the overall C-S-R strategy of each species.
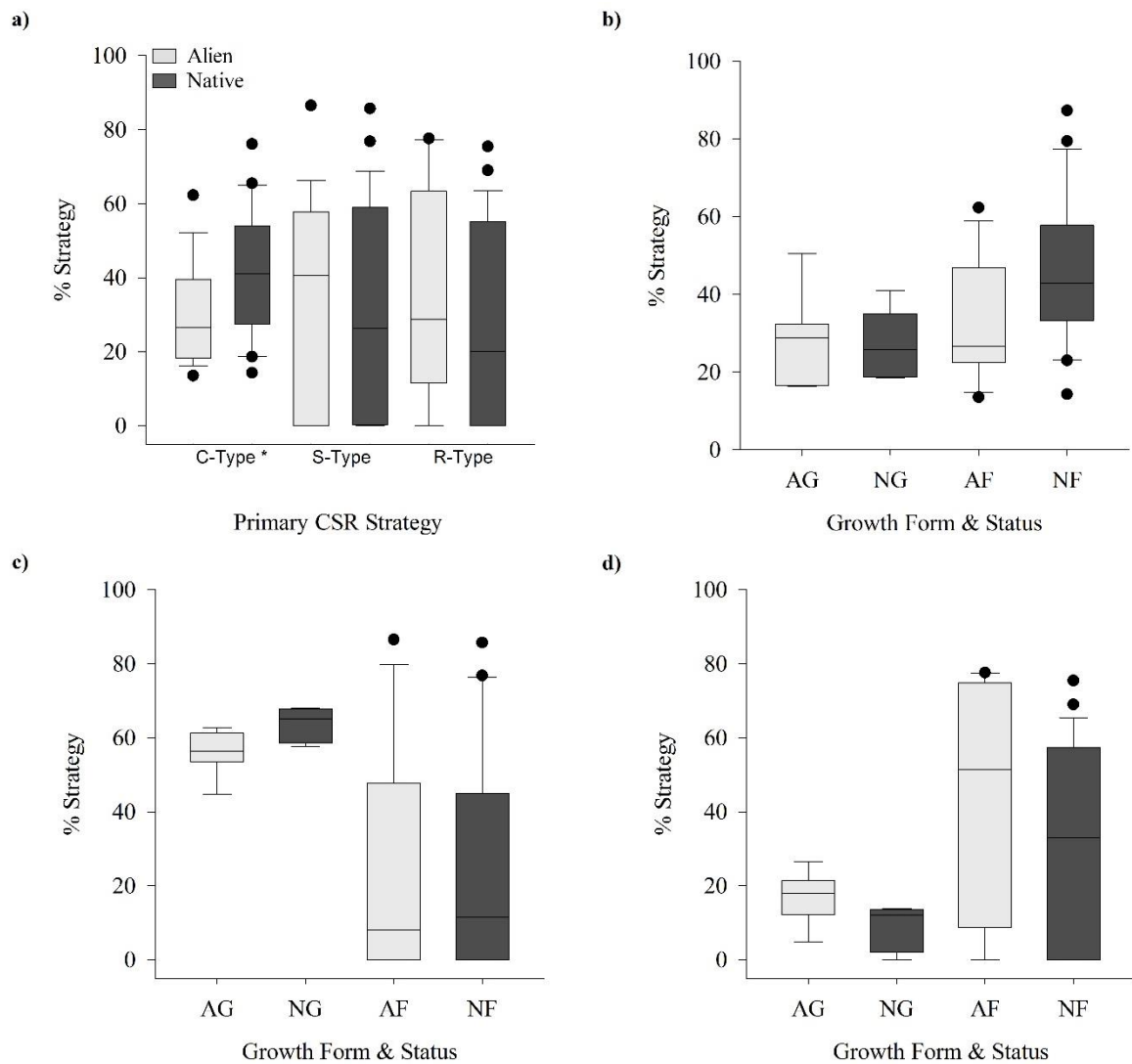
Figure 4: Differences in Grime's CSR strategies between alien and native taxa. a) Differences in primary CSR strategies between all alien and all native species. C-Type = competitor, S-Type = stress-tolerator, R-Type = ruderal. * denotes a significant difference ($p = \leq 0.05$) obtained from ANOVA analyses (Table 2). b-d) Percentage b) competitive, c) stress-tolerator and d) ruderal strategies of species of different status (alien or native) and growth form (graminoid or forb). AG = alien graminoid, NG = native graminoid, AF = alien forb, NF = native forb.
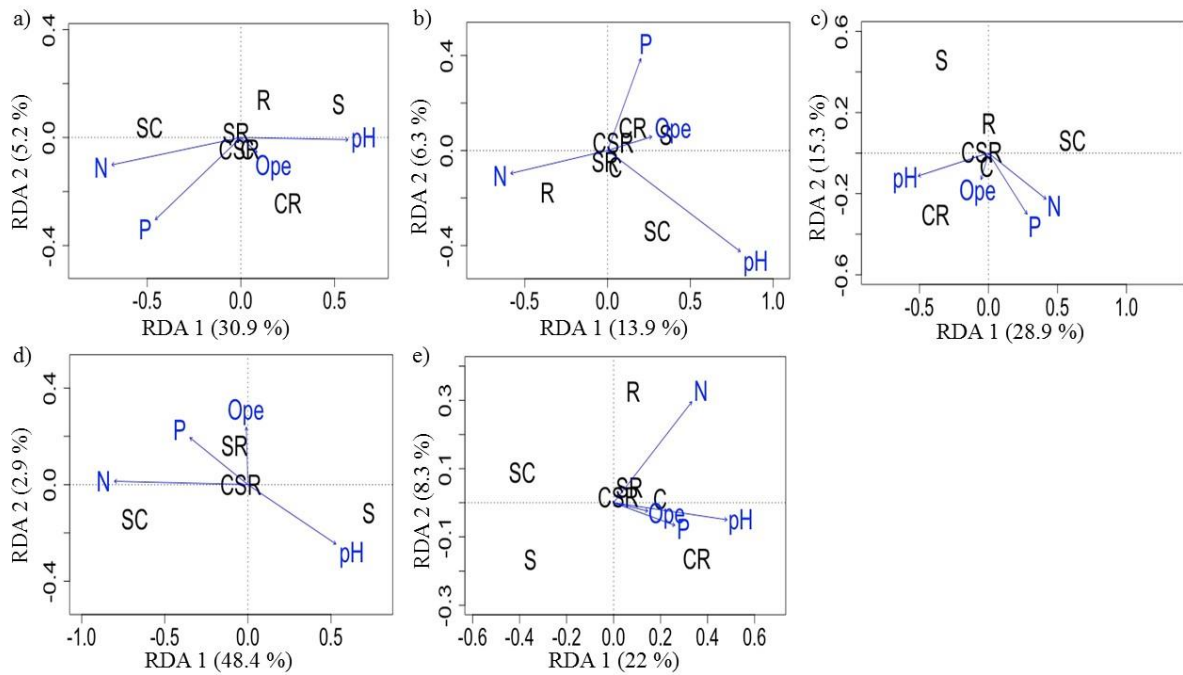
Figure 5. Redundancy analysis ordinations of C-S-R strategies, constrained by environmental variables: a) all species, b) aliens, c) natives, d) graminoids, e) forbs. C = competitors, CR = competitor-ruderals, SC = stress-tolerant-competitors, CSR = competitor-stress-tolerant-ruderals, R = ruderals, SR = stress-tolerant-ruderals, S = stress-tolerators. Constrained variables are: P = soil phosphorous, N = soil nitrogen, Ope = canopy openness, pH = soil pH.

Appendix B

Table B1: Six point classification scheme for maximum height, lateral spread and flowering start. Class definitions are as defined by Hodgson et al. (1999). The classification for flowering start has been adapted for Victoria, Australia.

Trait	Classification	Class	Class definition
Maximum height (mm)		1	1-49 mm
		2	50-99 mm
		3	100-299 mm
		4	300-599 mm
		5	600-999 mm
		6	> 999 mm
Lateral spread		1	Plant short-lived
	in graminoids	2	Loosely tufted ramets radiating about a single axis, no thickened rootstock
	in non-graminoids	2	Compactly tufted about a single axis, no thickened rootstock
	in graminoids	3	Compactly tufted ramets appressed to each other at base
	in non-graminoids	3	Compactly tufted about a single axis, thickened rootstock present
		4	Shortly creeping, < 40 mm between ramets
		5	Creeping, 40-79 mm between ramets
		6	Widely creeping, > 79 mm between ramets
Flowering start	southern hemisphere	1	First flowering in September or earlier
		2	In October
		3	In November
		4	In December
		5	In January
		6	In February or later, or before leaves in spring

Table B2: List of study species and their corresponding C-S-R strategies.

Species	Origin	Growth Form	C-S-R Strategy
Aira elegantissima	Alien	Graminoid	S
Ajuga australis	Native	Forb	C
Anthoxanthum aristatum	Alien	Graminoid	S
Briza maxima	Alien	Graminoid	S
Briza minor	Alien	Graminoid	S
Bromus diandrus	Alien	Graminoid	SC
Bromus madritensis	Alien	Graminoid	S
Burchardia umbellata	Native	Forb	C
Carduus pycnocephalus	Alien	Forb	CR
Centaurium erythraea	Alien	Forb	S
Cerastium glomeratum	Alien	Forb	R
Cirsium vulgare	Alien	Forb	CR
Daucus glochidiatus	Native	Forb	S
Desmodium varians	Native	Forb	C
Dichelachne hirtella	Native	Graminoid	SC
Dichondra repens	Native	Forb	CSR
Drosera peltata	Native	Forb	CR
Euchiton japonicus	Native	Forb	R
Geranium sp. 2	Native	Forb	CR
Gonocarpus tetragynus	Native	Forb	SC
Holcus lanatus	Alien	Graminoid	S
Hydrocotyle laxiflora	Native	Forb	CR
Hypericum gramineum	Native	Forb	S
Hypericum perforatum	Alien	Forb	C
Hypochaeris spp.	Alien	Forb	CR
Juncus aridicola	Native	Graminoid	S
Lomandra filiformis	Native	Forb	SC
Lomandra longifolia	Native	Forb	CR
Lomandra multiflora	Native	Forb	CR
Luzula densiflora	Native	Forb	CR
Luzula flaccida	Native	Forb	CR
Lysimachia arvensis	Alien	Forb	R
Microlaena stipoides	Native	Graminoid	SC
Oxalis perennans	Native	Forb	R
Pentapogon quadrifidus	Native	Graminoid	S
Poa sieberiana	Native	Graminoid	SC
Poranthera microphylla	Native	Forb	S
Ranunculus pumilio	Native	Forb	R
Rystidosperma pallidum	Native	Graminoid	SC
Rytidosperma spp.	Native	Graminoid	S
Sherardia arvensis	Alien	Forb	R
Stackhousia monogyna	Native	Forb	CR
Stellaria media	Alien	Forb	R
Stypandra glauca	Native	Forb	C

Species	Origin	Growth Form	C-S-R Strategy
Trifolium arvense	Alien	Forb	SC
Trifolium campestre	Alien	Forb	SR
Trifolium dubium	Alien	Forb	CR
Viola hederacea	Native	Forb	CR
Vulpia bromoides	Alien	Graminoid	S
Vulpia spp.	Alien	Graminoid	S
Wahlenbergia spp.	Native	Forb	CR
Xerochrysum viscosum	Native	Forb	CR

Table B3: Pearson's cross-correlation matrix for environmental variables. Upper diagonal portion shows correlation coefficient estimates (r). Lower diagonal portion contains the corresponding *p* values. Strong correlations (≤ -0.6 or ≥ 0.6) between environmental variables are indicated by bold coefficient values. LBA = live basal area, C = soil carbon, N = soil nitrogen, C:N = C:N ratio, Alt = altitude, Slo = slope, Ope = canopy openness, Mg = soil magnesium, pH = soil pH, P = soil phosphorous.

	LBA	C	N	C:N	Alt	Slo	Ope	Mg	pH	P
LBA	*****	0.574	0.151	**0.747**	**0.718**	-0.169	-0.131	-0.2	**-0.645**	-0.173
C	0.025	*****	**0.781**	**0.651**	**0.643**	-0.306	-0.211	-0.207	**-0.733**	0.148
N	0.59	0.001	*****	0.056	0.217	-0.507	-0.339	0.086	-0.377	0.07
C:N	0.001	0.009	0.844	*****	**0.811**	-0.028	0.127	-0.484	**-0.749**	0.164
Alt	0.003	0.01	0.438	<0.001	*****	-0.267	-0.244	**-0.702**	**-0.846**	0.048
Slo	0.548	0.268	0.054	0.921	0.337	*****	0.341	-0.037	0.259	0.2
Ope	0.641	0.45	0.216	0.652	0.381	0.214	*****	0.063	0.246	0.444
Mg	0.474	0.46	0.761	0.068	0.004	0.897	0.824	*****	**0.639**	-0.263
pH	0.009	0.002	0.167	0.001	<0.001	0.352	0.378	0.01	*****	-0.286
P	0.537	0.6	0.804	0.56	0.864	0.476	0.097	0.343	0.301	*****

Table B4: C-S-R composition for species of different status (alien/native) and growth form (graminoid/forb), constrained by environmental variables. Scores from redundancy analyses for a) all species, b) aliens, c) natives, d) graminoids and e) forbs. Only the first two ordination axes are shown. 'NA' indicates when a C-S-R strategy was not included in analyses, due to its absence within the particular status-growth form group. C-S-R strategies are: C = competitors, CR = competitive-ruderals, SC = stress-tolerant-competitors, CSR = competitive-stress-tolerant ruderals, R = ruderals, SR = stress-tolerant-ruderals, S = stress-tolerators. Constrained variables are: P = soil phosphorous, N = soil nitrogen, Ope = canopy openness, pH = soil pH.

	a) All		b) Aliens		c) Natives		d) Graminoids		e) Forbs	
C-S-R strategies										
Score	Axis1	Axis2	Axis1	Axis2	Axis1	Axis2	Axis1	Axis2	Axis1	Axis2
C	0.035	-0.042	0.047	-0.069	-0.011	-0.064	NA	NA	0.199	0.013
CR	0.251	-0.242	0.153	0.097	-0.383	-0.303	NA	NA	0.355	-0.162
SC	-0.487	0.04	0.301	-0.338	0.609	0.065	-0.68	-0.142	-0.387	0.09
CSR	-0.008	-0.043	0.034	0.034	-0.049	0.005	-0.042	-0.001	0.02	0.018
R	0.122	0.141	-0.362	-0.177	0.003	0.148	NA	NA	0.084	0.327
SR	-0.025	0.02	-0.014	-0.046	NA	NA	-0.079	0.162	0.068	0.045
S	0.521	0.123	0.353	0.069	-0.339	0.463	0.728	-0.115	-0.354	-0.166
Constraining environmental variables										
Score	Axis1	Axis2	Axis1	Axis2	Axis1	Axis2	Axis1	Axis2	Axis1	Axis2
P	-0.407	-0.725	0.246	0.613	0.412	-0.572	-0.299	0.503	0.32	-0.285
N	-0.856	-0.004	-0.623	-0.37	0.698	-0.373	-0.94	-0.299	0.28	0.824
Ope	0.102	-0.165	0.284	0.193	-0.118	-0.259	0.053	0.489	0.184	-0.119
pH	0.724	-0.294	0.742	-0.622	-0.891	-0.378	0.493	-0.626	0.617	-0.286

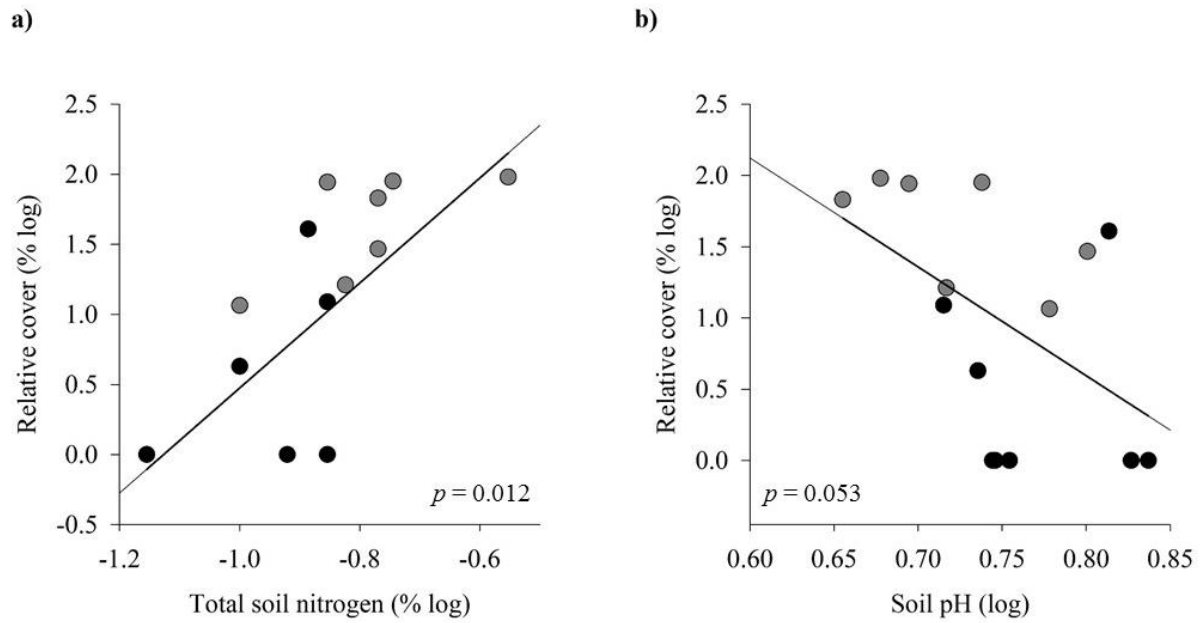**Figure B1:** Relationship between the combined relative cover (%) of dominant SC-strategist species *Microlaena stipoides* and *Rytidosperma pallidum* and a) total soil nitrogen (%) and b) soil pH. Grey data points represent communities with an SC-strategy. The *p* values shown are from linear regression models.

Chapter 3

Multispecies invasion increases and homogenizes function in an understorey plant metacommunity.

Introduction

One of plant ecology's central goals is to determine the relative importance of processes governing local community assembly (Weiher et al. 1998). Functional traits are used to examine how assembly processes such as habitat filtering and niche differentiation structure native plant communities (McGill et al. 2006; Westoby & Wright 2006). These assembly processes are known to influence the invasion of native communities by alien species (Grotkopp et al. 2002; Daehler 2003). They are also used to explain relationships between species, and between species and the environment, at a metacommunity scale (Logue et al. 2011). Certain traits increase an alien's chances of successfully invading a novel environment (van Kleunen et al 2010; Dainese & Bragazza 2012). Invasion by multiple alien species exhibiting such traits can also lead to changes in the functional structure and diversity of the invaded community (Fried et al. 2014; Castro-Díez et al. 2016). Therefore, identifying community-wide traits associated with invasion and how they relate to assembly processes is important not only to predict likelihood of successful establishment, but also to understand the impact that multiple alien species have on native communities.

Two major, deterministic processes of community assembly are widely recognised to influence community functional structure. First, abiotic habitat conditions cause non-random membership of communities and act as filters that restrict the range of trait values to those that enable persistence under prevailing conditions (Keddy 1992; Cornwell & Ackerly 2009; Shipley 2010). This 'habitat filtering' leads to functionally-similar species co-occurring in similar environments (i.e. trait-convergence), as shared traits allow these species to survive local conditions (Laughlin et al. 2012; Roscher et al. 2013). This clustering of similar trait values along specific environmental or ecological gradients is referred to as trait-convergence (Díaz et al. 1998; Weiher et al. 1998; Pillar et al. 2009). The second process altering community functional structure is niche differentiation (MacArthur & Levins 1967; Schoener 1974). In contrast to habitat filtering, competition between co-occurring species within sites necessitates the partitioning of limited resources, which reduces interspecific competition and promotes the coexistence of species that are functionally dissimilar (MacArthur & Levins 1967; Silvertown 2004; Stubbs & Wilson 2004). Niche differentiation generates trait-divergence patterns within the community (Gallagher & Leishman 2012; Laughlin et al. 2012) characterized by an increase in the range of trait values. However, competition can also exclude species when functionally-distinct traits are linked to competitive dominance (Mayfield & Levine 2010; Kunstler et al. 2016). This must be taken into account when inferring processes such as competition from patterns of trait-convergence and divergence.

Habitat filtering and niche differentiation are hypothesised to drive community trait assembly in opposing directions (convergence and divergence, respectively), but the two processes are not mutually exclusive. Habitat filtering reduces the range of viable trait values within a local environment, while niche differentiation can affect the spacing of trait values within this reduced range (a more even spacing of trait values results in higher apparent divergence) (Cornwell & Ackerly 2009). While environmental factors filter out species to allow only those with traits suited to local conditions (restricting the range of trait values; Díaz et al. 1998), species coexistence within the filtered assemblage can be promoted by resource partitioning through divergent trait values (increasing the evenness of trait value space) (Pacala & Tilman 1994). In this way, habitat filtering and niche differentiation can simultaneously influence species assemblages, resulting in communities exhibiting both convergence and divergence (Cornwell & Ackerly 2009). Importantly, the size and composition of the species pool can determine variation in trait values within a community, through evolutionary and ecological processes such as selection and dispersal (Vellend 2010).

Habitat filtering and niche differentiation can also determine whether aliens will converge or diverge in trait values with those of recipient communities. Habitat filtering results in trait-convergence between natives and aliens (Thompson et al. 1995; Duncan & Williams 2002), whereas niche differentiation promotes successful alien establishment when, for example, aliens are better suited to disturbed environments than their native counterparts (Crawley et al. 1996; Lake & Leishman 2004). If resource conditions in the invaded habitat are poor, aliens may gain a competitive advantage over natives by exhibiting trait values more suited to conserving limited resources, such as a long-lived, smaller leaves (Funk & Vitousek 2007). Conversely, in resource-rich habitats aliens may have traits such as higher specific leaf area (SLA) that allow them to take advantage of abundant resources more readily than natives (Leishman et al. 2007). Identifying patterns of trait-convergence and divergence in invaded communities can determine how invasion alters community functional structure, and can reveal which traits of invading aliens are responsible for this change.

Several traits have been linked to successful invasion by aliens. These traits enhance performance (e.g. higher reproductive output and faster growth strategies), giving aliens a competitive advantage over co-occurring natives (Leishman et al. 2007; van Kleunen et al. 2010; Leishman et al. 2014). Arguably the most widely-supported trait characteristic of invasive plant species is SLA. High SLA is strongly correlated with growth-promoting traits such as high relative growth rate and short-lived leaves (Wright & Westoby 1999). Higher SLA has been found among invasive aliens compared to natives in several different habitats

(Dainese & Bragazza 2012; Feng & van Kleunen 2016; Marx et al. 2016) and across multiple disturbance and/or resource regimes (Grotkopp et al. 2002; Lake & Leishman 2004). Other traits associated with invasive species and fast growth strategies include short lifespan (annual life history), increased leaf area and higher leaf nitrogen content (Cadotte & Lovett-Doust 2001; Daehler 2003; Leishman et al. 2014). Reproductive traits promoting successful invasion include longer flowering duration, which increases reproductive output by providing higher visitation rates by pollinators and increased overlap between flowering periods and activities of multiple pollinators (Chrobock et al. 2013; Feng et al. 2016). Smaller seed mass in aliens may promote greater fecundity through production of many seeds easily dispersed by wind (Rejmánek 1996; Schmidt & Drake 2011). Several studies have also found that invasive aliens are more likely to be clonal than to natives, which can increase dispersal and occurrence of aliens at local scales (Liu et al. 2006).

Studies determining which traits enable a species to invade have seldom incorporated gradients of multispecies invasion. Most trait-based invasion research, including the use of invasion gradients, focuses on single-species invasions and impacts, or have compared invasive aliens with native congeners (Pyšek & Richardson 2007; Robertson & Hickman 2012; Kuebbing et al. 2013; Bansal & Sheley 2016). Those studies that do consider multiple alien species usually involve pairwise comparisons of species, or invaded versus non-invaded communities (Pyšek & Richardson 2007). Invasion, however, is a cumulative process developing along an invasion continuum, with habitats regularly invaded by more than one species over time, and with varying levels of invasion severity (Traveset & Richardson 2011; Campos et al. 2013). Collectively, aliens may exhibit certain trait values that differ from natives and could impact community functional structure and assemblage patterns more severely than the impacts of any single invader (Kuebbing et al. 2013). Examining which traits are divergent or convergent along a multispecies invasion gradient could i) identify what components of community functional structure are altered by multispecies invasion and ii) what consequences this has for functional diversity. Furthermore, investigating community trait similarities and dissimilarities could reveal at what point along the multispecies invasion gradient the greatest shift in patterns of divergence and convergence occurs.

Here, I examine if invasion by multiple alien species is related to changes in community-wide functional traits, and trait-convergence/divergence patterns, across an invasion gradient in a dry forest plant metacommunity. I investigate three key questions: 1) how do community-wide plant traits change with an increase in the level of multispecies plant invasion, 2) do trait patterns in the metacommunity converge or diverge across the invasion gradient and 3) if these

patterns are present, which traits contribute most to convergence or divergence? I predict that flowering duration, clonality, proportion of annuals, maximum height, leaf area and SLA will significantly increase as the invasion level increases, while seed mass, leaf dry mass and leaf thickness will decrease (Table 1).

Methods

Study location and multispecies invasion gradient

Chiltern-Mt. Pilot National Park is a 21,560 ha protected area in north-east Victoria, Australia. The park was established in 2002 and contains granitic hills woodlands and box-ironbark forest consisting of open canopies of native eucalypt (*Eucalyptus*) and cypress pine (*Callitris*) trees. Regional land use around Chiltern-Mt. Pilot historically involved gold mining, forestry and agriculture and has resulted in > 80 % loss of native habitats (Parks Victoria 2008). Subsequent land use and human activity has increased disturbance in the region leading to pressures such as invasive alien species negatively affecting the surviving intact ecosystems (Parks Victoria 2008). While there are few alien tree species within the park, the understorey community has been invaded by many, predominantly herbaceous, aliens. Despite this, several significant flora and fauna are protected, including a variety of orchid species (Parks Victoria 2008).

Fifteen sites were selected for sampling. These sites were spread across the park and ranged in distances of 1 to 22 km apart. Sites are 500 m² and divided into 25 subplots each measuring 20 m². The chosen sites represent individual communities within the study system and are henceforth referred to as 'communities'. The fifteen communities collectively represent the metacommunity. Here, I investigate trait changes and patterns of convergence and divergence applied at a metacommunity scale, with communities arranged along the invasion gradient (Pillar et al. 2009).

To determine how traits change across a multispecies invasion gradient, a range of invasion levels was represented across the 15 communities. Relative alien abundance is recommended as an indicator of invasion level as it expresses the contribution that aliens make to a community, is independent of scale and is comparable across ecosystems and regions (Catford et al. 2012). Here I use relative alien cover (%) as a proxy for relative alien abundance. This measure was calculated for each community and used to represent the level of multispecies invasion within that community. Measurements were obtained for the cover (%) of individual understorey species (forbs, graminoids and shrubs ≤ 3 m) in each community. Within each subplot in each community, two 1 m x 1 m quadrats were randomly placed (50 quadrats per

community). Percent cover was estimated for every individual species per quadrat, using the following categories: 0 %, < 1 %, 1 %, 2 %, 5 % with subsequent intervals of 5 % from 10 to 100 (Daubenmire, 1959; Stohlgren 2007). Cover was summed across all 50 quadrats to give a total community cover for each species, as well as a total community cover for all species combined. All alien species were used in defining the invasion gradient in this study (i.e. included in the total alien cover). Aliens are likely to be situated at different stages of the invasion process due to different introduction times and subsequent lag phases, meaning some aliens may yet significantly impact the invaded community (Catford et al. 2012; Campos et al. 2013). Including all alien species addresses the subjectivity of categorising aliens as invasive (Campos et al. 2013). The multispecies invasion gradient across all 15 communities ranged from 3.92 % to 61.08 % relative alien cover.

Collection of trait data

Data were collected for five field-based traits (1. maximum vegetative height (mm), 2. leaf thickness (mm), 3. leaf area (mm²), 4. leaf dry mass (mg), 5. SLA (mm² mg⁻¹)) and four literature-sourced traits (1. flowering duration (months), 2. seed mass (mg), 3. clonal (yes/no), 4. annual life history (proportion of species); Table 1). Traits were selected based on research from prior studies that provide evidence of their link to invasive species (Table 1). Trait data were collected for the most common species in each of the communities (i.e. 85-95 % of total community cover; Pakeman & Quested 2007). Across all 15 communities, a total of 59 plant species were sampled in-field for trait data.

Field samples were collected in the austral spring of 2014 and 2015. Maximum plant height measurements were collected *in-situ* for each species per community from the tallest observed individual. Forty leaf samples (four leaves per individual across ten individuals; Pérez-Harguindeguy et al. 2013) were collected for each species in each community to obtain measurements for the four leaf traits. Twenty samples per species in each community were measured for leaf thickness using digital callipers. All leaf samples were scanned using a Canon LiDE210 flatbed scanner and ImageJ software was used to calculate the one-sided area of each leaf. Leaf samples were oven-dried for 72 hours at 70°C then weighed using a microbalance to obtain leaf dry mass. Specific leaf area was calculated by dividing the leaf area of each sample by its leaf dry mass. Seed mass data was collected from the Kew Royal Botanic Gardens Seed Information Database (http://data.kew.org/sid/, accessed 25 Jan 2017). Life history,

clonality and flowering duration data was collated from Walsh & Entwisle (1992-1996) and supplementary literature-based sources.

Statistical analyses

Generalized linear models (Gaussian error distribution with log link function) were used to test relationships between traits and the invasion gradient, with the trait as the response variable. Each trait was analysed separately. Community mean trait values were used and were unweighted by species abundances. Spatial autocorrelation analysis was run for the residuals of each GLM model using global Moran's I (Dormann et al. 2007). No significant spatial autocorrelation was found for any of the traits ($p = \geq 0.05$): i.e. trait data can be regarded as spatially independent. Analyses were performed using R Studio 3.3.1 (R Core Team, 2016).

Trait patterns were investigated using three data matrices: matrix **B** containing species described by traits; matrix **W** containing species cover data in each community, and matrix **E** describing communities according to their level of invasion (Pillar et al. 2009). The mean trait value across communities for each species was used for the quantitative traits in matrix **B**. Matrix **W** was standardized so that row totals (communities) = 1. To ensure that the alien species cover data used in Matrix **E** and the cover data used in Matrix **W** were independent, a Pearson's correlation was performed. The correlation was not significant ($r = 0.152, p = 0.589$) and the cover data used in each matrix can be treated as independent for the purpose of analysis. The three matrices (**B**, **W** and **E**) form the basis for analysis in the R package "SYNCSA" (Debastiani & Pillar 2012).

Traits were scaled up to metacommunity level separately to measure convergence and divergence. To enable detection of convergence, matrix **T** containing community-weighted mean trait values was created, using the matrix multiplication **T = B'W**. Traits in matrix **T** were standardized due to a combination of binary and quantitative data using different units of measurement. To identify divergence, a matrix **U** was first created with degrees of belonging of species to fuzzy sets defined by the traits in Matrix **B**. This was done using the Gower similarity coefficient which is appropriate for handling different measurement units of traits in matrix **B** (Gower 1971; Podani 1999). Matrix **X** was created using the matrix multiplication **X = U'W**, and describes the composition of the communities in terms of species taken as fuzzy sets. The subsets of traits from matrix **B** that maximised the expression of convergence and divergence related to the invasion gradient in matrix **E** were then identified using an iterative method developed by Pillar & Sosinski (2003).

The matrices **T**, **X** and **E** were used to compute distance matrices of communities ($\mathbf{D}_T$, $\mathbf{D}_X$ and $\mathbf{D}_E$, respectively), that relate both **T** and **X** to **E**. Only the subsets of traits maximising expression of convergence and divergence were used. Relating **T** to **E** involved a matrix correlation $\rho(\mathbf{TE}) = \rho(\mathbf{D}_T; \mathbf{D}_E)$ which measures how congruent community distances based on **T** ($\mathbf{D}_T$) are with community distances based on **E** ($\mathbf{D}_E$), comparable to the correlation in a Mantel test (Pillar et al. 2009). The resulting correlation between $\mathbf{D}_T$ and $\mathbf{D}_E$ is a measure of trait-convergence related to variation along the multispecies invasion gradient. A large $\rho(\mathbf{TE})$ indicates communities sharing trait similarities are also similar in their level of multispecies invasion. Using the same method of matrix correlation for **X** and **E** (i.e. $\rho(\mathbf{XE}) = \rho(\mathbf{D}_X; \mathbf{D}_E)$) reveals both trait-convergence and divergence related to the variation in **E**. To remove the trait-convergence component from $\rho(\mathbf{XE})$ a partial Mantel correlation $\rho(\mathbf{XE.T}) = \rho(\mathbf{D}_X; \mathbf{D}_E)$ is used. This provides a measure of trait-divergence related to the variation in **E** while controlling for the effects of trait-convergence (Pillar et al. 2009). The subsets of traits maximising expression of convergence and divergence were used in the analyses of community assembly patterns. Once values of convergence [$\rho(\mathbf{XE})$] and divergence [$\rho(\mathbf{XE.T})$] were computed, statistical significance was tested against null models of 999 iterations by obtaining a randomly-generated null $\rho(\mathbf{XE})$ and $\rho(\mathbf{XE.T})$.

Because closely-related species are expected to share similar traits with each other than with distantly-related species, it is important to quantify the effects of species' evolutionary history on community patterns (de Bello et al. 2015). Aliens in this system are distantly-related to natives (Chapter 1), and this may impact trait patterns along the gradient. Trait phylogenetic signal related to convergence and divergence was measured at the metacommunity level (Pillar & Duarte 2010). The correlation between the phylogenetic structure of the metacommunity and the invasion gradient was also quantified. A phylogenetic tree for the metacommunity (all species with trait measurements across all communities) was created using the APG III phylogeny (Stevens 2001) and Phylomatic (Webb & Donoghue 2005). The branch length adjustment algorithm (BLADJ) in Phylocom was used to assign branch lengths, calibrated in millions of years, to the metacommunity phylogenetic tree (Wikstrom et al. 2001; Webb et al. 2008). A phylogenetic distance matrix based on the branch lengths was then created and standardized (range 0-1). The resulting matrix $\mathbf{S}_F$ was used to scale up the phylogeny to community level using a method analogous to the scaling up of traits to the community level (Pillar et al. 2009; Pillar & Duarte 2010). Matrix **Q** was obtained and standardized with degrees of belonging of species to fuzzy sets defined by the phylogenetic pairwise dissimilarities in

matrix $\mathbf{S_F}$. The matrix multiplication $\mathbf{P=W'Q}$ gives matrix $\mathbf{P}$ containing the phylogenetic structure of communities after fuzzy-weighting of species abundances by the phylogenetic similarities of species. A distance matrix ($\mathbf{D_P}$) is then computed from $\mathbf{P}$ and the matrix correlations $\rho(\mathbf{PT}) = \rho(\mathbf{D_P}; \mathbf{D_T})$ and $\rho(\mathbf{PX.T}) = \rho(\mathbf{D_P}; \mathbf{D_T}.\mathbf{D_T})$ measure the phylogenetic signal at the metacommunity level related to convergence and divergence, respectively. The strength of the association between the phylogenetic structure of the communities and the invasion gradient was measured by the matrix correlation $\rho(\mathbf{PE}) = \rho(\mathbf{D_P}; \mathbf{D_E})$.

Upon the identification of convergence and divergence and the subset of traits maximising these patterns, exploratory analysis was performed to interpret results. To interpret patterns of trait-convergence, I performed linear regressions looking at the relationship between community-weighted mean (CWM) trait values from matrix $\mathbf{T}$ and the invasion gradient. This was done separately for each trait that maximised the expression of trait-convergence. To interpret trait-divergence patterns I first calculated two values of Rao's quadratic entropy (FD_Q) for each community: once using all traits and once using the optimal subset of traits driving divergence. Rao's quadratic entropy gives a measure of functional diversity for each community that is based on species abundances and trait dissimilarities among them (Rao 1982). I used nonlinear regression to explore relationships between FD_Q and the invasion gradient. I also calculated coefficients of variation of mean FD_Q for communities of low (n = 6), intermediate (n = 6) and high (n=3) levels of invasion to explore variation in FD_Q along the gradient.

Results

Community-wide trait changes across the invasion gradient

Two of the nine traits were significantly related to the multispecies invasion gradient (Table 2). The proportion of species with an annual life history increased significantly with relative alien cover ($p = 0.003$, Figure 1). Mean SLA also increased significantly across the multispecies invasion gradient, with high mean SLA found in communities with a high level of invasion ($p = 0.003$, Figure 1).

Trait-convergence and trait-divergence patterns across the invasion gradient

Both trait-convergence and trait-divergence patterns were significantly related to the multispecies invasion gradient (Table 3). The subset of traits maximising convergence included annual life history and flowering duration ($\rho(\mathbf{TE}) = 0.941$, $p = < 0.001$). There was a significant

relationship between annual CWMs and the multispecies invasion gradient ($p = < 0.001$; Table C1). Communities with higher levels of multispecies invasion supported higher abundances of annual species (Figure 2a). Flowering duration CWMs, however, were found to be non-significant across the invasion gradient ($p = 0.669$; Figure 2b) despite being one of the traits optimising trait-convergence. Mean flowering duration for aliens was consistently between 4.45 and 5.5 months and for natives between 4.79 and 6.85 months (Figure C1), revealing little difference in flowering duration.

The traits responsible for maximising divergence were leaf dry mass, SLA, seed mass and annual life history ($\rho(\mathbf{XE.T}) = 0.937$, $p = 0.001$). Considering all nine traits, functional diversity (FD$_Q$) significantly increased with the level of invasion ($p = 0.023$; Table C1; Figure 2c). This significant pattern remained when considering only those traits maximising divergence ($p = 0.004$; Table C1; Figure 2d). Variation in functional diversity was greater within little-invaded communities (relative alien cover < 20%) than in communities with intermediate or high invasion levels (Figures 2c, d; 3). Communities with < 20 % relative alien cover had FD$_Q$ ranging from $0.05 - 0.4$, while communities with invasion levels greater than 20 % had FD$_Q$ in the range of 0.3 - 0.4 (Figure 2c, d). Functional diversity in communities of intermediate and high invasion had coefficients of variation ranging from 7-12 %, while little-invaded communities had coefficients of variation of 56 % (only optimal traits) and 63 % (all traits; Figure 3a) - equivalent to an eightfold and fivefold increase in variation, respectively.

The correlation between the phylogenetic structure of the communities and the multispecies invasion gradient was non-significant ($\rho(\mathbf{PE}) = 0.096$, $p = 0.483$). Additionally, phylogenetic signal at the metacommunity level was not significant for either trait-convergence or divergence ($\rho(\mathbf{PT}) = 0.171$, $p = 0.555$ and $\rho(\mathbf{PX.T}) = 0.021$, $p = 0.519$, respectively). In other words, phylogenetically-structured assembly patterns are not correlated with patterns of trait-convergence or trait-divergence in this system.

Discussion

As far as I am aware, this study is the first to show that traits previously associated with invasion success, and patterns of trait convergence and divergence, are significantly correlated with a gradient of increasing multispecies invasion. Specifically, the proportion of annual species and SLA increased significantly across the multispecies invasion gradient. Annual life history and flowering duration maximised patterns of trait-convergence in contrasting ways. Annual life history, SLA, leaf dry mass and seed mass maximised trait-divergence.

Furthermore, functional diversity increased as multispecies invasion increased, but variation in functional diversity was lower at intermediate and high levels of invasion (> 20 %).

Community-wide traits across the multispecies invasion gradient

Studies associating traits to invasion success have predominantly involved pairwise comparisons of aliens and natives, or invaded and uninvaded communities. Here, I have demonstrated that specific leaf area and annual life history are significantly correlated with increases in multispecies invasion of communities. Herbaceous alien annuals such as *Lysimachia arvensis*, *Cerastium glomeratum* and *Sherardia arvensis*, and annual grasses such as *Briza minor*, were characteristic of highly-invaded communities, and were among the species that had the highest SLA values in those communities. Invasion success by aliens is often attributed to traits promoting rapid growth and reproduction, particularly in disturbed or temporarily resource-rich environments (Lambdon et al. 2008; Pyšek et al. 2009; J; Dainese & Bragazza 2012). Such traits include high SLA, which is situated toward the 'fast return' end of the leaf economic spectrum that promotes faster growth and increased photosynthetic rates (Westoby et al. 2002; Wright et al. 2004). Invading aliens have been associated with high SLA across several studies, spanning different functional groups and environmental regions, such as peri-urban bushland and arid shrubland (Lake & Leishman 2004; Dainese & Bragazza 2012). Annual life history is also associated with faster growth rates and has been linked to invasions at global, country, regional and habitat scales (Cadotte & Lovett-Doust 2001; Sutherland 2004; Pyšek et al. 2009; Dainese & Bragazza 2012). The increase in the proportion of annual species and SLA with invasion level shows that not only dominance by a single invader, but also multispecies invasion, has the potential to significantly alter the functional structure of invaded communities. This in turn may impact ecosystem functioning, supported by the fact that both annual life history and SLA were among the subset of traits maximising patterns of trait-convergence or divergence.

The seven remaining traits showed no significant relationship with the invasion gradient. This was particularly surprising for flowering duration because the association between longer flowering periods and invading species is well-supported (Pyšek & Richardson 2007). There are three potential reasons for this. First, the seven traits may be more relevant when conducting analyses between specific species or taxonomic groups, rather than realized communities of species in the field, as shown here. Studies linking these traits with invasion have predominantly tested for trait differences between invasive and native congeners or used

pairwise comparisons between invasive aliens and natives (Pyšek & Richardson 2007). Second, processes impacting trait patterns, such as habitat filtering and niche differentiation, differ in strength at different spatial scales and can influence different traits in contrasting ways (Kraft & Ackerly 2010). For example, Hamilton et al. (2005) found smaller seed mass to be significantly correlated with invasion success at regional and continental scales and high SLA at the continental scale only.

The third potential reason is that the multispecies invasion gradient is based on the relative alien cover of each community and incorporates alien species that are not considered invasive, even though they have naturalized. Frequently-occurring aliens, such as *Aira elegantissima*, *Hypochaeris spp.* and *Lysimachia arvensis*, are classified as non-invasive at both the state and bioregional scale (Adair et al. 2008; Victoria State Government Department of Environment and Primary Industries 2017). The use of all alien species may affect the significance of the trait-invasion associations across the gradient by obscuring trait values closely linked to invasive aliens. If this is the case, significant differences between aliens and natives for these traits may occur only when considering highly invasive species, but excluding non-invasive aliens that may still be locally abundant. For this approach, all alien species were included as I am interested in the cumulative effect of multiple alien species on trait patterns across the metacommunity.

Trait-convergence and trait-divergence across the multispecies invasion gradient

Both trait-convergence and divergence were found across the multispecies invasion gradient. This suggests that contrasting mechanisms such as habitat filtering and niche differentiation are influencing community trait patterns along the gradient. These mechanisms are often used to investigate trait patterns in communities and metacommunities (Pillar et al. 2009; Logue et al. 2011). This means that trait-convergence among communities may be observed in one part of the gradient, whereas trait-divergence may occur in another part of the gradient, resulting in both convergence and divergence at the metacommunity scale (Pillar & Duarte 2010; Carlucci et al. 2012). Additionally, the relevance to aliens of mechanisms promoting convergence or divergence may be dependent on the stage of invasion. Convergence may restrict aliens during the establishment stage to those with trait values suited to local conditions (Theoharides & Dukes 2007). Trait-divergence may be more important in enabling aliens to spread throughout the new environment once they are established (Martin & Canham 2010). However, without more detailed information on alien introduction times, and the lag phases which they

experience, it is difficult to link convergence/divergence patterns to particular stages of invasion.

Trait-convergence can occur when communities in close proximity along the ecological gradient consistently share species with similar trait values, and changes in these traits are associated with the gradient (Pillar et al. 2009). This pattern was evident for annual life history, as communities with similar relative alien cover along the invasion gradient converged toward similar proportions of annual species. In contrast, flowering duration converged along the gradient because all communities contained species with similar flowering periods, regardless of the level of invasion a community experienced. This indicates that annual life history and flowering duration express patterns of convergence in different ways, but their combination maximises the expression of convergence along the invasion gradient.

Trait-divergence occurs when turnover in community trait values coincides with changes along the ecological gradient, but the communities consist of species with dissimilar traits (Pillar et al. 2009). Along the invasion gradient, I found trait-divergence to increase with invasion level, as indicated by FD_Q. This increase suggests that aliens collectively exhibit a broader range of trait values than natives. However, this is in direct contradiction to the findings of earlier work (Chapter 2), in which natives showed more diversity in life strategies than aliens. Although not all the same traits were used in both studies, the contradictory outcomes reveal that using a continuum of invasion (i.e. the invasion gradient) may provide different conclusions about invasion impacts to studies comparing aliens and natives directly. Therefore, more research incorporating continuums or gradients of invasion are needed. Only one other study that I am aware of (in Mediterranean dune ecosystems) has found invasion by multiple alien species to increase the functional diversity of communities (Marcantonio et al. 2014). The use of the invasion gradient provides a novel insight into the impact of multispecies invasion.

Annual life history maximised patterns of both trait-convergence and divergence. This is possible when convergence and divergence are represented at different points along the gradient. The proportion of annuals consistently converged between communities with similar invasion levels along the gradient. Divergence along the same gradient is evident in how the proportion of annuals changes significantly along the entire gradient. Traits such as SLA, plant inclination, leaf shape and leaf resistance have been associated with both convergent and divergent patterns along the same gradients of soil water availability, nitrogen fertilization and grazing intensity (Cornwell & Ackerly 2009; Pillar et al. 2009). My results support the idea that individual traits are often responsible for influencing trait patterns in opposing ways across ecological gradients.

Functional diversity across the invasion gradient was more variable in little-invaded communities than in intermediate- or highly-invaded communities. Rao's quadratic entropy is considered to be independent of species richness in most cases (Götzenberger et al. 2016). However, in this system, FD_Q significantly increased as species richness increased (Figure C2). Despite this, FD_Q increased significantly with invasion level, even when species richness was accounted for. This suggests that trait dissimilarity increases then remains constant in communities that have reached a particular threshold of multispecies invasion (in this case ~ 20 % relative alien cover). Differences in functional diversity between little- and highly-invaded communities stem mostly from variation in functional diversity among little-invaded communities. To my knowledge, the combined increase and homogenization of functional diversity has not been found in previous studies of plant invasions. The findings here emphasize the need for focus on multispecies invasion studies, in particular studies incorporating invasion gradients, and how they impact metacommunity functional structure.

Conclusions

Growing evidence suggests that traits such as high SLA and annual life history are related to increased invasion success. My research builds on this evidence by revealing these two traits are characteristic of aliens *in situ* when examined across a multispecies invasion gradient. Specific leaf area and annual life history promote rapid growth and completion of life cycles and this could have implications for ecosystem functioning, such as productivity (Wright et al. 2004; Liao et al. 2008). The correlation of trait-convergence and divergence patterns with the invasion gradient reveals that alien invasion of communities can alter community functional structure in opposing directions (i.e. more or less similar in traits to natives) and that these patterns are driven by traits known to promote invasion. Finding high functional diversity in communities of intermediate and high levels of invasion contrasts with other studies that find invasion by single species to often reduce community functional diversity (Chabrerie et al. 2010; Michelan et al. 2010). With invasion by aliens expected to rise in the future (Hellmann et al. 2008), native communities in many parts of the world may experience increases in functional diversity when invasion by multiple aliens occurs. The use of an invasion gradient in this study therefore provided a novel insight into the impact of multispecies invasion on the functional structure of a metacommunity. More field research focussing on multispecies invasion will help to determine if increased and homogenized functional diversity is a common phenomenon in communities containing co-occurring aliens.

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Tables

Table 1. The traits used and their proposed response mechanisms to multispecies invasion. Positive (+) and negative (-) symbols indicate increases and decreases in species trait values. "Higher invasion" refers to an increase in relative alien cover (%).

Trait	Proposed trait response to multispecies invasion (+/-)	Evidence source of proposed trait response in alien species
Life history (proportion annuals)	Higher proportion of species with annual life history as community invasion increases (+)	Cadotte & Lovett-Doust (2001); Pyšek et al. (2009); Dainese & Bragazza (2012)
Maximum plant height (mm)	Taller species found in communities with higher invasion (+)	Westoby (1998); Feng & van Kleunen (2016)
Flowering duration (months)	Longer flowering duration at sites with higher invasion (+)	Chrobock et al. (2013) ; Bezeng et al. (2015) ; Feng et al. (2016)
Seed mass (mg)	Smaller seeds in communities with higher invasion (-)	Rejmánek (1996); Cadotte & Lovett-Doust (2001); Thuiller et al. (2006) ; Schmidt & Drake (2011)
Clonality (proportion species)	Higher proportion of species are clonal in communities with higher invasion (+)	Lake & Leishman (2004); Burns (2006); Liu et al. (2006); Shah et al. (2014)
Leaf area (mm²)	Higher leaf area with an increase in community invasion (+)	Daehler (2003); Liu et al. (2015); Wang et al. (2013); Leishman et al. (2014)
Leaf dry mass (mg)	Lower leaf dry mass with higher invasion (-)	Fynn et al. (2009); Matzek (2011)
Leaf thickness (mm)	Lower leaf thickness in communities with higher invasion (-)	Smith et al. (1998); Niinemets (2001); Funk & Throop (2010) ; Pérez-Harguindeguy et al. (2013)
Specific leaf area (SLA) (mm² mg⁻¹)	Higher SLA in communities with higher invasion (+)	Lake & Leishman (2004); Grotkopp & Rejmánek (2007); Pyšek & Richardson (2007); Marx et al. (2016)

Table 2. Changes in mean trait values across the multispecies invasion gradient. Generalized linear model results (family = Gaussian, link = log). Significant p values ($p \leq 0.05$) are in bold.

Trait	Estimate	Std. Error	df	t	p
Annual life history (proportion species)	0.016	0.004	13	3.695	**0.003**
Height (mm)	-0.002	0.004	13	-0.51	0.618
Flowering duration (months)	< 0.001	0.001	13	0.254	0.804
Seed mass (mg)	-0.009	0.007	13	-1.245	0.235
Clonal (proportion species)	-0.001	0.002	13	-0.499	0.626
Leaf area (mm²)	-0.003	0.007	13	-0.358	0.726
Leaf dry mass (mg)	-0.001	0.007	13	-0.205	0.841
Leaf thickness (mm)	-0.001	0.002	13	-0.435	0.671
Specific leaf area (mm² mg⁻¹)	0.013	0.004	13	3.564	**0.003**

Table 3. The optimal trait subsets that maximise trait-convergence and trait-divergence along the multispecies invasion gradient. Significant p values ($p = \leq 0.05$) are in bold.

	Trait-convergence			Trait-divergence		
	Optimal Traits	Annual, Flowering duration		**Optimal Traits**	Annual, SLA, Leaf dry mass, Seed mass	
Correlation	**Metric**	**Obs**	***p***	**Correlation**	**Obs**	***p***
Convergence/divergence	ρ(**TE**)	0.941	**0.001**	ρ(**XE.T**)	0.937	**0.001**
Phylogeny & convergence/divergence	ρ(**PT**)	0.171	0.555	ρ(**PX.T**)	0.021	0.519
Phylogeny & invasion gradient	ρ(**PE**)	0.096	0.483	ρ(**PE**)	0.096	0.493
Phylogenetic signal of species pool	ρ(**FB**)	0.054	**0.043**	ρ(**FB**)	0.069	0.066
Convergence/divergence w/o phylogeny effects	ρ(**TE.P**)	0.943	**0.001**	ρ(**XE.P**)	0.939	**0.001**
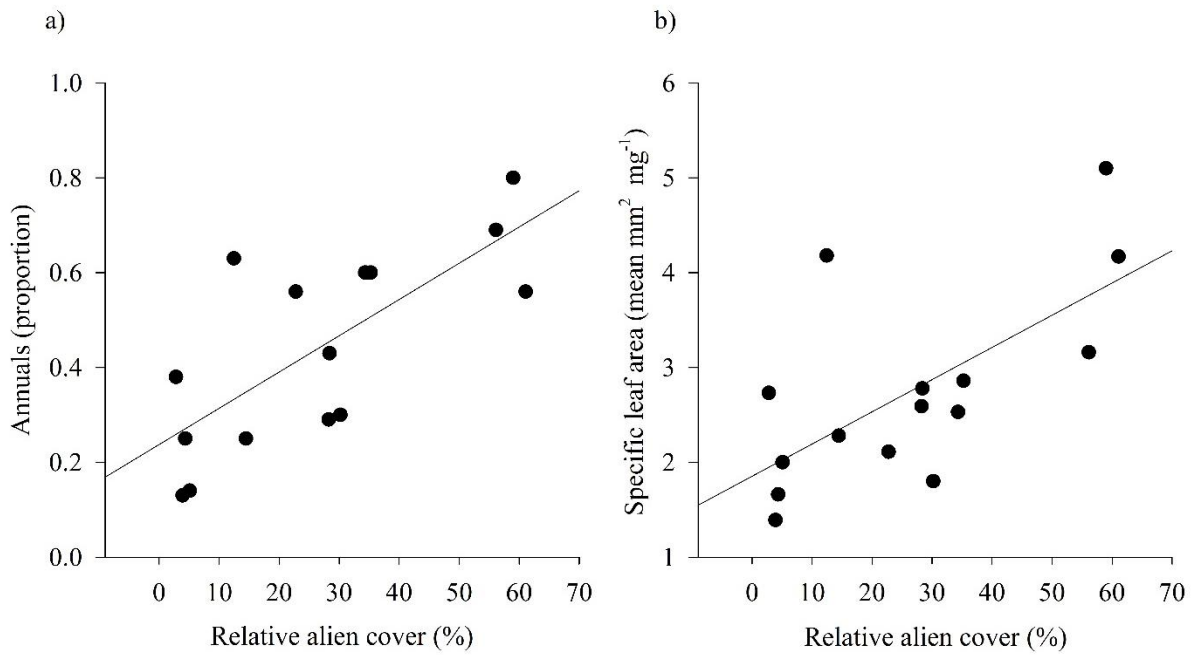
Figure 1. The relationship between relative alien cover and a) proportion of annuals ($p = 0.003$) and b) specific leaf area ($p = 0.003$). The p values have been taken from GLM models (Gaussian error distribution with log link function; Table 2).

Figure 2. The relationship between relative alien cover and a,b) community-weighted means (CWM), c,d) functional diversity. a) CWM of annual life history ($p = < 0.001$); b) CWM of flowering duration ($p = 0.669$); c) functional diversity for all traits ($p = 0.026$); d) functional diversity for the trait subset maximising divergence ($p = 0.005$). The p values have been taken from regression models (Table C1).

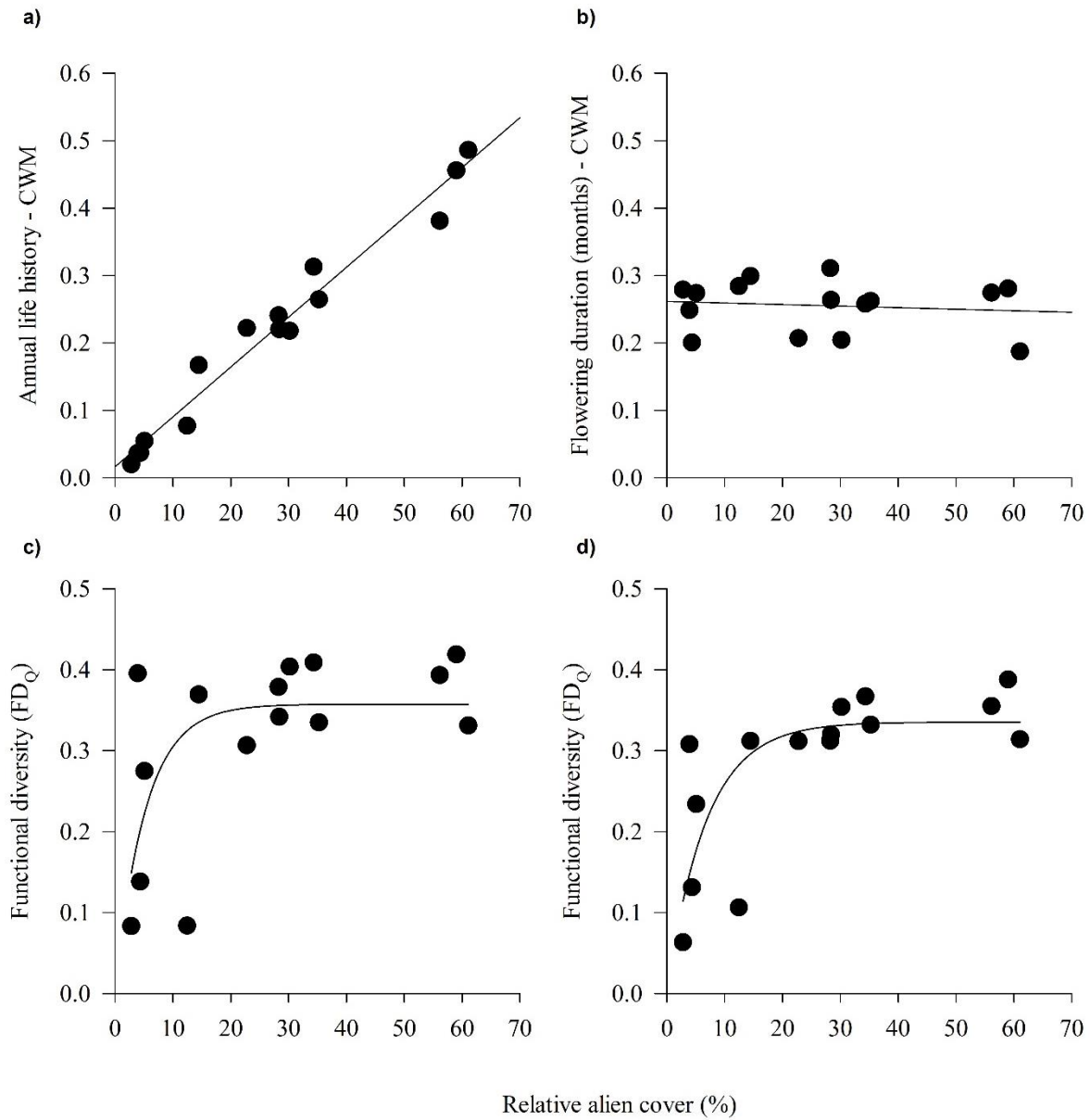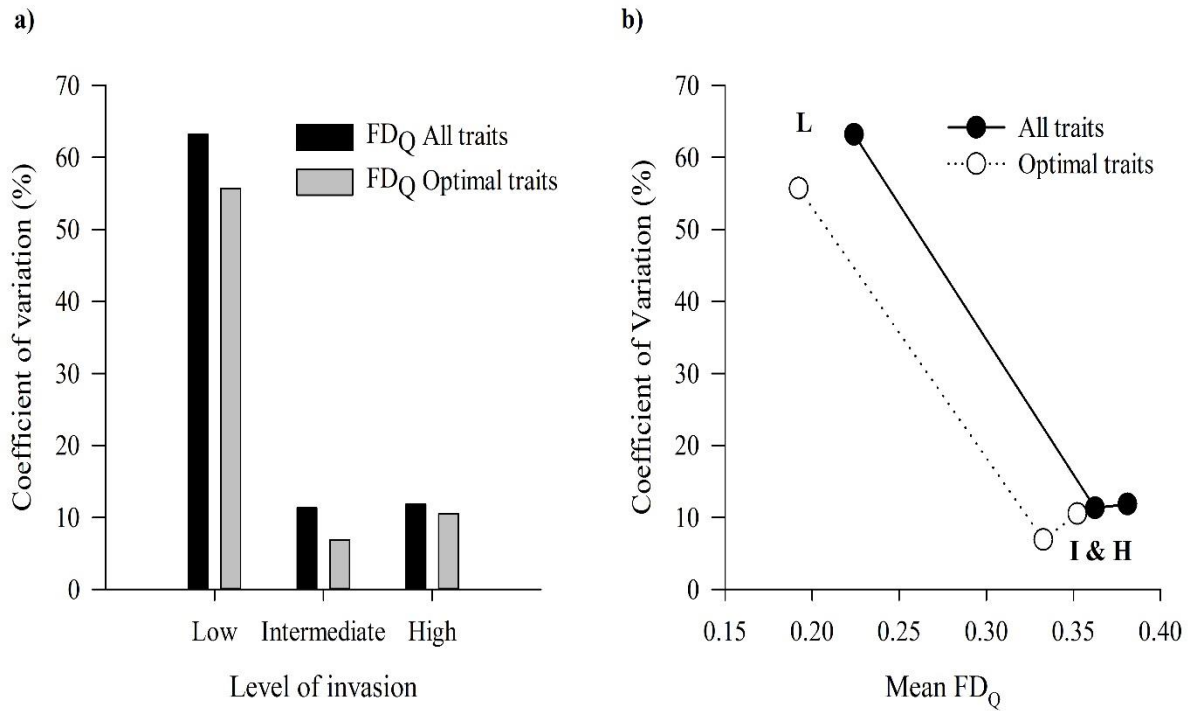**Figure 3.** Variation in functional diversity (FD$_Q$) across the invasion gradient. a) Coefficient of variation for FD$_Q$ across communities of low (n = 6; relative alien cover = < 20 %), intermediate (n = 6; relative alien cover = 20 – 50 %) and high (n = 3; relative alien cover = > 50 %) invasion; b) The relationship between mean FD$_Q$ and the coefficient of variation for. L FD$_Q$ = low invasion levels; I = intermediate invasion levels; H = high invasion levels

Appendix C

Table C1: Changes across the multispecies invasion gradient of annuals and flowering duration community-weighted means (CWMs), in functional diversity (FD_Q) for all traits and only those traits optimising divergence. Regression model results. Significant p values ($p = \leq$ 0.05 are in bold).

Response Variable	Estimate	Std. Error	df	t value	p value
CWM annuals	0.016	0.012	13	1.321	**< 0.001**
CWM flowering duration	-0.000	0.000	13	-0.437	0.669
FD_Q all traits	0.192	0.08	13	2.4	**0.031**
FD_Q optimal traits	0.148	0.05	13	2.967	**0.011**

Figure C1. Differences between alien and native species in community mean flowering duration. Communities are sorted from lowest relative alien cover to highest relative alien cover along the *x* axis. Error bars represent standard deviation.
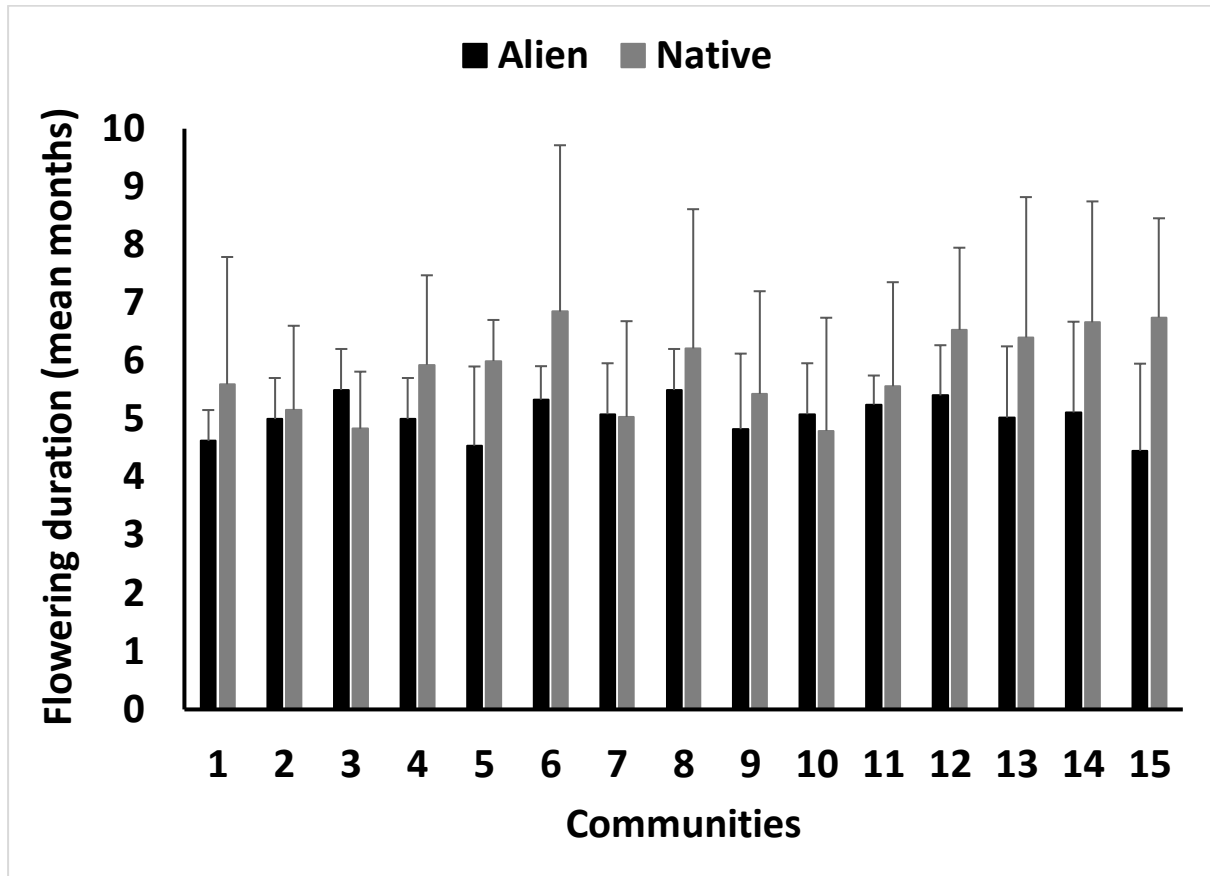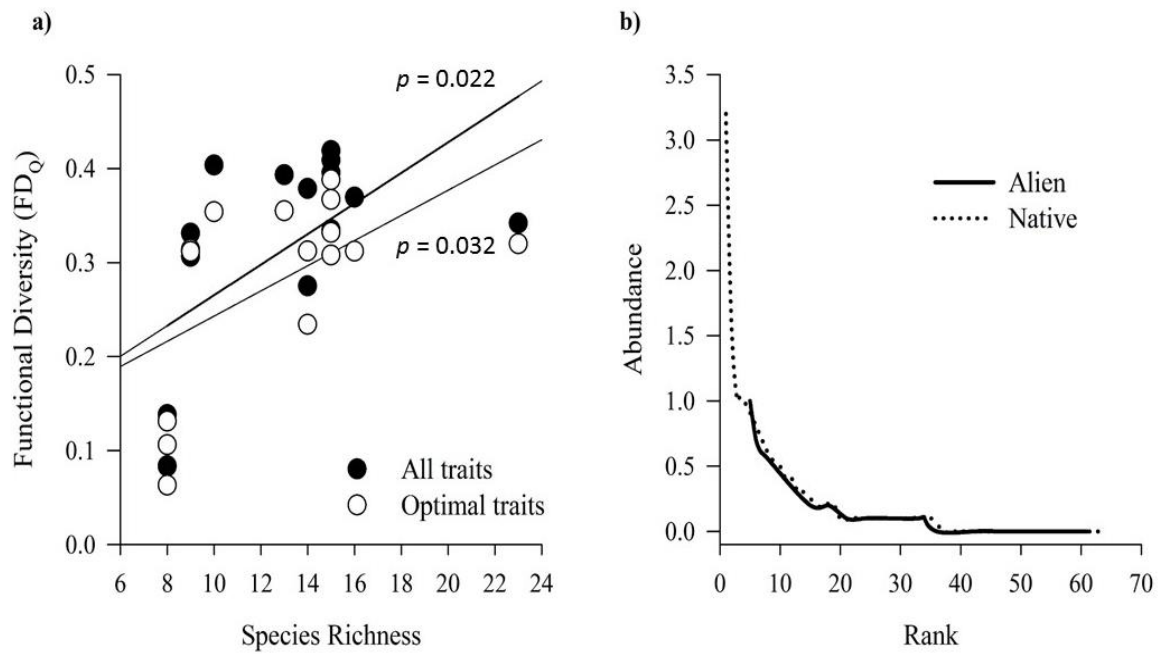
Figure C2: How species richness and abundance affects functional diversity (FD_Q) across the invasion gradient. a) The relationship between species richness and FD_Q; b) Rank abundance curves for alien and native species within the metacommunity.

Chapter 4

The impact of traits, environment and invasion on community productivity

Introduction

Ecosystem functions are influenced by multiple factors, including the physical environment, the functional structure of communities and changes to functional composition from invading alien species (Díaz & Cabido 2001; Chapin 2003; Díaz et al. 2007). In the past two decades, there has been a shift from using species richness *per se* to instead using plant traits to better understand relationships between species assemblages and ecosystem functioning (Lavorel & Garnier 2002). This approach has revealed, for example, that changes in the functional structure of plant species in a community – i.e. the value, range and relative abundance of traits - can contribute substantially to determining primary productivity and other ecosystem properties (Díaz et al. 2007; de Bello et al. 2010).

Two leading hypotheses explain the effects of plant traits on productivity. First, the biomass-ratio hypothesis (Grime 1998) proposes that productivity is strongly determined by the trait values of the dominant species (i.e. the functional identity of the dominant species) within the community, while being comparatively unresponsive to the traits of rarer species (Dias et al. 2013). The biomass-ratio hypothesis relies on the community-weighted mean (CWM) values of species traits for determining the effect of plant traits on productivity (Díaz et al. 2007; Dias et al. 2013). Second, the complementarity hypothesis (Tilman 1997) suggests that a greater range of trait values (i.e. functional diversity) in a community will positively affect productivity via complementary resource use of the species involved (Chanteloup & Bonis 2013). As trait diversity increases, niche partitioning will increase along specific axes of resource use, thereby increasing productivity through more complete resource use in space or time (Mokany et al. 2008; Fu et al. 2014). Several different indices of functional diversity have been used to predict trait impacts on productivity, including Rao's quadratic entropy (FD_Q; Botta-Dukát 2005).

The biomass-ratio and complementarity hypotheses are not mutually exclusive, meaning that both functional identity and functional diversity can be important determinants of productivity. However, functional identity and functional diversity are unlikely to drive variation in productivity to the same degree (Mouillot et al. 2011; Kröber et al. 2015). Most studies of trait impacts on productivity and other ecosystem properties have concluded that the functional identity of species contributes more to ecosystem function than functional diversity (Mokany et al. 2008; Roscher et al. 2012; Zhu et al. 2016). Furthermore, the level of influence that either mechanism has on productivity is dependent on the specific trait being considered. For example, Ali et al. (2017) found that increased aboveground biomass in subtropical forests in China was driven by the CWM of young leaf traits and the functional diversity of wood traits. Considering functional identity and functional diversity together is therefore important

to understand how both mechanisms influence the functional structure of communities, and in turn productivity.

Although species trait values are important, local environmental conditions also strongly mediate community productivity (Loreau et al. 2001; Díaz et al., 2007). Environmental factors such as soil chemistry and light availability often explain significant amounts of variation in aboveground net primary productivity (ANPP) and biomass (Schumacher & Roscher, 2009; Chanteloup & Bonis, 2013). Indeed, environmental factors often explain more variation in productivity than functional structure. For example, soil nitrogen (N) concentration was the single most important predictor of aboveground biomass in semi-natural grasslands in Germany, explaining 40 % of total variation (Schumacher & Roscher 2009). In contrast, elevation, slope, solar insolation and soil carbon (C) and N content explained only 4 % of the variation in crown growth in subtropical tree communities in China, while functional identity (42 %) and diversity (31 %) accounted for more variation (Kröber et al. 2015). No significant effect was found of soil water and mineral N content on biomass production in grasslands of the French Atlantic coast, which was instead driven by CWM traits (Chanteloup & Bonis 2013). Examining environmental factors in conjunction with functional indices is therefore important, and likely to provide a more thorough explanation of variation in community productivity than considering each in isolation. For example, functional diversity has been negatively related to biomass production when considered in isolation, but when combined with abiotic and CWM variables in the same model, the influence of functional diversity became positive (Schumacher & Roscher 2009).

Species richness is a well-known driver of trait diversity (Mayfield et al. 2010). Increases in species richness (e.g. due to invasion) may impact ecosystem function by increasing functional diversity, because an increase in richness is likely to result in a greater range of trait values (Petchey & Gaston 2002). Here, I focus on the influence of trait diversity on productivity, rather than the impact of species diversity *per se*. Most studies investigating trait-ecosystem relationships that have accounted for species richness have found only weak relationships between richness and ecosystem functioning, while trait indices such as CWM and FD_Q are better at predicting changes to function (Mokany et al. 2008; Chanteloup & Bonis 2013). Nevertheless, it is important to consider the effect of species richness on ecosystem functioning.

Ecosystem function may also be impacted by invading alien species (Lockwood et al. 2013). Aliens may differ in their traits to native species, and these differences can influence ecosystem functioning, such as productivity or nutrient cycling (Ehrenfeld 2003). Therefore, it is

important to test how the traits of aliens differ from natives, and how the alien component of communities affects ecosystem functioning through traits of interest. Invasion by alien species can cause changes to community composition, thereby affecting ecosystem functioning (Levine et al. 2003; Liao et al. 2008; Ehrenfeld 2010). Individual alien species often outcompete natives once established in a natural community, with the alien reaching high local abundance and dominance (Vilá & Weiner 2004). The dominance by one alien species alters the composition of native assemblages, and also has the potential to change community functional structure (Levine et al. 2003). If aliens are functionally similar to natives, then changes to ecosystem functioning may be minimal (Figure 1). In this case, alien species may maintain the existing community functional structure. However, high abundances of aliens that are functionally dissimilar to natives have the potential to alter ecosystem functioning because differences in traits lead to different effects on ecosystem properties (Hillebrand et al. 2008; Liao et al. 2008).

Under the assumption that aliens replace natives, communities invaded by multiple alien species of which one (or few) becomes dominant impact ecosystem functioning by causing a shift in community mean traits toward the values of the dominant alien(s) (Figure 1; Hillebrand et al. 2008). The influence of dominant aliens may increase the relative importance of functional identity in communities in which they dominate. This could impact productivity either negatively or positively, depending on the trait(s) of the dominant alien(s). If invading aliens establish and do not become dominant, the addition of multiple, functionally-distinct aliens may increase functional diversity because aliens are able to fill ecological niches unoccupied by natives (Figure 1; Hejda & de Bello 2013). Depending on the relative impact that functional diversity has on ecosystem functioning, increases in functional diversity from invasion could positively influence productivity through a more complete use of available resources (Mason et al. 2005). Alternatively, productivity may decline as a result of invasion if the native community is already characterised by trait values that are close to optimal for productivity under prevailing conditions. Increases in functional diversity from invasion in this case would increase the evenness of trait values in the community, thereby 'diluting' the effect of community trait values on productivity.

Studies involving alien species traits have focussed predominantly on the identification of traits that determine invasion success, rather than traits that may alter ecosystem functioning (Pyšek et al. 2012). Fewer than 200 alien plant species have been quantitatively assessed for ecological impacts and only nine species account for one third of ecological impact research (Vilà et al. 2009; Hulme et al. 2013). Of those publications, more than 80 % involve the

examination of a single alien species (Hulme et al. 2013). This focus on single-species invasions potentially limits our understanding of how alien assemblages of species, and their traits, affect ecosystem function (Hulme et al. 2013). This is particularly relevant because invasion of plant communities by multiple alien species is common, and becoming increasingly so (Perrings et al. 2010). An assemblage of alien plant species may have traits different to co-occurring natives, and the cumulative impact that these trait differences have on community productivity could be more severe than the impact of any one alien, depending on its dominance. Determining if aliens are collectively impacting productivity more strongly through the biomass-ratio hypothesis or the niche complementarity hypothesis will provide insight into the consequences of multispecies invasion for ecosystem function.

Here I examine the importance of traits and environment for productivity in a dry forest ecosystem, and investigate how multispecies invasion affects trait-productivity relationships. Specifically, I ask three questions: 1) What are the relative contributions of functional identity, functional diversity and environment to explaining productivity? 2) What traits contribute most to effects of functional identity and functional diversity? 3) How do alien species' traits impact productivity? I predict that functional identity will better explain productivity than functional diversity (i.e. more support for the biomass-ratio hypothesis than the niche complementarity hypothesis; Mokany et al. 2008; Finegan et al. 2015). Furthermore, functional diversity has been shown to increase in this system as the level of invasion increases (Chapter 3). As a result, I expect that aliens are more likely to affect productivity through increases in functional diversity.

Methods

Study location and multispecies invasion gradient

Chiltern-Mt. Pilot National Park was established in 1980 as a protected area of 21 560 ha in north-east Victoria, Australia. The park contains box-ironbark forest and granitic hills woodlands consisting of open canopies of a single native cypress pine (*Callitris*) and several eucalypts (*Eucalyptus*). Historical land use in and around Chiltern-Mt. Pilot include forestry, agriculture and gold mining, and these activities have resulted in more than 80 % loss of native ecosystems (Parks Victoria 2008). Ongoing disturbance in the region, including the impacts of invasive alien species, has also increased (Parks Victoria 2008). While few alien tree species exist within the park, the understorey community has been invaded by numerous,

predominantly herbaceous alien species. Despite this, Chiltern-Mt. Pilot protects several significant flora (Parks Victoria 2008).

Fifteen sites (communities) were chosen for sampling within the study system (Figure 1). Communities ranged in distances of 1 to 18 km apart. Each community is 500 m² and was further divided into 25, 20 m² subplots. Total species richness was recorded for each community. Within each subplot, two 1 m x 1 m quadrats were randomly placed to collect percent cover measurements for all individual understorey plant species present. Species with a known maximum height greater than 3 m (including trees and epiphytic species on trees) were not measured. A total of 50 quadrats per community were used. Percent cover in each quadrat was estimated for each species using the following categories: 0 %, 0.5 %, 1 %, 2 %, 5 % with subsequent intervals of 5 % from 10 to 100 (Daubenmire, 1959). Percent cover for each species and for all species combined was then obtained for each community.

Measurements of productivity

Aboveground, live photosynthetic biomass (referred to as simply 'biomass', g), and aboveground net primary productivity (ANPP, $g\,m^{-2}\,d^{-1}$) were chosen as metrics of community productivity (Garnier et al. 2004). These metrics are not fully independent (Figure D3), but they measure different aspects of productivity. Biomass represents the standing biomass at the peak of the growing season, while ANPP represents the rate of change in biomass between the onset of the growing season and the peak. Both have important influences on other ecosystem processes, such as water fluxes, nutrient cycles and soil chemical balances (Raich et al. 1991; Lienin & Kleyer 2012). Furthermore, although biomass and ANPP are correlated, we don't understand the relative contributions of aliens and natives to each of them, and how these contributions differ between them. Biomass was collected once in late July 2015 (beginning of growing season) and again in mid-late October 2015 (peak of growing season). Sampling within this period minimises the effect of water availability on productivity, by measuring biomass and productivity when water limitation is not an issue for plant growth and survival. Three 50 cm x 50 cm quadrats were sampled in each community for biomass: one quadrat randomly placed in each of the southeast corner, centre and northwest corner subplots. Biomass was collected by removing the vegetative matter and the top 3-4 cm of soil intact. The samples were then sorted to remove the live biomass. Biomass samples were oven-dried for 72 hours at a temperature of 70°C. Once dried, samples were weighed to obtain dry mass. Mean total dry

biomass (g) was calculated for each community. Only the October harvest measurements were used for analyses of biomass, as this period represents the peak in community biomass.

Aboveground net primary productivity was calculated from the harvested live biomass following Garnier et al. (2004). Aboveground net primary productivity expresses community productivity as per ground area per unit time (here: in days; Garnier et al. 2004; Vile et al. 2006). Aboveground net primary productivity is represented by:

$$\frac{(\text{live biomass in Oct}) - (\text{live biomass in Jul})}{t_{\text{Oct}} - t_{\text{Jul}}}$$

where t_{Oct} and t_{Jul} represent the harvest dates.

Collection of trait data

Six traits were chosen to test functional effects on productivity. Five traits were field-based: 1) maximum vegetative height (cm), 2) leaf thickness (mm), 3) leaf area (mm²), 4) leaf dry mass (mg) and 5) specific leaf area (SLA; mm² mg⁻¹). The sixth trait, clonality (clonal/non-clonal), was collected from literature-based sources. Traits were selected based on their demonstrated influences on productivity (Garnier & Navas 2012; Reichman & Sala 2014; Mason et al. 2016), and the feasibility of acquiring enough field sample replicates.

Trait data was collected for species cumulatively adding to 85-95 % of total cover in each community. A minimum of 80% cumulative relative abundance (cover is used as a proxy for abundance in this context) has been suggested for species selection for trait sampling, as this best captures any impacts of traits on ecosystem properties (Garnier et al. 2004; Pakeman & Quested 2007). The exclusion of rare species is unlikely to reduce the potential effect of functional diversity, as I use functional diversity metrics that are weighted by the relative abundance of species. A total of 59 plant species were sampled for trait data across all 15 communities.

Field trait data were collected in the Austral spring in both 2014 and 2015. Maximum vegetative height was measured *in-situ* from the tallest individual of each species in each community. Forty leaf samples (ten individuals; four leaves per individual) were collected for each species in each community (Pérez-Harguindeguy et al. 2013). These samples were used for measurements of leaf thickness, leaf area, leaf dry mass and SLA. Leaf thickness was measured from 20 samples of each species in each community using digital callipers. All leaf samples were scanned using a Canon LiDE210 flatbed scanner. ImageJ software was then used

to calculate the one-sided area of each leaf (Schneider et al. 2012). To calculate leaf dry mass, samples were oven-dried for 72 hours at 70°C. Once dry, leaf samples were weighed and leaf dry mass was recorded. Specific leaf area was calculated by dividing the leaf area of each sample by its leaf dry mass. Clonality information was collected from several literature-based sources.

Environmental measurements

Eight environmental variables were sampled from each community. These included 1) slope (degrees), 2) altitude (m a.s.l.), 3) total soil nitrogen (%), 4) soil C:N ratio, 5) canopy openness (mean %), 6) live basal area (m² ha), 7) soil pH and 8) soil phosphorous (P) content (mg/kg). Five soil samples (0-5 cm of upper mineral horizon) were collected from each community from the four corner subplots and the centre subplot, and pooled into one mixed, composite sample. Chemical analyses were conducted on 40 °C oven-dried samples. Total soil C and N were measured using catalytic combustion and thermal conductivity with a LECO IR Analyser (Rayment & Lyons 2011). Soil C:N ratio was calculated using the resulting measurements. Soil pH was determined using a conductivity meter in a 1:5 soil-water suspension. Soil P concentrations were measured using the Bray 1 method (Rayment & Lyons 2010). To determine canopy openness, three hemispherical photographs were taken at dawn or dusk in the south-west, centre and north-east subplots of each community. These photos were analysed using Winscanopy Pro 2014a software to produce a measure of canopy openness from each photograph. Mean canopy openness was then calculated for each community. Live basal area was determined from circumference measurements of all live tree stems with a diameter breast height > 10 cm.

Statistical analyses

To test for spatial autocorrelation in biomass and ANPP, Moran's I was used (Moran 1950). No significant autocorrelation was found for either variable ($p = > 0.05$); i.e. data points can be regarded as spatially independent for variables of community productivity. To represent functional identity and functional diversity, CWM values and Rao's quadratic entropy (FD_Q) were calculated for each trait using the 'FD' package in R (Laliberté et al. 2014). CWM and FD_Q were weighted by the percentage cover of species in each community. All traits were standardised prior to analysis. For clonality (a nominal trait), CWM scores were calculated for each individual class (i.e. clonal and non-clonal). I used only the CWMs of the non-clonal class

in analyses, as the two classes are represented by CWM scores that are the inverse of each other.

To determine the relative contribution of functional identity, functional diversity and environment to productivity, I conducted variation partitioning analysis (Oksanen et al. 2013; Kröber et al. 2015). I first determined what traits (using CWM and FD_Q metrics) and environmental factors were important for predicting productivity, following the methods of Díaz et al. (2007). I tested trait- and environment-productivity relationships using both single predictor models and multipredictor models. Single predictor models may indicate significant influences on productivity from single variables, but multipredictor models may further reduce uncertainty in predicting productivity, by identifying the combination of traits that explain most variation in productivity (Díaz et al. 2007). Linear regression was used to identify significant relationships between each predictor variable and both variables of productivity. Several environmental (N, C:N ratio, slope) and FD_Q (leaf area, leaf dry mass and SLA) variables were square root-transformed prior to analysis. The effect of species richness on productivity was tested, as increases in richness may lead to increases in productivity (Flombaum & Sala 2008).

I then combined all CWM variables and performed multiple regression for all possible combinations of predictors, to find the most parsimonious functional identity model, based on Akaike's information criterion, corrected for small sample sizes (cAIC). This was performed twice: once for biomass and once for ANPP. The process was repeated for functional diversity (FD_Q) variables and environmental variables. During regression analyses I tested for multicollinearity between variables using the variance inflation factor. An inflation factor > 10 may decrease statistical power by creating inaccurate model parameters (Graham 2003). Variance inflation factor values were < 10, indicating that collinearity among predictors had little impact on the results. Finally, I used the most parsimonious models of the three predictor groups in variation partitioning analysis to determine the relative contribution of CWMs, FD_Q and environment to both biomass and ANPP.

Principal components analysis (PCA) was used to identify which traits contributed most to variation in trait space. I used the traits retained in the most parsimonious multipredictor models to identify principal axes of trait variation (five traits for biomass, four traits for ANPP). Principal components analysis was performed on all species, and for alien and native species separately. For each group of species (all species, alien, native) generalized linear models (GLM; Gaussian error distribution with identity link function) were used to test relationships between productivity and the PCA scores of the primary and secondary axes (PCA 1 and PCA 2). Differences between alien and native traits were examined using ANOVA analysis. The

traits with the highest loadings from PCA 1 of ordinations were included in the ANOVA analysis. These same traits were then used to identify relationships between traits and productivity, for all species, aliens and natives, using linear regression. All analyses were performed in R Studio 3.3.1 (R Core Team, 2016).

Results

There was a twelve-fold difference in standing mean biomass across the 15 communities, and the range of ANPP values was even greater with a 120-fold difference across communities (Table 1). Communities, on average, contained more non-clonal than clonal species, and there was high variation in species leaf dry mass (Table 1). Height was the most variable trait for the FD_Q metric, while FD_Q leaf thickness and FD_Q clonality had the lowest variation across communities (Table 1). The mean soil C:N ratio across communities was 21.75, indicating that these communities, on average, tend to have slow decomposition rates of organic matter (Table 1). Live basal area (m^2 ha) showed little variation across communities (Table 1).

Contributions of functional identity, functional diversity and environment to productivity

Together, functional identity, functional diversity and environment explained 78 % of the variation in biomass (Table 2). Functional identity explained the most variation, both in terms of total and independent variation explained (Figure 2a). Environment also explained a high amount of variation in biomass, but very little of this variation was independently explained by environment (Figure 2a). Functional diversity independently explained variation intermediate to that of functional identity and environment, and explained the lowest amount of total variation (Figure 2a). Most variation in biomass was explained exclusively by functional identity (25 %), followed by an interaction of functional identity and environment (19 %). No variation in biomass was explained by an interaction between all three predictor groups (functional identity, functional diversity and environment; Figure 2a).

A total of 65 % of variation in ANPP was explained by the three predictor groups (Table 2). Environment explained the most variation, followed by functional identity and functional diversity (15 %). Functional identity exclusively explained no variation (Figure 2b). Functional diversity and environment independently explained variation in ANPP similar to the variation each explained in biomass. Variation in ANPP was best explained by an interaction between functional identity and environment (43 %; Figure 2b). Interactions between functional identity and environment, as well as all three predictor groups, explained no variation in ANPP.

Trait contributions to effects of functional identity and functional diversity

Community-weighted mean of leaf thickness was the only individual trait predictor significantly related to biomass. This relationship was negative, with biomass decreasing as leaf thickness increased (Figure 3a). The individual functional diversity (FD_Q) models for leaf thickness and clonality were only significant at the 90 % confidence level (Table D1). For environment models, both soil C:N ratio and altitude were significantly related to biomass (Table D1). Both of these relationships were negative (Figure 3b,c).

The best-fit model predicting biomass using combinations of CWM traits retained both leaf thickness and plant height, although height was only significant at the 90 % confidence level (Table 2). This indicates that mean biomass was higher in communities with thinner leaves and taller species. Although no individual FD_Q variables were significant, the best significant multipredictor model retained leaf thickness, SLA and clonality. Both FD_Q leaf thickness and FD_Q clonality were negatively related to total biomass, suggesting that higher biomass is a result of higher diversity in SLA, but lower diversity of leaf thickness and clonality. Only soil C:N ratio was retained in the most parsimonious environment model, suggesting higher biomass in communities with less soil C per unit of soil N (Table 2).

Aboveground net primary productivity was significantly and negatively related to both CWM and FD_Q leaf thickness in single regression models (Table D1). Soil C:N ratio was the only significant individual environmental predictor of ANPP (Figure 3). Multipredictor models revealed CWM leaf thickness as the only trait retained in the best-fit model for functional identity (Table 2). For functional diversity, the FD_Q traits (leaf thickness, SLA and clonality) that were retained in the best-fit model for biomass were also retained in the best-fit model for ANPP, and they were similarly related (negative or positive; Table 2). FD_Q SLA was only significant at the 90 % confidence level (Table 2). Soil C:N ratio and total soil N were retained in the most parsimonious environment model, though Soil N was significant at the 90 % confidence level only (Table 2). The relationships between species richness and both biomass and ANPP were non-significant (Table D1).

Due to the strong collinearity between CWM and FD_Q leaf thickness (r = 0.634), FD_Q leaf thickness was removed from the variation partitioning analysis. This is justified on the basis that the relationship between FD_Q leaf thickness and productivity was negative. In principle, this negative relationship can be viewed as amplifying the significant signal of CWM leaf

thickness (Mokany et al. 2008), and as a result should be removed from the variation partitioning analysis. FD_Q leaf thickness was included in the principal components analysis, because a main function of PCAs is to reduce the number of highly-correlated variables (Jackson 1991).

Impact of alien traits on productivity

For biomass, CWM traits accounted for 40-45 % of variation in ordinated traits and were associated with PCA 1 for all three groups considered (all species, aliens and natives; Table D2). PCA 2 for all three groups was predominantly associated with FD_Q traits and explained 25-30 % variation (Table D2). For traits related to ANPP, variation in trait space for all species and natives was primarily associated with low leaf thickness (CWM and FD_Q leaf thickness; PCA 1 = 44 % and 49 % variation; Table D2; Figure D1d,f). For aliens, PCA 1 showed CWM leaf thickness increased as FD_Q SLA declined (38 %; Table D2; Figure D1e). FD_Q SLA and FD_Q clonality varied together along PCA 2 for all species and natives (Table D2). For aliens, decreasing FD_Q clonality was associated with PCA 2 (Table D2).

Aliens and natives differed significantly in CWM height (Table 3; Figure 4b). Native species, on average, tended to be taller than aliens (Figure 4b). No significant differences were found between aliens and natives for the other three traits analysed (Table 3; Figure 4). When examining trait-biomass relationships of all species, aliens and natives, a significant negative relationship was found for CWM leaf thickness for all three groups (Table 4; Figure 5a). Relationships between biomass and FD_Q leaf thickness for all species, and CWM height for aliens, were only significant at the 90 % confidence level (Table 4). Similar to biomass, CWM leaf thickness-ANPP relationships were significant and negative across groups (Table 4; Figure 5d). The FD_Q leaf thickness of all species and natives were also significantly-negatively related to ANPP (Table 4; Figure 5f). Aliens had positive trait-productivity relationships opposite to all species and natives for CWM height, FD_Q leaf thickness and FD_Q SLA, but these relationships were non-significant (Figure 5b-c, e-f).

Significant negative relationships between biomass and PCA 1 revealed that lower biomass was associated with higher leaf thickness for natives, and also thicker leaves and shorter species for aliens (Table 5; Figure D2b-c). For all species, both CWM and FD_Q leaf thickness and CWM height declined with an increase in biomass, but this relationship was only significant at the 90 % confidence level (Table 5; Figure D2a). There were significant relationships between ANPP and PCA 1 of each group (Table 5; Figure D2d-f). For all species and natives, ANPP

increased significantly with a decrease in leaf thickness. For aliens, ANPP was higher in communities with thinner leaves and greater range of SLA values (Figure D2e). Overall therefore, productivity was largely related to variation in leaf thickness.

Discussion

Both local abiotic conditions and community functional structure drive ecosystem functioning, but their contributions are likely to be context dependent, and spatially and temporally variable (Díaz et al. 2007; Kröber et al. 2015). Here I showed that in this dry forest ecosystem, functional identity, functional diversity and environmental factors associated with understorey communities jointly contributed to explaining productivity, but differed in their importance. Functional identity explained more variation in biomass and ANPP than functional diversity, supporting the biomass-ratio hypothesis. However, interactions between functional identity and the environment were also important for explaining variation in productivity. Low leaf thickness is a key trait for predicting productivity in this system, and aliens are mirroring the existing CWM leaf-thickness-productivity relationship. Although aliens differed in their functional diversity-productivity relationships to natives, these relationships were not significant. Therefore, the traits of alien species do not alter the contributions of functional identity or functional diversity to community productivity, but instead reinforce the importance of functional identity for trait-productivity relationships.

The relative importance of functional identity, diversity and environment to productivity

The finding that functional identity is more important to productivity than functional diversity supports previous research. Community-weighted means of traits, particularly leaf traits, are known to explain more variation in aboveground biomass and primary productivity than functional diversity in several different habitats, including Australian grasslands, subtropical forests in China and alpine grasslands of Northern Tibet (Mokany et al. 2008; Kröber et al. 2015; Zhu et al. 2016). Like many studies, I found both CWM and FD_Q traits influence productivity, adding to the consensus that functional identity and functional diversity are not mutually exclusive in contributing to productivity (Mokany et al. 2008; Chiang et al. 2016). Functional identity is often considered as the main contributor to predicting productivity and other ecosystem functions, while functional diversity is viewed as a secondary or indirect driver of productivity (Thomspon et al. 2005; Roscher et al. 2012; Chiang et al. 2016).

Soil C:N ratio was the only environmental factor that significantly explained both biomass and ANPP. In both cases, the relationship was negative. Given that biomass and ANPP are significantly and positively related in this system (Figure D3), it is perhaps unsurprising that both are affected by soil C:N ratio. Biomass represents the major source of standing carbon stock in ecosystems, while ANPP measures the rate at which carbon is sequestered in biomass (Field et al. 1998; Li et al. 2015). Higher soil C:N ratios mean that decomposition of organic material is comparatively slow, limiting the release of nitrogen into the soil (Yamakura & Sahunalu 1990). A reduction in soil N availability can lead to a reduction in ANPP (LeBauer & Treseder 2008). Negative relationships between soil C:N ratio and biomass production have been found in grassland experiments in Germany, while ANPP in French subalpine grasslands were significantly related to an index of soil nitrogen nutrition (Díaz et al. 2007; Hejcman et al. 2010). Communities in this system have slow decomposition rates of organic matter and predominantly low soil N (Hazelton & Murphy 2007). Their negative relationships with ANPP shows how high soil C:N ratios and low soil N can constrain productivity in this system.

The combined effect of leaf thickness and soil C:N ratio on ANPP emphasizes the need to examine traits and environment together when investigating impacts to ecosystem functioning. Environmental factors explained a large proportion of the variation in productivity, especially ANPP, for which it explained more variation than both functional identity and functional diversity (Figure 2). However, most of the variation explained by the environment was explained together with CWM leaf thickness ($R^2 = 0.43$). Interactions between environmental factors and traits are often difficult to interpret because it is not known if trait values present in communities are a response to local environmental conditions, or vice versa (Grime & Pierce 2012; Kardol et al. 2013). In these dry forest communities, increased decomposition and soil N mineralization due to low soil C:N ratios may allow species with low leaf thickness to grow faster than other species in the community, and this would be evident in the accumulation rate of biomass (i.e. ANPP; Yamakura & Sahunalu 1990; Wright et al. 2004).

Trait contributions to functional identity and functional diversity

Almost all significant trait-productivity relationships were negative. For CWM traits, negative relationships demonstrate a correlation between high productivity and the low trait values of dominant species (Mokany et al. 2008). For FD_Q traits, negative relationships indicate that a broader range of trait values reduces productivity, and such a relationship can be viewed as reinforcing the CWM signal of the same trait (Chanteloup & Bonis 2013; Kröber et al. 2015).

In the context of this system, increasing diversity of leaf thickness and clonality (i.e. an even abundance of clonal and non-clonal species) reduces productivity. This suggests that less functionally-diverse communities, containing species with low leaf thickness and higher abundances of non-clonal species, increases biomass and ANPP. For leaf thickness, this is corroborated by the significant negative relationship between CWMs and both metrics of productivity. The positive relationship between both productivity metrics and the proportion of non-clonal species (i.e. CWM clonality) was significant only at the 90 % confidence level (Table D2), but indicates that non-clonal species are dominant in communities with higher productivity.

Leaf thickness was the only CWM trait that significantly contributed to the relationship between functional identity and productivity. The relationship was negative, with productivity (both biomass and ANPP) decreasing as leaf thickness increased. This is in line with the leaf economics spectrum, of which leaf thickness is a key component (Wright et al. 2004; Vile et al. 2005; Sakschewski et al. 2014). Resource acquisition and high photosynthetic rates are increased by a combination of traits, including low leaf thickness, high SLA and high leaf area (Garnier et al. 1997; Wright et al. 2004). Although CWM SLA and CWM leaf area were non-significant, the negative relationship between CWM leaf thickness and productivity provides some evidence that productivity within these communities is coupled to the leaf economics spectrum.

Specific leaf area was the only FD_Q trait that was positively related to productivity. The association between high biomass and high diversity of SLA values may be due to invasion by alien species. Aliens have significantly higher mean SLA than natives across communities (Figure D4). Increases in SLA, and functional diversity, significantly increase with invasion in this system (Chapter 3). Aliens with high SLA, such as *Briza minor* and *lysimachia arvensis*, which co-occur with natives with low SLA (e.g. *Lomandra filiformis* and *Rytidosperma pallidum*) could increase the functional diversity of SLA across these communities, and impact on standing biomass.

All other FD_Q-trait productivity relationships were negative. In fertile habitats, these relationships have been described as dependent on two conditions: i) productive species dominating less-diverse assemblages and ii) an increase in the range of life strategies as functional diversity increases (Chanteloup & Bonis 2013). If these two conditions are met, then productive, competitive species will dominate in less-diverse communities (Grime 2006; Chanteloup & Bonis 2013). Functional diversity will increase when stress (e.g. reduction in soil nutrients or water availability) or disturbance (e.g. fire or grazing) occurs, creating

opportunities for stress-tolerant and ruderal species to become more abundant. These species are typically less-productive than dominant, competitive species in depauperate communities (Grime 2006). Under these circumstances, increased functional diversity may cause a "dilution" effect, by reducing the optimal capacity for growth, resulting in a negative FD-productivity relationship (Chanteloup & Bonis 2013). Species in this dry forest understorey use a variety of life strategies (i.e. Grime's competitor-stress tolerator-ruderal strategies; Grime 1979). Although most are situated on low- to moderately-fertile soils (Hazelton & Murphy 2007), communities in this system with higher productivity contained dominant species, (e.g. *Microlaena stipoides*, *Hydrocotyle laxiflora* and *Rytidosperma pallidum*) that have life strategies that incorporate competitiveness (e.g. competitor-ruderal or stress tolerator-competitor strategies). Productivity may decrease when these species become less abundant, as this allows species using different, less-productive strategies to increase in abundance. This dilution effect has been described for fertile habitats, but I found support for it here in communities situated in low to moderately fertile habitats.

It has been suggested that FD_Q-productivity relationships may be bell-shaped, with positive relationships (i.e. support for the niche complementarity hypothesis) occurring below a FD_Q threshold of 0.4, and the dilution effect occurring when this threshold is exceeded (Chanteloup & Bonis 2013). Interestingly, my results support this argument. FD_Q SLA ranged from > 0 to 0.4 (with the exception of one community) and was the only significant positive predictor of productivity. The FD_Q values of both leaf thickness and clonality were predominantly above 0.4 and were negatively correlated to productivity. Trait values corroborating this bell-shaped relationship have been found in wet grasslands of the French Atlantic coast (Chanteloup & Bonis 2013). Positive relationships have been found between soil nitrification and traits with FD_Q values ranging from 0 and 0.4 in a ponderosa pine forest understorey (Laughlin 2011). I show that the bell-shaped relationship between functional diversity and productivity applies to the dry forest understory and that the dilution effect of functional diversity decreases productivity within this ecosystem.

Impact of alien traits on productivity

The traits of alien species were not found to significantly alter aboveground productivity of the understorey. Aliens were not significantly different to natives in any of the traits associated with productivity, with the exception of CWM height (Figure 4). However, given that the CWM height-biomass relationship was only marginally significant (and non-significant for

ANPP; Table 2), height differences of dominant species, regardless of whether they were alien or native, had little impact on productivity. For the remaining traits, aliens seemed to be adding similar trait values to the community, resulting in little change to functional structure (Finerty et al. 2016). This, in turn, resulted in no detectable relationship with productivity. Regardless of whether aliens become dominant or maintain low abundances, the similarity of alien and native traits in the community ensures that multispecies invasion is unlikely to successfully change the existing state of community productivity in this system (Peltzer et al. 2009; Finerty et al. 2016).

Relationships between alien traits and productivity in these dry forest communities result in two alternative outcomes, and depend on the trait and metric in question. First, rather than changing productivity, aliens maintain existing productivity rates by having similar CWM leaf thickness values to natives – the most important trait influencing both biomass and ANPP. In this respect, aliens are also reinforcing the importance of functional identity in these communities. Many common alien species (e.g. *Aira elegantissima*, *Trifolium spp.*) had low leaf thickness values, little different to common native species, such as *Microlaena stipoides* and *Rytidosperma spp*. Aliens, natives and all species together had similar CWM leaf thickness-productivity relationships (both biomass and ANPP; Table 4; Figure 5a,d). This provides evidence that the alien species in this understorey maintain the existing leaf thickness-productivity relationships, and in doing so emphasize the importance of functional identity for productivity.

Second, for all other traits, alien trait-productivity relationships were positive, while for natives these relationships were negative. Despite these differences, the positive FD_Q-productivity relationships across the alien species were not strong enough to change community productivity (Figure 5c,e,f). Functional diversity has been found to increase across these understorey communities as the level of invasion increases (Chapter 3). However, the results here suggest changes in trait functional diversity associated with invasion do not lead to changes in productivity. In addition, while functional diversity increases as relative alien cover increases (Chapter 3), biomass and ANPP do not (Figure 6). For these traits at least, this reaffirms the negligible effect that multispecies invasion has on productivity across these communities.

Although aliens do not seem to significantly alter productivity in this system, the indirect consequences of alien trait-productivity relationships for other ecosystem properties are unknown. This includes impacts of invasion to fuel loads, fire regimes and soil nutrient cycles, through changes to biomass and litter decomposition (Brooks et al. 2004; Liao et al. 2008;

Ehrenfeld 2010). Aliens also have traits not measured here, e.g. leaf N and P concentrations, resprouting capacity, that may be better predictors of alien impacts on productivity (van Kleunen et al. 2010; Clarke et al. 2013). The ratio of aboveground biomass to belowground biomass, measured as the root:shoot ratio, can also influence productivity and may differ between aliens and natives (Wilsey & Polley 2006; Kang et al. 2013). In addition, high phylogenetic diversity in plant communities has been found to increase productivity (Cadotte et al. 2013). Phylogenetic diversity may be a complementary predictor of ecosystem function, as it provides a measurement of species differentiation irrespective of traits (Cadotte et al. 2013). Selecting traits for analysis is often dependent on factors such as sampling and time constraints, meaning some traits important for productivity are overlooked (Lavorel et al. 2008). The use of phylogenetic metrics may capture additional information not provided by un-sampled traits. Alien and native species in these communities are distantly-related (Chapter 1), and these phylogenetic differences may provide further insight into how multispecies invasion impacts ecosystem functioning. For example, phylogenetically-diverse communities have been shown to provide greater stability in productivity (Cadotte et al. 2012). This relationship could potentially exist within the dry forest system, in communities where distantly-related aliens and natives co-occur.

Conclusions

By examining different components of functional structure, I have shown that functional identity contributes more to variation in productivity than functional diversity in this system. However, the environment explained more variation in ANPP than either functional identity or functional diversity, and interactions between environment and functional identity were also important. This emphasizes the importance of considering functional structure and the environment together when testing for effects on ecosystem functions (Díaz et al. 2007; Schumacher & Roscher 2012). Aliens that have integrated into these dry forest communities do not significantly differ from natives in traits affecting productivity. This has resulted in aliens maintaining existing and important trait-productivity relationships, through CWM leaf thickness, which has reinforced the importance of functional identity for community productivity. When aliens do exhibit trait-productivity relationships that differ to natives, they are too weak to change the existing community trait-productivity relationships. Investigating other traits relevant to productivity, such as leaf nutrient contents or root traits, or examining traits in combination with other diversity metrics, such as those based on phylogenetic

information, may provide further insight into the impacts of multispecies invasion for community productivity.

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Tables

Table 1: Summary statistics for aboveground biomass, aboveground net primary productivity (ANPP), functional identity (CWM) traits, functional diversity (FD_Q) traits and environmental predictors ($n = 15$ for all variables).

Variable	Unit	Min.	Max.	Mean	Range	std. error	% CV
Productivity							
Biomass	mean g	4.01	48.45	25.86	44.44	14.15	14.11
ANPP	$g\ m^{-2}\ d^{-1}$	0	0.12	0.06	0.12	0.04	16.67
Functional Identity							
CWM height	mm	223.1	700.1	404.59	476.9	42.36	40.55
CWM leaf thickness	mm	0.07	0.25	0.16	0.17	0.01	31.25
CWM leaf area	mm^2	9.89	69.03	36.96	59.14	3.77	39.48
CWM leaf dry mass	mg	4.99	59.47	23.94	54.48	3.76	60.78
CWM specific leaf area	$mm^2\ mg^{-1}$	0.9	3.77	2.37	2.87	0.2	32.49
CWM non-clonal	Prop. spp.	0.53	1	0.82	0.47	0.04	17.07
Functional Diversity							
FD_Q height	FD_Q	0.02	2.68	0.63	2.666	0.2	125.4
FD_Q leaf thickness	FD_Q	0.07	1.36	0.6	1.292	0.09	60
FD_Q leaf area	FD_Q	0.03	1.03	0.39	1.005	0.08	79.49
FD_Q leaf dry mass	FD_Q	0.01	1.27	0.27	1.267	0.08	118.52
FD_Q specific leaf area	FD_Q	0.01	1.02	0.24	1.013	0.06	100
FD_Q clonality	FD_Q	0	1.59	0.83	1.589	0.13	62.65
Environment							
Live basal area	$m^2\ ha$	0.01	0.02	0.14	0.01	0	0.71
Total soil nitrogen	%	0.07	0.28	0.14	0.21	0.01	35.71
Soil C:N ratio	.	14.67	30.3	21.75	15.63	1.39	24.78
Altitude	m a.s.l.	213	572	387.87	359	32.46	32.41
Slope	degrees	0	10	3.13	10	0.67	82.75
Canopy openness	%	23.58	41.15	32.85	17.56	1.3	15.31
Soil pH	.	4.52	6.87	5.65	2.35	0.18	12.57
Soil phosphorous	mg/kg	1.4	5	2.69	3.6	0.24	40.15

Table 2: Coefficients for most parsimonious functional identity (CWM), functional diversity (FD_Q) and environment multi-predictor models. Significant p values ($p = \leq 0.05$) are in bold.

Biomass

Models	R^2	Predictors	Estimate	Std. Error	df	t	p
CWM	0.47	Leaf thickness	-255.385	74.714	12	-3.418	**0.005**
		Height	0.441	0.226	12	1.956	0.074
FD_Q	0.29	SLA	38.212	12.674	11	3.015	**0.012**
		Clonality	-19.092	4.765	11	-4.007	**0.002**
Environment	0.38	Soil C:N ratio	-27.47	10.125	13	-2.713	**0.018**
Combined	0.78						

ANPP

Models	R^2	Predictors	Estimate	Std. Error	df	t	p
CWM	0.44	Leaf thickness	-0.539	0.177	13	-3.052	**0.009**
FD_Q	0.15	SLA	0.082	0.041	11	2.025	0.068
		Clonality	-0.048	0.015	11	-3.14	**0.009**
Environment	0.50	Soil C:N ratio	-0.077	0.027	12	-2.845	**0.015**
		Soil N content	0.084	0.039	12	2.173	0.051
Combined	0.65						

Table 3. Differences between community-level traits of alien and native species. Results from ANOVA models. Significant p values ($p \leq 0.05$) are in bold.

Trait	df	Sum Sq	F	P
CWM leaf thickness	28	0.002	0.71	0.407
CWM height	28	3465	12.75	**0.001**
FD_Q leaf thickness	28	0.001	0.013	0.911
FD_Q SLA	28	0.12	2.238	0.146

Table 4. Relationships between traits and productivity for all species, aliens and natives. The traits presented are those that had moderate-high loadings (≥ 0.5) on the first principal component axes for either all species, aliens or natives (i.e. not all traits presented here had moderate-high loadings across all three groups). Results from linear regression models. Significant p values ($p \leq 0.05$) are in bold.

Biomass	Estimate	Std. Error	df	t	p
All Species					
CWM leaf thickness	-164.74	64.661	13	-2.548	**0.024**
CWM height	-0.037	0.239	13	-0.155	0.879
FD_Q leaf thickness	-19.16	9.606	13	-1.995	0.068
Aliens					
CWM leaf thickness	-229.305	79.374	13	-2.889	**0.013**
CWM height	0.627	0.312	13	2.009	0.066
FD_Q leaf thickness	9.095	11.382	13	0.799	0.439
Natives					
CWM leaf thickness	-127.171	55.412	13	-2.295	**0.039**
CWM height	-0.099	0.189	13	-0.527	0.607
FD_Q leaf thickness	-18.124	10.336	13	-1.754	0.103

ANPP	Estimate	Std. Error	df	t	p
All Species					
CWM leaf thickness	-0.539	0.177	13	-3.052	**0.009**
FD_Q SLA	-0.002	0.056	13	-0.052	0.959
FD_Q leaf thickness	-0.066	0.026	13	-2.523	**0.025**
Aliens					
CWM leaf thickness	-0.573	0.251	13	-2.282	**0.04**
FD_Q SLA	0.066	0.046	13	1.438	0.174
FD_Q leaf thickness	0.033	0.033	13	0.998	0.337
Natives					
CWM leaf thickness	-0.435	0.149	13	-2.911	**0.012**
FD_Q SLA	-0.074	0.046	13	-1.626	0.128
FD_Q leaf thickness	-0.062	0.029	13	-2.169	**0.049**

Table 5. Relationships between trait ordination axes and productivity for all species, aliens and natives. Results from generalised linear models (Gaussian family with identity function). PCA = scores from first (PCA 1) and second (PCA 2) principal components identified in principal component analysis. Significant *p* values are in bold.

| Biomass	χ	Estimate	Std. Error	df	t	p
All						
Species	PCA 1	4.561	2.33	12	1.957	0.074
	PCA 2	3.059	2.689	12	1.137	0.278
Aliens	PCA 1	-5.496	2.026	12	-2.712	**0.019**
	PCA 2	-2.259	2.742	12	-0.824	0.426
Natives	PCA 1	-5.285	2.084	12	-2.536	**0.026**
	PCA 2	3.328	2.717	12	1.225	0.244
ANPP						
All						
Species	PCA 1	0.02	0.006	12	3.24	**0.007**
	PCA 2	-0.001	0.007	12	-0.639	0.535
Aliens	PCA 1	-0.019	0.007	12	-2.517	**0.027**
	PCA 2	-0.009	0.009	12	-1.005	0.335
Natives	PCA 1	0.02	0.006	12	3.494	**0.004**
	PCA 2	-0.001	0.008	12	-0.175	0.864
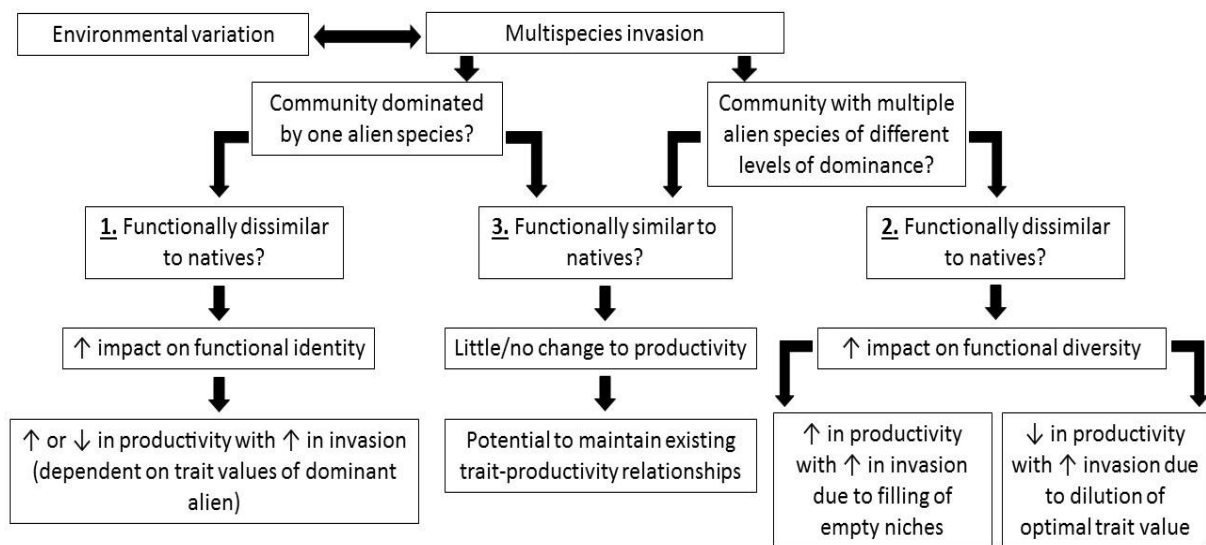
Figure 1. The impact of multispecies invasion on community productivity. 1. Invasion by multiple alien species where one alien that is functionally-dissimilar to natives becomes dominant could increase the importance of functional identity in the community. This in turn will either increase or decrease productivity, depending on the trait values of the dominant alien. 2. Invasion by multiple alien species with different abundances that are functionally-dissimilar to natives may increase the importance of functional diversity in the community. This could increase productivity due to aliens filling empty niches. Alternatively, a decrease in productivity may occur when natives have optimal trait values for productivity and these are 'diluted' by aliens, increasing the evenness of trait values within the community. 3. Alien species that are functionally similar to natives are hypothesised to cause little change to productivity, regardless of the abundance or dominance of aliens, and may instead reinforce existing trait-productivity relationships.
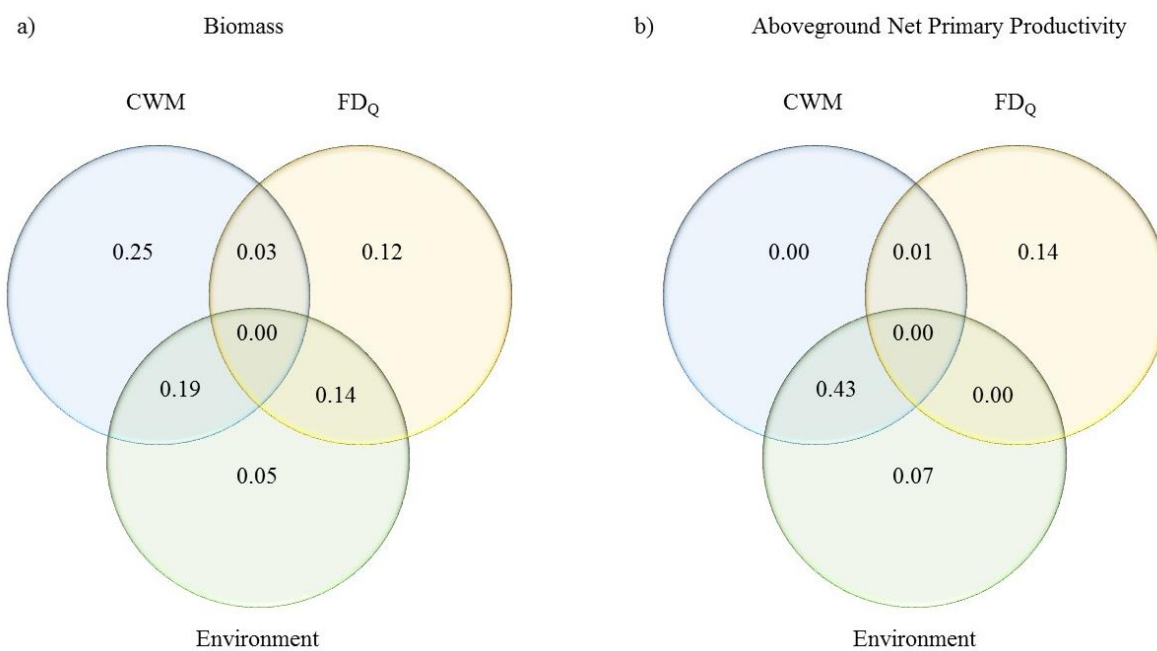
Figure 2: The relative contribution of functional identity (CWM), functional diversity (FD_Q) and environment to a) total standing biomass and b) aboveground net primary productivity; R^2 values from variation partitioning analysis.
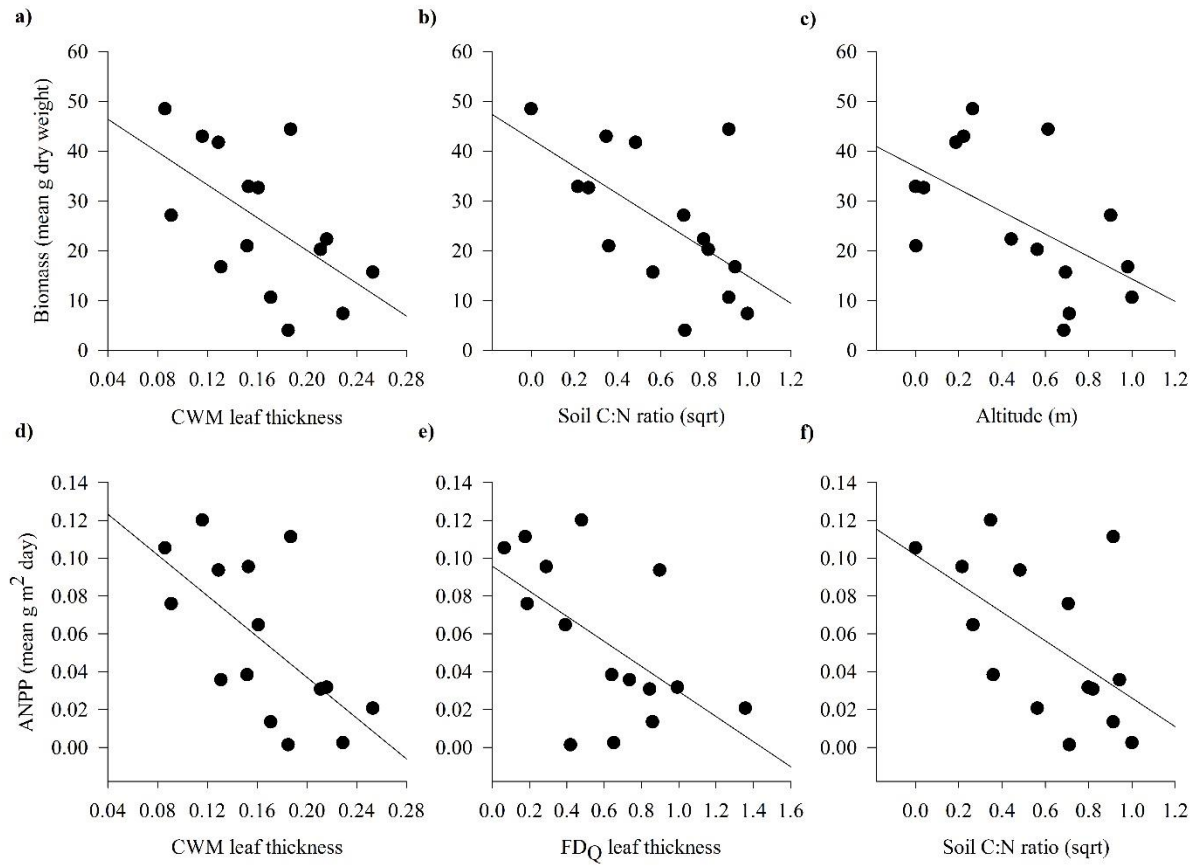
Figure 3: Significant relationships between individual community traits and environment predictors and a-c) biomass and d-f) aboveground net primary productivity (ANPP). Linear regression models. Statistical details are found in Table 1.
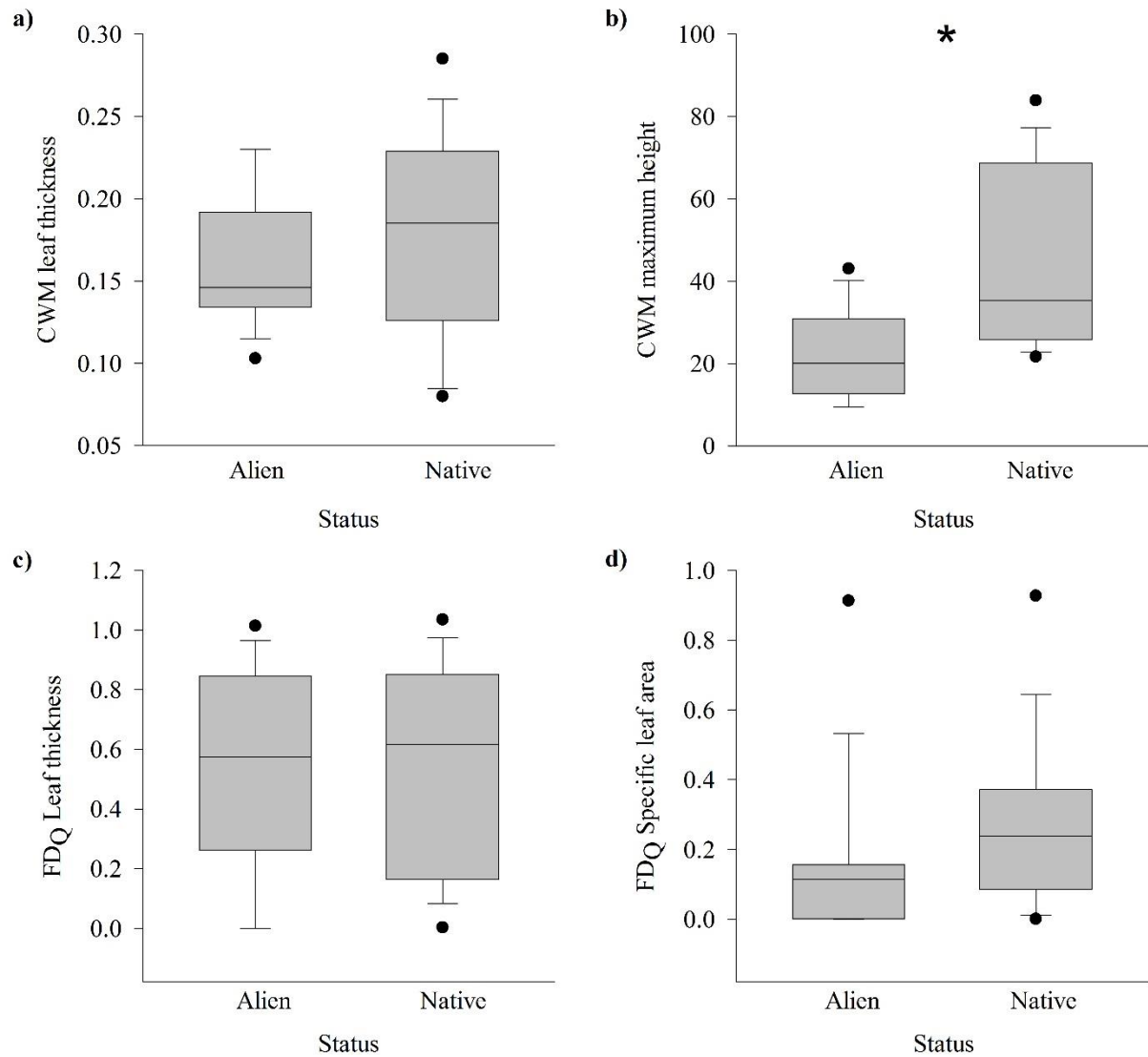
Figure 4. Differences between community-level traits of alien and native species. a) Functional identity (community-weighted means (CWM)) leaf thickness, b) CWM height, c) Functional diversity (FD_Q) leaf thickness, d) FD_Q specific leaf area. Significant differences ($p = \leq 0.05$) are indicated by *.
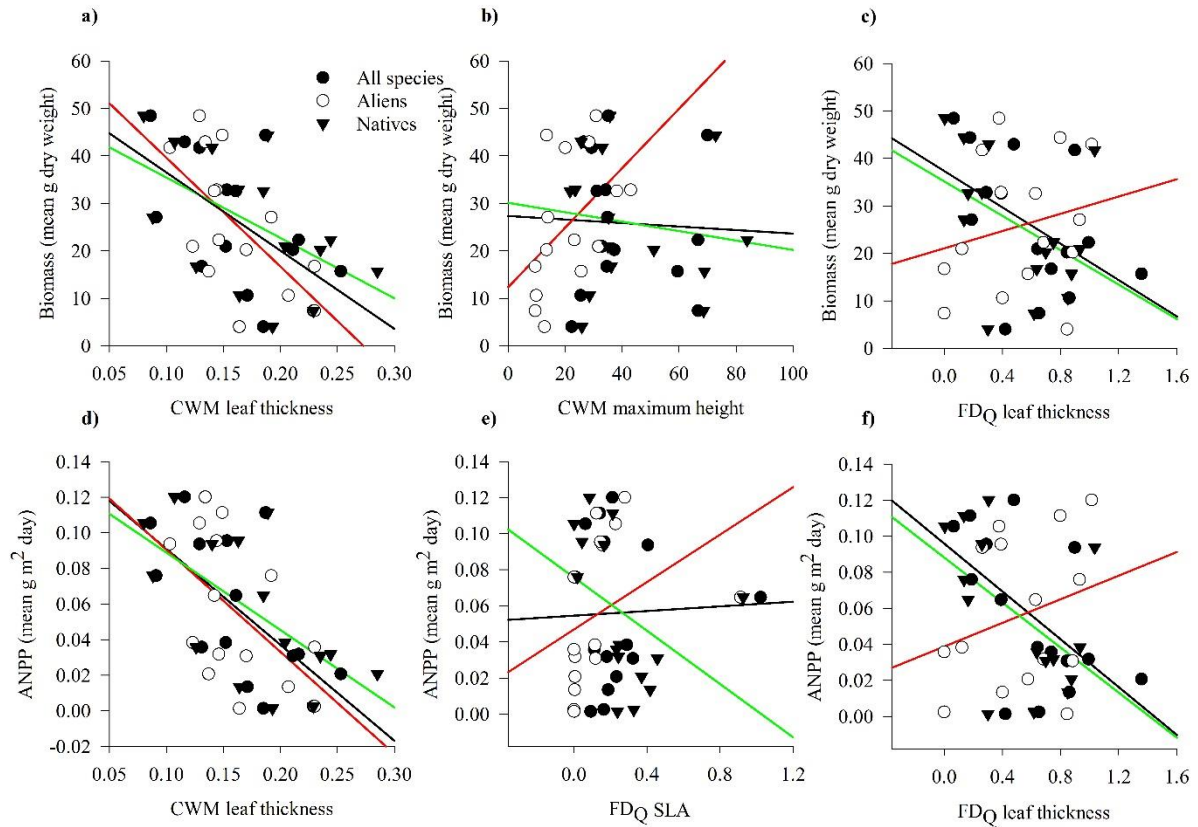
Figure 5. Relationships between traits and productivity for all species, aliens and natives. Productivity is shown as biomass (a-c) and aboveground net primary productivity (d-f). The traits presented are those that had moderate-high loadings (≥ 0.5) on the first principal component axes for either all species, aliens or natives (i.e. not all traits presented here had moderate-high loadings across all three groups). Regression slopes are as follows: black = all species; red = aliens; green = natives. Statistical analysis is presented in Table 5.
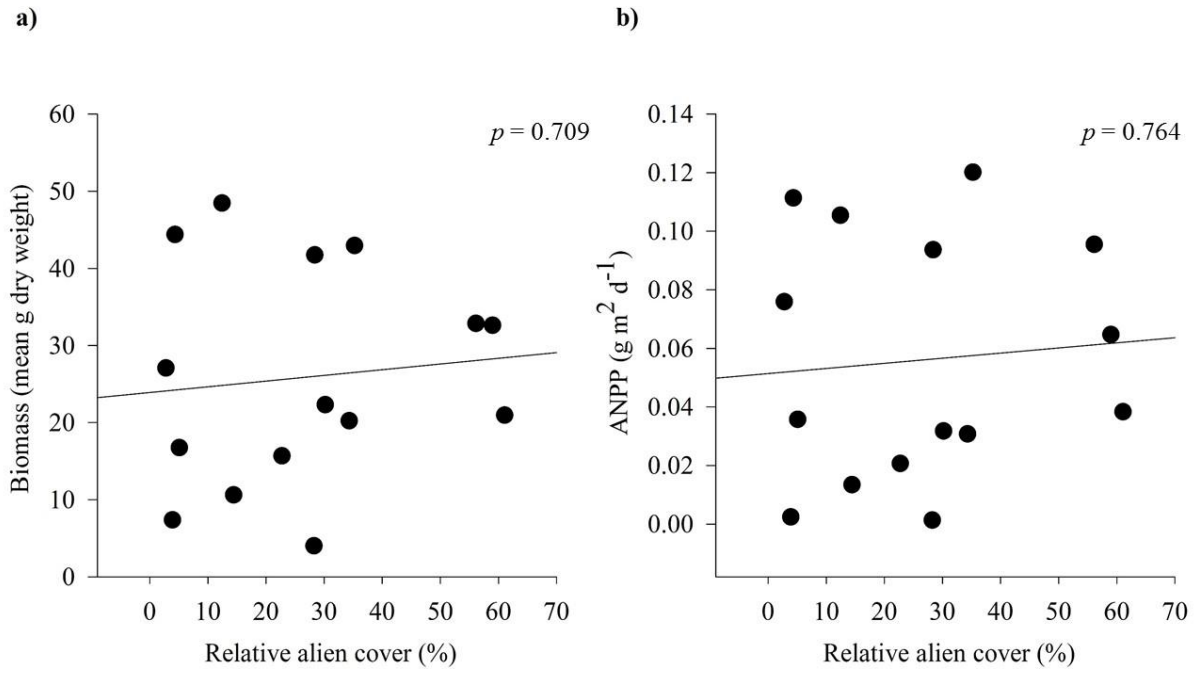
Figure 6. The relationship between the multispecies invasion gradient and community productivity for a) biomass and b) aboveground net primary productivity (ANPP). The *p* values have been taken from linear regression models.

Appendix D:

Literature sources used to compile information on clonality for species included in the current study.

Benson, D. & McDougall, L. 1993. Ecology of Sydney plant species: part 1. *Cunninghamia* 3: 257-422

Benson, D. & McDougall, L. 1994. Ecology of Sydney plant species: part 2 Dicotyledon families Asteraceae to Buddlejaceae. *Cunninghamia* 3: 789-1004.

Benson, D. & McDougall, L. 1995. Ecology of Sydney plant species: part 3 Dicotyledon families Cabomaceae to Eupomatiaceae. *Cunninghamia* 4: 217-431.

Benson, D. & McDougall, L. 1997. Ecology of Sydney plant species: part 5 Dicotyledon families Flacourtiaceae to Myrsinaceae. *Cunninghamia* 5: 331-544.

Benson, D. & McDougall, L. 2000. Ecology of Sydney plant species: part 7b Dicotyledon families Proteaceae to Rubiaceae. *Cunninghamia* 6: 1017-1202.

Benson, D. & McDougall, L. 2005. Ecology of Sydney plant species: part 10 Monocotyledon families Lemnaceae to Zosteraceae. *Cunninghamia* 9: 17-212.

Catford, J.A., Downes, B.J., Gippel, C.J. & Vesk, P.A. 2011. Flow regulation reduces native plant cover and facilitates exotic invasion in riparian wetlands. *Journal of Applied Ecology* 48: 432-442.

Lunt, I.D. & Morgan, J.W. 1999. Vegetation change after 10 years of grazing exclusion and intermittent burning in a *Themeda triandra* (Poaceae) grassland reserve in South-eastern Australia. *Australian Journal of Botany* 47: 537-552.

McIntyre, S., Lavorel, S. & Tremont, R.M. 1995. Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. *Journal of Ecology* 83: 31-44.

Meers, T.L., Kasel, S., Bell, T.L. & Enright, N.J. 2010. Conversion of native forest to exotic Pinus radiata plantation: Response of understorey plant composition using a plant functional trait approach. *Forest Ecology and Management* 259: 399-409.

Stelling, F. (ed.). 1998. *South West Slopes revegetation guide (South of the Murrumbidgee River)*. Murray Catchment Management Committee & Department of Land & Water Conservation, Albury, NSW, AU.

Table D1: Individual trait- and environment-productivity relationships. Linear regression models. Significant p values ($p = \leq 0.05$) are in bold.

Biomass ~	Estimate	Std. Error	df	t	*p*
Species richness	-0.278	0.406	13	-0.684	0.506
CWM height	-0.037	0.239	13	-0.155	0.879
CWM leaf thickness	-164.74	64.66	13	-2.548	**0.024**
CWM leaf area	-0.057	0.269	13	-0.212	0.836
CWM leaf dry mass	-0.001	0.27	13	-0.004	0.999
CWM SLA	2.294	5.035	13	0.456	0.656
CWM clonality	52.56	24.61	13	2.136	0.052
FD_Q height	-6.07	4.689	13	-1.295	0.218
FD_Q leaf thickness	-19.16	9.606	13	-1.995	0.068
FD_Q leaf area	-3.474	15.637	13	-0.222	0.828
FD_Q leaf dry mass	-6.961	15.006	13	-0.464	0.65
FD_Q SLA	7.451	19.156	13	0.389	0.704
FD_Q clonality	-13.336	6.581	13	-2.026	0.064
Live basal area	-21.86	11.078	13	-1.973	0.07
Total soil nitrogen	22.43	17.13	13	1.309	0.213
Soil C:N ratio	-27.49	10.124	13	-2.715	**0.018**
Altitude	-22.541	9.298	13	-2.424	**0.031**
Slope	-11.325	14.309	13	-0.791	0.443
Canopy openness	13.505	13.189	13	1.024	0.325
Soil pH	16.196	12.259	13	1.321	0.209
Soil phosphorous content	2.903	3.535	13	0.821	0.426
Aboveground net primary productivity ~	**Estimate**	**Std. Error**	**df**	**t**	***p***
Species richness	-0.001	0.001	13	-0.259	0.800
CWM height	-0.001	0.001	13	-0.431	0.673
CWM leaf thickness	-0.539	0.177	13	-3.052	**0.009**
CWM leaf area	0.001	0.001	13	0.037	0.971
CWM leaf dry mass	0.001	0.001	13	0.164	0.873
CWM SLA	0.007	0.015	13	0.442	0.666
CWM clonality	0.139	0.074	13	1.875	0.084
FD_Q height	-0.023	0.013	13	-1.733	0.107
FD_Q leaf thickness	-0.066	0.026	13	-2.523	**0.025**
FD_Q leaf area	0.005	0.046	13	0.114	0.911
FD_Q leaf dry mass	-0.006	0.044	13	-0.14	0.891
FD_Q SLA	-0.002	0.056	13	-0.052	0.959
FD_Q clonality	-0.035	0.02	13	-1.787	0.097
Live basal area	-0.054	0.034	13	-1.069	0.132
Soil nitrogen content	0.082	0.048	13	1.71	0.111
Soil C:N ratio	-0.076	0.031	13	-2.479	**0.028**
Altitude	-0.059	0.028	13	-2.082	0.058
Slope	-0.049	0.041	13	-1.202	0.251
Canopy openness	0.031	0.039	13	0.784	0.447
Soil pH	0.046	0.036	13	1.27	0.226
Soil phosphorous content	0.007	0.01	13	0.624	0.544

Table D2. Loadings from ordinations involving the traits that influence productivity for all species, aliens and natives. Only the first three principal components are shown.

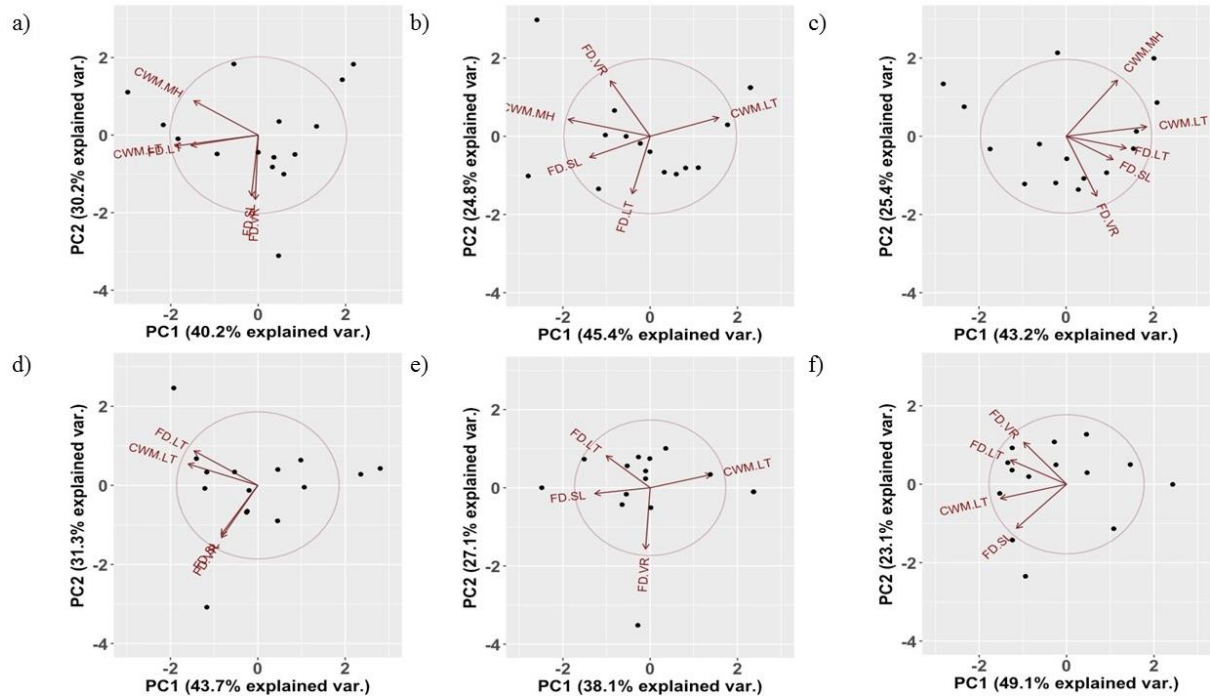| Biomass			
All Species	**PCA 1**	**PCA 2**	**PCA 3**
CWM leaf thickness	-0.665	-0.114	-0.193
FD_Q leaf thickness	-0.538	-0.108	0.639
CWM height	-0.514	0.358	-0.423
FD_Q specific leaf area		-0.632	0.269
FD_Q clonality		-0.669	-0.55
Proportion variation	0.402	0.302	0.143
Aliens	**PCA 1**	**PCA 2**	**PCA 3**
CWM leaf thickness	0.526	0.216	
FD_Q leaf thickness	-0.138	-0.666	0.652
CWM height	-0.629	0.195	
FD_Q specific leaf area	-0.464	-0.244	-0.555
FD_Q clonality	-0.305	0.642	0.508
Proportion variation	0.454	0.248	0.163
Natives	**PCA 1**	**PCA 2**	**PCA 3**
CWM leaf thickness	0.64	0.109	
FD_Q leaf thickness	0.477	-0.138	0.473
CWM height	0.407	0.647	0.134
FD_Q specific leaf area	0.373	-0.269	-0.801
FD_Q clonality	0.242	-0.691	0.328
Proportion variation	0.432	0.254	0.18
ANPP			
All Species	**PCA 1**	**PCA 2**	**PCA 3**
CWM leaf thickness	-0.647	0.26	0.237
FD_Q leaf thickness	-0.593	0.419	-0.655
FD_Q Specific leaf area	-0.34	-0.597	0.153
FD_Q Clonality	-0.338	-0.633	-0.3
Proportion variation	0.437	0.313	0.17
Aliens	**PCA 1**	**PCA 2**	**PCA 3**
CWM leaf thickness	0.653	0.186	
FD_Q leaf thickness	-0.47	0.454	0.682
FD_Q Specific leaf area	-0.592		-0.606
FD_Q Clonality		-0.868	0.408
Proportion variation	0.381	0.271	0.203
Natives	**PCA 1**	**PCA 2**	**PCA 3**
CWM leaf thickness	-0.607	-0.212	-0.208
FD_Q leaf thickness	-0.515	0.361	-0.603
FD_Q Specific leaf area	-0.46	-0.658	0.375
FD_Q Clonality	-0.393	0.625	0.672
Proportion variation	0.491	0.231	0.185

Figure D1. Ordination of traits associated with a-c) biomass and d-f) aboveground primary productivity. Ordinations are for a, d) all species, b, e) aliens and c, f) natives. CWM_MH = CWM maximum height; CWM_LT = CWM leaf thickness; FD_LT = FD_Q Leaf thickness; FD_SL = FD_Q Specific leaf area; FD_VR = FD_Q Clonality.
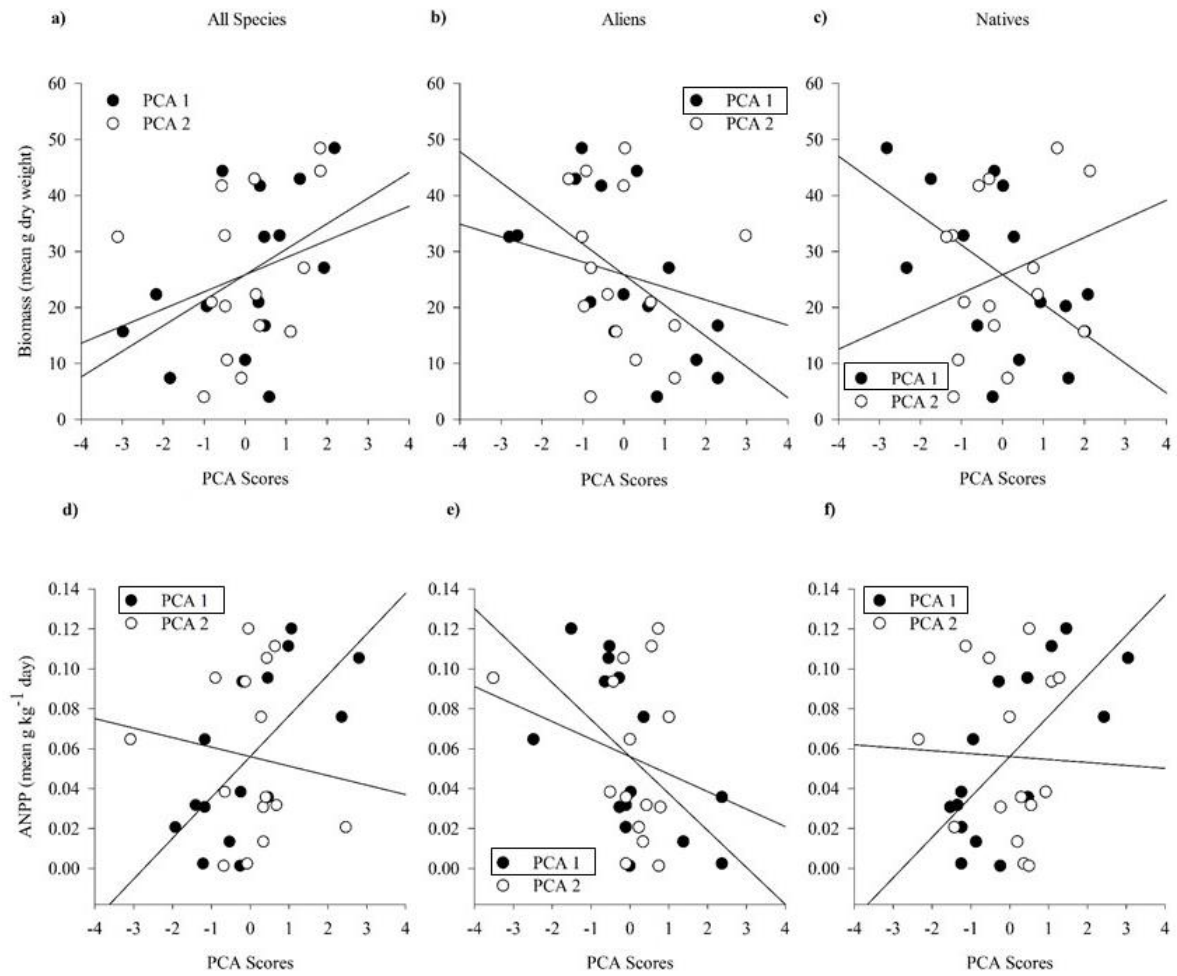
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Figure D2. Relationship between biomass (a-c) and aboveground net primary productivity (d-f) and principal component scores from trait ordinations for a,d) all species, b,e) aliens and c,f) natives. Significant relationships ($p = \leq 0.05$) are represented by boxes in each plot legend
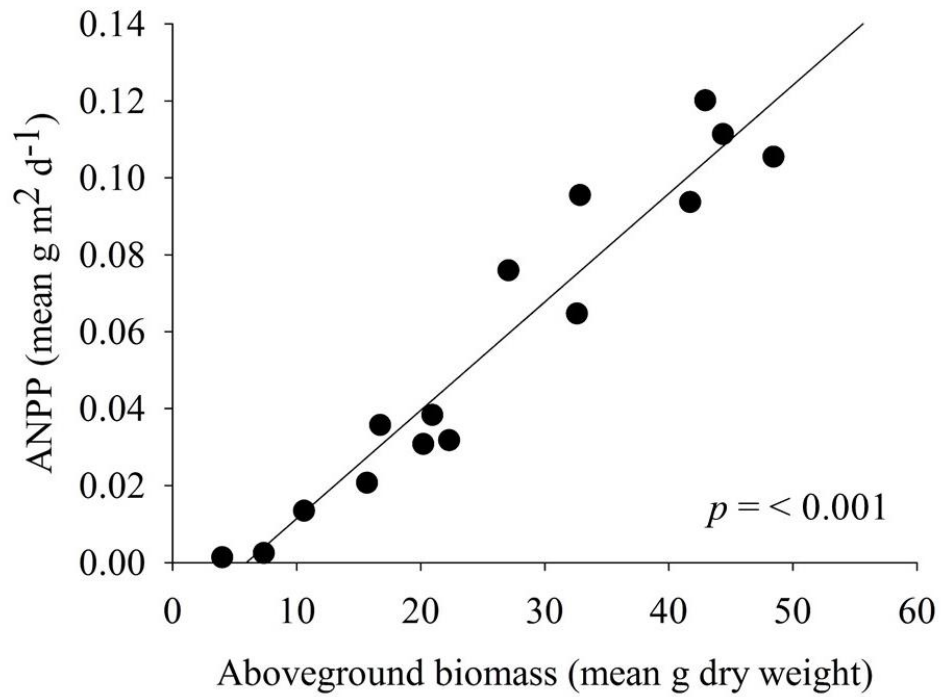
Figure D3. The relationship between aboveground biomass and aboveground net primary productivity (ANPP). The *p* value shown has been taken from linear regression analysis.
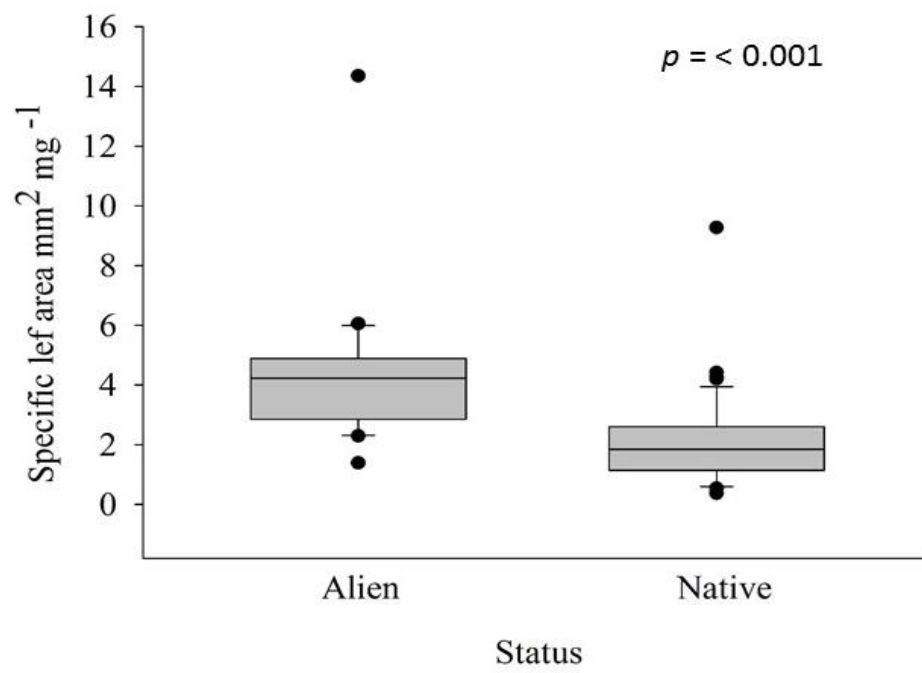
Figure D4. Difference in specific leaf area between alien and native species. The *p* value has been taken from an ANOVA analysis.

Concluding Discussion

In this thesis, I show how multispecies invasion impacts the functional structure of dry forest communities, but leaves community phylogenetic structure and productivity largely unchanged. This was done using well-understood trait and phylogenetic metrics, and a novel methodological approach, to test established hypotheses in functional and community ecology. Below, I discuss how my findings contribute to a broader understanding of the impacts of multispecies invasion for native communities and ecosystem functioning, and the implications of these findings in the context of Chiltern-Mt. Pilot National Park.

Incorporating multispecies invasion into impact studies

The ecological impacts of multispecies invasion is a focal challenge in invasion ecology but is dealt with in few studies (Pyšek et al. 2012). Invasion by multiple alien plant species is commonplace in natural systems (Hellman et al. 2008), and the continued rise in alien introductions stresses the need for a multispecies approach. Of particular importance is the quantification of multispecies invasion from field-based, observational studies, which provide insight into invasion impacts from real systems. In this thesis, investigating the collective impact of alien species using a field-based approach has provided both support for existing evidence on invasion success, and novel insights into how multispecies invasion changes community functional structure.

Investigating invasion impacts by using a gradient of community invasion yielded observed changes in the functional structure of the understorey. Significant, positive relationships between the proportion of annual species, SLA and the invasion gradient supports previous findings that these traits are characteristic of invasion success (Pyšek & Richardson 2007; van Kleunen et al. 2010). Previously, these relationships had largely been identified from comparing single or few species to congeneric natives, or through comparisons that treated communities only as invaded or uninvaded. As shown here (Chapter 3), taking into consideration communities of different invasion levels can reveal which findings supported from previous invasion research are applicable or supported in the context of invasion continuums. While some trait-invasion relationships were supported, others were not. These results may be habitat-specific, but it highlights the caution needed when drawing conclusions about multispecies invasion across communities of different invasion levels from single-invader studies. Future investigations into invasion impacts should, therefore, incorporate how

traits and mechanisms promoting invasion success change across invasion continuums or gradients.

Identifying an appropriate standard metric for quantifying multispecies invasion is essential for examining invasion impacts (Coulatti & Richardson 2009). Relative alien abundance is recommended, as it expresses the contribution that aliens make to a community, it is independent of scale and is comparable across ecosystems and regions (Campos et al. 2013). Relative alien cover is considered a reliable and easy-to-measure proxy of relative alien abundance (Catford et al. 2012). Thus, it may capture information on the extent of invasion, and any incurred impacts, more accurately than relative alien occupancy or richness (Catford et al. 2012; Cross et al. 2017). The use of relative alien cover to quantify the multispecies invasion gradient helped to identify patterns of trait diversity, that are not detected when using occupancy or richness data instead (Figure 1). These findings support the use of relative alien cover as a standard metric for quantifying community invasion level.

It could be argued that using all recorded alien species to quantify impacts, as done in this thesis, as opposed to only those that are deemed invasive (i.e. that are amongst the most dominant species in the community), may reduce the ability to identify significant impacts to communities and ecosystems (Valéry et al. 2008). However, invasion is temporally dynamic, with alien species invading the same system at multiple points in time (Richardson et al. 2000). Alien species are likely to experience lag phases that delay the onset of impacts, and focussing only on currently-invasive species will fail to capture interactions between the characteristics of the invaded system and species in lag phases (Simberloff et al. 2011; Catford et al. 2012). The exclusion of non-invasive aliens may also prevent the ability to detect trends that act as early warning signals of severe and detrimental impacts. Furthermore, invasive species often occur in systems with high proportions or richness of alien species (Rejmánek & Randall 2004; Catford et al. 2012; Chytrý et al. 2012). Encompassing the full suite of aliens will therefore likely capture the trends revealed from examinations exclusively based on invasive alien species, as well as the collective effect of all aliens.

The consequences of multispecies invasion for Chiltern-Mt. Pilot National Park

Chiltern-Mt. Pilot's status as a protected area is relatively recent. Some sections have been awarded protection since 1980 and the current extent of the park has been protected since 2002. There has been a long history of disturbance within and around Chiltern-Mt. Pilot, with historical activities such as gold mining and forestry dating back to the 1850s (Parks Victoria

2008). Disturbance from agriculture in bordering private lands and human recreational activities has been ongoing. These disturbances have resulted in a region-wide problem of alien species invasion, with many aliens having successfully established in the park prior to protection being applied (Parks Victoria 2008). Chiltern-Mt. Pilot has been invaded by multiple alien species principally introduced by humans for agricultural purposes (Randall 2002). These species are closely related, and are phylogenetically distinct from natives (Chapter 1). This is not surprising, as 37 % of plant species introduced into Australia are from families with no representative species in the native flora (Gallagher & Leishman 2014). Despite the phylogenetic differences between aliens and natives, and that aliens represent 25 % of the species pool, the understorey currently maintains its' phylogenetic integrity. Assuming that aliens have not replaced native species, the phylogenetic structure of the understorey has likely remained unchanged to the point of its' current phylogenetic state. Future invasions, however, could sufficiently increase the proportion of aliens in the species pool, leading to a detectable impact of the alien sub-community on the understorey phylogenetic structure. Incorporating species abundance data into phylogenetic approaches may reveal whether or not communities are dominated by certain phylogenetic lineages, and how this might change with increasing invasion (Cadotte et al. 2010).

Competitive natives may provide biotic resistance to competitive aliens that they are closely-related to (biotic resistance hypothesis; Levine et al. 2004). This would result in distantly-related alien species that are adapted to disturbance or stress assimilating into the understorey. These communities have natives with significantly higher use of competitive life strategies, and a clear absence of strictly-competitive aliens (Chapter 2). Despite the absence of strict competitors, aliens have integrated into this system using a range of life strategies, similar to native species. However, unlike natives, alien C-S-R composition does not appear to be affected by soil characteristics, such as acidity. Other environmental characteristics that influence resource availability and stress, such as water availability, may influence alien C-S-R composition (Cartorci et al. 2011). Furthermore, I did not test the potential effects of disturbance, such as fire, grazing or human activity, on relative C-S-R composition in the native and alien sub-communities. Fire in particular is an important and recurring disturbance in Chiltern-Mt. Pilot, and has been recognised as a potential agent for the further spread of alien species in the park (Parks Victoria 2008). Severe fire events are known to facilitate increases in vegetation in the understorey post-fire (Parks Victoria 2008). Examining C-S-R composition along disturbance gradients may help to understand which factors influence the life strategies of aliens in this system.

Aliens represent a subset of native life strategies, but they still have specific traits that are significantly different to natives. These traits – proportion of species with annual life history and high specific leaf area – are associated with rapid life cycle completion, and have been linked to invasion success (Westoby et al. 2002; Pyšek et al. 2009). Similarities to native life strategies allow aliens to persist under prevailing conditions, but their short lifespans and higher SLA values give them an advantage when conditions become favourable for growth and expansion. Being annuals, this may be restricted to the growing season, but would allow these aliens to increase their cover at local scales, while supressing or excluding native species cover. Higher proportions of annuals and SLA values at higher relative alien cover supports this idea (Chapter 3). Annuals with high SLA relative to natives are characteristic of Mediterranean-type climates, where they can complete their life cycles before the onset of summer drought (Holmes & Rice 1996; Garnier et al. 1997). Invasions by annual alien grasses with higher SLA have been particularly detrimental to many Californian grasslands, where these species have replaced native perennials (Sandel & Dangremond 2012).

Annual life history and high SLA are traits associated with disturbance adaptation (Lake & Leishman 2004; Spasojevic et al. 2010). Thus, it could be expected that aliens in this system would be predominantly ruderal strategists. Counterintuitively, most aliens were stress-tolerators. This may be due to overall low species SLA, when compared to the range of SLA values known to occur in plants. The known range of SLA values is <1 to 300 mm^2 mg^{-1} (Pérez-Harguindeguy et al. 2013). Specific leaf area values at the lower end of the leaf economics spectrum are typical of species found in Australian sclerophyll forests, where soil fertility is often low (Wright et al. 2004). Furthermore, high leaf mass per area (considered the inverse of SLA) has been associated with open woodland habitats, similar to this dry forest habitat, where drought and nutrient limitation can restrict growth (Poorter et al. 2009). Mean SLA for natives in this system ranged from 0.37 to 4.41 mm^2 mg^{-1} and for aliens this was 1.39 to 14.35 mm^2 mg^{-1} which, in both cases, is low relative to the known range of SLA. Aliens have significantly higher SLA than natives and this difference is particularly apparent along the multispecies invasion gradient. Despite having higher values than natives, the SLA of aliens may be too low to classify most of them as ruderals. Aliens were most commonly stress-tolerant in this system, and their low SLA values likely reflect this (Negreiros et al. 2014).

The increase and stabilisation of functional diversity at intermediate and high invasion levels (Chapter 3) could indicate the filling of vacant niches by aliens. Rapid increases in functional diversity could be possible if niche dimensionality (i.e. the diversity of niches) in a community is low (Clarke 2013), and would be achieved once the threshold of 20 % relative alien cover

(as shown in Chapter 3) is reached. Increased variation in functional diversity in little-invaded communities (<20 %) suggests that these communities have different levels of niche saturation, potentially as a result of environmental heterogeneity or recent disturbances (Moles et al. 2012; Clarke 2013). Little-invaded communities with high functional diversity may be more resistant to invasion, because empty niches are unavailable to invading aliens (Pokorny et al. 2005; Funk et al. 2008). Little-invaded communities with low functional diversity and vacant niches could experience a rapid increase in functional diversity, particularly if the life strategies used by aliens are not limited by soil resource availability (Chapter 2). Niche saturation would be reached at ~ 20 % relative alien cover and subsequent increases in alien cover will not increase functional diversity, but rather maintain it at high diversity. This saturation of functional diversity at intermediate and high levels of invasion may provide some level of resistance to future invaders with similar functional attributes, if there are no vacant niches left to fill.

The fact that functional diversity remained high as alien cover increased suggests that aliens are not only filling vacant niches, but also the niches of natives that have declined in cover. If this is the case, then alien species in this system may have higher plasticity in certain traits, relative to natives. Higher plasticity would allow aliens to take advantage of unoccupied niches, and to overtake the niches previously occupied by natives that have experienced reduced cover from invasion. This in turn would allow functional diversity to remain high even as alien cover increases. Phenotypic plasticity has long been suggested to facilitate invasions, allowing aliens to survive in a wide range of habitat conditions, including those in low-resource environments (Hulme 2008; Funk 2008). Examining the link between alien trait plasticity and the functional structure of the understorey could provide additional insight into how multispecies invasion impacts this system.

Based on my findings, impacts of aliens were not detectable for some patterns, processes and metrics, but were detectable for a few. The leaf thickness of dominant species was important in predicting productivity across the understorey, and aliens mirrored natives in CWM leaf thickness (Chapter 4). This functional repetition may provide a positive impact on productivity, by increasing the stability of standing biomass and ANPP (Schlaepfer et al. 2011; Lockwood et al. 2013). A positive effect, however, relies on the assumption that aliens have no significant, negative impact on native biodiversity. Additional patterns and dimensions of biodiversity need to be considered before it can be concluded that aliens have little or no impact on biodiversity. In addition, invasion may have already detrimentally impacted native biodiversity by causing the loss of some native species from this system. Although aliens

reinforce the importance of functional identity for productivity, it cannot be concluded that they positively provide stability via this mechanism.

Increase in functional diversity with invasion did not cause a shift in the relative importance of functional diversity for productivity. This is despite aliens having positive FD_Q trait-productivity relationships that are different to the negative relationships of natives. These differences, however, were not significant enough to affect community productivity. If niche saturation due to invasion has occurred, then subsequent invasions – if or when they occur – are unlikely to influence the weak diversity-productivity relationships of aliens. Other ecosystem properties, such as soil nutrient cycles or litter decomposition, may be more affected by the traits of aliens in this system (Liao et al. 2008; Ehrenfeld 2010). Given that changes to the functional structure of the understorey have been related to increased invasion, examining changes to ecosystem function across the invasion gradient may further our knowledge on the impacts of multispecies invasion.

Changes to the functional structure of the understorey from multispecies invasion may have implications for the management of Chiltern-Mt. Pilot. The park protects a number of threatened populations of plant species, particularly native orchids, which are often spatially isolated. Management of these threatened populations should include the observation and potential control of spreading annual species with high SLA. These species are likely to reduce the cover of native species and may detrimentally impact on the high conservation value of the park.

Conclusion

In this thesis I have demonstrated how the quantification of multispecies invasion reveals changes to community functional structure, but has no detectable effect on the phylogenetic structure or productivity of the understorey. Almost all natural terrestrial systems have been invaded by multiple alien plant species that now co-occur. The cumulative impact of these species may have severe detrimental impacts for native plant assemblages, species at other trophic levels, and the ecosystem properties that allow these ecosystems to function naturally. Furthermore, the ecosystem services and intrinsic value provided by natural systems, which humans rely on, can be lost or altered when alien species impact on these systems. Often, it is difficult to adequately manage long invaded, alien rich landscapes, particularly when they are protected and associated with high native biodiversity. Using a multispecies approaches, particularly those incorporating gradients of invasion may provide novel insight into how these

landscapes are best managed and preserved. Future research using a multispecies approach will also help to address the existing imbalance in invasion impact studies, which focus on single, dominant invaders. In doing this, a more complete assessment of the implications of invasions for natural communities and ecosystem can be achieved.

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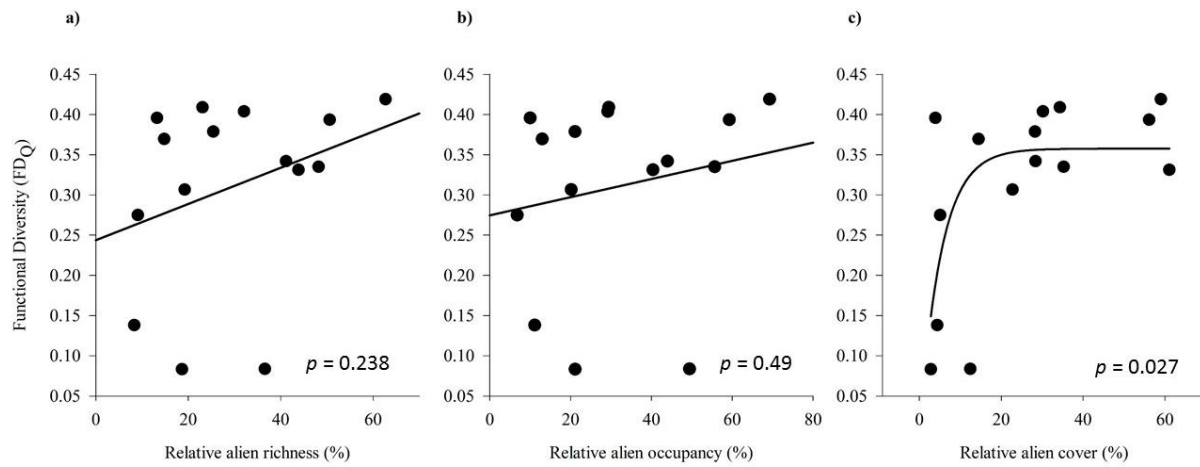
Figures

Figure 1. The relationship between functional diversity and different metrics of invasion level. The multispecies invasion gradient is quantified by a) relative alien richness, b) relative alien occupancy and c) relative alien cover. The *p* values shown are from regression models.