Forecasting native and exotic plant species richness and interactions

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“Tiger got to hunt, bird got to fly;

Man got to sit and wonder 'why, why, why?'

Tiger got to sleep, bird got to land;

Man got to tell himself he understand.”

– Kurt Vonnegut

Abstract

Plant species richness patterns tend to follow environmental (climatic and topographic) gradients. Species richness-environmental relationships are used to predict species richness in different locations which can benefit conservation efforts. For instance, predicted native species richness can be used to identify native richness 'hotspots', and predicted exotic (i.e. non-native) richness can be used to determine which areas are most at risk of invasion by the most exotic species. Context-specific factors also influence native and exotic richness, suggesting that other factors may be important for predicting native and exotic species richness patterns. For native plants, species richness is affected by biogeographic factors, such as landmass area and degree of isolation; and exotic richness is higher in locations that have higher levels of human impact.

I tested the relative importance of different factors on plant richness by developing models that linked combinations of native and exotic C3 and C4 grass species richness to environmental and human impact factors at a large (100 × 100 km) spatial scale across Australia. I found that native and exotic species richness were (i) positively correlated in areas they co-occurred possibly because (ii) they had similar associations with environmental and human impact variables, implying (iii) predicted native species richness may provide a template for potential exotic species richness. For exotic C4 grasses, Northern regions of Australia had particularly high native richness but relatively low exotic richness, suggesting these regions are suitable for supporting much greater numbers of exotic C4 grass species.

I tested criteria (i) and (ii) for a further 20 common plant families within Australia to determine whether native and exotic richness respond similarly to environmental gradients more generally, and to develop guidelines for using the native richness template in other locations. Use of the native richness template was supported by four additional plant families, again highlighting Northern Australia as a region that should be able to support many more exotic species. Families that did not meet criteria (i) or (ii) suggested that use of native richness template may be restricted when native species richness are influenced by non-environmental factors and when exotic species are strongly dispersal-limited.

I tested the importance of environmental and biogeographic factors (land area and isolation) on species richness by comparing native and exotic C3 and C4 grass richness in Australia and New Zealand. I found that that richness patterns in Australia predicted native richness patterns in New Zealand, likely because native species have conserved tolerances to environmental

gradients. For its environmental conditions, New Zealand supported fewer native species relative to Australia, consistent with island biogeographic theory which posits smaller and more isolated landmasses support fewer species because of increased dispersal barriers. New Zealand supported many exotic species, likely because human activities overcome dispersal barriers that have previously isolated plant species assemblages.

Finally, I tested the effect of changes in a critical resource (water availability) on the competitive impacts of exotic species on a native community. Under drought conditions, the exotic grasses had higher survival and greater biomass than native species, and one exotic species still competitively suppressed the native community. These findings suggest that native species may not escape competitive effects of exotic species during resource-poor periods.

Keywords: Invasion, native richness, exotic richness, plant families, species distribution models, biogeographic factors, environmental gradients, Australia, invasion, island biogeography, New Zealand, competition, resource use, water availability, competitive effects, invader impact

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Chapter 1 – Introduction

1.1 Predicting plant species richness patterns

Flowering plants (angiosperms) are a group of 342,953 currently described species and form the basis of most terrestrial ecosystems (Govaerts et al. 2021; WFO 2021). Regions of the planet support vastly different numbers of plant species (Francis and Currie 2003). For example, Ecuador contains 15,788 currently described plant species, whereas Antarctica is more than 45 times larger but only hosts four plant species – two of which have been recently introduced (Engemann et al. 2015; Galera et al. 2017; Pertierra et al. 2017).

A common measure of the structure of communities is the number of species in a given area, termed 'species richness' (Palmer 1990). Understanding the general influences on species richness patterns has important ecological applications. For example, factors that explain species richness in one location can be used to predict species richness patterns in other locations (Francis and Currie 2003; Huang et al. 2021). Many locations lack the data to estimate species richness with useful levels of accuracy (Reddy and Dávalos 2003; Schmidt-Lebuhn et al. 2012). Predicting species richness in this way can be used to overcome sampling constraints that inhibit estimating richness in hard to access or particularly diverse communities (Jiménez et al. 2009; Engemann et al. 2015). Maps of predicted species richness can assist in conservation planning (Myers et al. 2000; Pelletier et al. 2018). For example, species distribution modelling has helped produce maps of Conservation Management Zones in South Western Australian temperate woodlands. The Zones have helped identify high-quality temperate woodlands which host a variety of endemic and endangered taxa, including 202 threatened plant species, as well as threats such as invasive species (Department of the Environment 2015). These maps then contribute to management of these regions for stakeholders, including natural resource managers, sate/territory or national governments, and private owners (Department of the Environment 2015).

Predicting species richness patterns can also be useful for understanding the potential distributions of exotic species. Exotic (introduced and established) plant species can cause large ecological and economic impacts in the areas they invade (Pimentel et al. 2005; Chytrý et al. 2008; Roy et al. 2018) including native species richness 'hotspots' (Stohlgren et al. 2003; Moser et al. 2018). The impacts of exotic species on native communities has motivated research

focused on forecasting the locations that exotic species can spread to (Duursma et al. 2013; Bellard et al. 2017). Like with native species, linking exotic richness to factors has been used to predict potential exotic richness (Bellard et al. 2013; Gallardo et al. 2015). Maps of potential exotic species richness have been used to anticipate the arrival of exotic species, and to design effective surveillance and removal efforts (Panetta et al. 1991).

Yet, there is debate about the relative importance of different factors in different locations, which inhibits the accuracy of linking species richness with factors in one location to predict species richness in others (Yates et al. 2018). If we can better understand the roles of different factors on native and exotic plant species assemblages, we may be able to better predict native and exotic plant richness in different locations. And, in doing so, we can increase our understanding of how plant communities – independent of their origin – are structured in different locations around the globe.

1.1.1 General influences on native plant species richness

1.1.1.1 Climatic gradients

At large spatial scales, there are consistent and predicable patterns between the locations where species are found and particular ecosystem properties (Mittelbach et al. 2007). For example, species richness of many taxa (mammals, insects, plants) generally increases towards the equator, suggesting climatic gradients might strongly influence species assemblages (Hillebrand 2004). At large spatial scales (1,000 – 10,000 m^2), climates that are year-round wet and warm support the highest numbers of plant species on the planet (Hawkins et al. 2003; Kreft and Jetz 2007). As climatic conditions become more variable, cooler, and drier (or combinations of these conditions), plant species richness declines (Hawkins et al. 2003; Kreft and Jetz 2007). Plant species richness is thus predictable from environmental gradients (Francis and Currie 2003; Field et al. 2009; Huang et al. 2021).

The large-scale correlative studies which link observed species richness with climatic and topographic gradients have been important in furthering our understanding of the factors that affect species richness (e.g. Francis and Currie 2003; Field et al. 2009; Huang et al. 2021). An additional step is understanding the mechanisms that link plant species richness to climatic gradients is important to avoid spurious richness-environment correlations and for supporting specific hypotheses about where the greatest numbers of plants are expected to be found.

Climate may play an important role in structuring plant species richness patterns because of the fundamental limits temperature regimes and water availability have on plant physiology. A fundamental physiological plant process is photosynthesis. Photosynthesis is dependent on sunlight and is inextricably linked with water availability because CO_2 uptake cannot occur without water loss. The trade-off between carbon capture and water use suggests that the types of plant species found in different regions should vary with rainfall, solar radiation, and temperature gradients (Nano and Pavey 2013; Chen et al. 2017). Equatorial regions typically provide plants with high and consistent water availability, and stable and benign ambient temperatures, which provide the fewest restrictions for species' meeting their physiological requirements (Huang et al. 2021). The high and stable solar radiation levels in equatorial zones are thought to allow species to adapt different forms to exploit different resources or spaces, which is thought to contribute to the high species richness in tropical regions (Mittelbach et al. 2007).

Maintaining physiological functioning outside of stable, hot, and wet climates, may progressively restrict plant functioning. For example, as water availability declines but temperature remains high, evapotranspiration demands increase, resulting in increased water loss from photosynthesis, oxidative damage, and heat stress (Wright et al. 2005). Plant performance is also affected by low temperatures. For example, in freezing conditions, vacuoles can freeze and puncture cells walls, and cell stress can result in oxidative damage (Lukatkin 2003). Lower plant biomass in cool or arid climates may be a result of lower available resources and the higher resource cost required to maintain physiological functioning (Zomer et al. 2008; McDowell 2011; Dwyer and Laughlin 2017). Lower resources and higher costs of biomass may also contribute to the lower species richness in cooler and more arid climates (Hawkins et al. 2003).

Topographic heterogeneity also affects species richness, but independently of large-scale climatic variation. Areas that vary in the physical complexity have more strongly varying micro-habitat conditions, including increased diversity of micro-climates, resources, and spatial refugia (Currie 1991; Deutschewitz et al. 2003; Kallimanis et al. 2008). This is thought to allow for a wider array of physiological types of species to be supported in a given area and hence greater species richness (Stein et al. 2014). Moreover, species richness can increase in more topographically diverse conditions because species can specialise into different micro-climates, or are more strongly spatially separated, and thus species can evolve through vicariance or via refugia from competition (Hughes and Eastwood 2006). Thus, for a given climate and at

virtually all spatial scales, higher topographical heterogeneity is consistently associated with higher taxonomic diversity and species richness (Stein et al. 2014; Ben-Hur and Kadmon 2020).

Assessing how species with particular functional traits (*sensu* Violle et al. 2007) vary with environmental gradients is another means to determine the importance of different factors on species richness patterns. For example, plants have evolved three types of photosynthetic pathways (C3, C4, and CAM [crassulacean acid metabolism] photosynthesis). C3, C4, and CAM photosynthesis provide differing carbon uptake-water use efficiencies, and are thus each adapted to progressively drier and/or hotter climates (Szarek and Ting 1975). The distributions of species with C3, C4 and CAM pathways is consistent with their theorised adaptations in different climates, suggesting the strong limit of physiology on plant species richness (Still et al. 2003). For instance, C3 species have a high rate of carbon-capture in relatively cool and wet climates, and thus are the dominant photosynthetic type in plant assemblages in temperate and cooler regions. C4 photosynthesis results in more efficient water use in regions that are warmer with more strongly seasonal (e.g. monsoon) rainfall (Oyarzabal et al. 2008; Bremond et al. 2012; Griffith et al. 2015; Simpson et al. 2020). CAM photosynthesis has very low rates of water loss but also carbon uptake, and species with CAM photosynthesis are common in arid (hot and dry) conditions (Nobel and Jordan 1983).

Comparing closely related species is another means to predict species richness patterns. More closely related plant species can have more similar phenologies, tolerances to resources and competitive and mutualistic interactions (Burns and Strauss 2012). This phenomenon is attributed to the idea of 'phylogenetic niche conservatism', where more closely related taxa tend to have more similar physiological and thus ecological characteristics (Wiens and Graham 2005). For example, Crisp et al. (2009) estimated the ancestral and current distributions of ~11,000 plant species across the Southern Hemisphere, finding that less than $1/25^{th}$ of the species have moved habitat types. The phylogenetic niche conservation theory also posits that more closely related species should also have more similar limits on their distributions (Wiens and Donoghue 2004). For example, Ricklefs and Latham (1992) found that the mean range sizes of genera found in both temperate North America and eastern-Asia were similar, attributing this phenomenon to conserved traits.

1.1.1.2 Biogeographic factors

In contrast to the influence on physiology, biogeographic factors such as land area and isolation have also explained species richness patterns in many locations, suggesting that species richness patterns need not necessarily follow climatic gradients (Roy and Goldberg 2007; Albert et al. 2017). Macroevolutionary theory suggests species assemblages are formed through species increasing their geographic ranges (dispersing), diverging (speciating), and terminating (becoming extinct) (Gaston 1998). Speciation, extinction, and dispersal are interlinked processes, meaning that dispersal barriers (rivers, mountains, or deserts) that impede dispersal can alter speciation and extinction rates, and hence species richness. For example, endemic African species in the genus *Canarina* are separated by 7,000 kilometres, which Mairal and colleagues (2015) found was explained by a seven-million-year history of dispersal from one region to the other, with aridification and vicariance driving the extinction of the species between these regions. Therefore, contemporary climatic conditions may not usefully predict species richness patterns of some plant communities because species richness patterns may be largely the result of historic processes.

The area of a landmass can influence rates of dispersal, speciation, and extinction and thus species richness. Larger areas can support larger populations which decreases species' extinction risk (Albert et al. 2017). Larger landmasses also increase the chance of speciation through vicariance, or the numbers of 'specialised' species that use particular micro-habitats (Kadmon and Allouche 2007). For example, the Theory of Island Biogeography (TIB) posits that areas with smaller landmasses of the same environmental conditions should receive fewer propagules from potential source populations compared to larger landmasses (MacArthur and Wilson 1963). With fewer successful colonisations, species pools on smaller landmasses tend to be smaller (Palmer and White 1994). Additionally, extinction rates are theorised to be higher on smaller landmasses such as islands because of stronger limits on population sizes (Warren et al. 2015). Indeed, compared to continental landmasses with similar climates, islands have smaller species pools that are composed of high proportions of unique (endemic) species (Kier et al. 2009). Consequently, species richness is typically lower on islands, suggesting land area and isolation are important and universal drivers of species richness (Warren et al. 2015).

1.1.2 Influences on exotic plant species richness

Studying newly established (i.e. exotic) species could provide an additional opportunity to test the importance of different factors on species richness. Across the globe, at least 16,926 plant species have been recorded in locations outside of their natural ranges (Seebens et al. 2017 onwards). There is debate about the extent to which newly established (exotic) assemblages of plant species are subject to different influences compared to old (i.e. native) assemblages (Catford et al. 2011; Pouteau et al. 2015). Human activities and environmental gradients both explain a large proportion of the variation in current exotic species richness patterns (Essl et al. 2019; Mologni et al. 2021; Wohlwend et al. 2021). But the relative importance of environmental gradients and human impacts is unclear, making it difficult to forecast the extent to which exotic species are likely to spread and impact other areas (Pyšek et al. 2010).

1.1.2.1 Human impacts

Plant species are establishing in new locations because of the impacts of human activities on environmental spaces and processes (Mack and Lonsdale 2001; Dodd et al. 2015; Pyšek et al. 2017). At large spatial scales, the degree of human impact is a reliable predictor of exotic species richness (Pouteau et al. 2015; Wohlwend et al. 2021). Introduced species have a greater chance of establishing if they are introduced more frequently, into more areas, and in greater numbers (Duncan et al. 2019; Blackburn et al. 2020). Humans intentionally import plants from different locations for agriculture or horticultural purposes and many of these species escape and establish wild populations (Dodd et al. 2015; van Kleunen et al. 2018). Species also "hitchhike" their way into new locations, being incidentally introduced via human trade and transport (Hulme 2009). Thus, areas that contain transport ports, and centres of human population and activity (e.g. urbanisation, agricultural land use) tend to also contain high numbers of exotic species (Perrings et al. 2005; Seabloom et al. 2006). Human activities are intensifying and long-distance trade is increasing, which means that introductions of species to new regions are expected to increase globally (Levine and D'Antonio 2003; Seebens et al. 2017 onwards, 2021).

Humans also disturb the environments they live in, which may benefit many exotic species (Mack and Lonsdale 2001; Hulme 2009). Human activities can create the conditions for exotic species to establish, including the removal of existing vegetation (e.g. land clearance) (Rashid et al. 2021). Human activities also alter ecosystem properties which can benefit some exotic

species. For example, agricultural fertiliser runoff can increase nutrient supply, which has globally increased primary productivity. However, increasing fertilisation tends to benefit exotic species and can have negative impacts on native species (Seabloom et al. 2006; Dawson et al. 2012). Exotic species can also interact, with the presence of one invader altering conditions which facilitate other exotic species. For example, exotic species can alter nutrient cycles (Liao et al. 2008), the fire-cycle (Rossiter et al. 2003), and water availability (Fritzsche et al. 2006). Understanding when and how resources alter native-exotic interactions is important for understanding where exotic species are likely to have the greatest impacts on native species (Vila et al. 2011), particularly to anticipate impacts within the areas forecasted for exotic species to be able to invade (Thompson et al. 2015).

1.1.2.2 Location

Different factors appear to be important for structuring exotic species assemblages in different locations, termed 'context-dependence' (Catford et al. 2022). Compared to native populations, species introduced into new locations can have markedly larger distributions, higher abundance in areas they occupy, and stronger impacts on co-existing species (Hulme 2008; Vilà et al. 2011). Locations themselves can also differ in the number of invaders they host, termed 'biotic resistance' (Visser et al. 2016). Islands are thought to have lower biotic resistance compared to continents, and islands supports the highest numbers of exotic species (Wohlwend et al. 2021). Continents themselves can also vary in biotic resistance. For instance, Kalusová and colleagues (2015) found that habitats in North America contained more exotic species than comparable habitat types in Europe. Additionally, many studies have shown that larger areas support higher numbers of exotic species, even per unit area (Moser et al. 2018; Mologni et al. 2021; Wohlwend et al. 2021), which suggests that landmass characteristics may affect the number of exotic species that different regions can support.

Europe is one of the largest sources of exotic species (Seebens et al. 2018). Pyšek and colleagues (2010) found that climatic gradients and human impacts explained similar amounts of variation in Europe's exotic richness patterns. Recently, Pouteau and colleagues (2021) found that 1,485 plant species in Europe had, on average, only filled 4.2% of their potential distributions in other regions across the globe. They found that exotic species' current distributions were strongly associated with environmental gradients, suggesting that much of the spread potential of exotic species is due to dispersal limitation to suitable areas. Interestingly, degree of human impact explained the large disparity between current and

predicted distributions: most areas that were environmentally suitable but had no strong human presence were yet to be invaded, further suggesting human activities as large scale dispersal mechanisms for exotic species. Another study on global exotic species distributions also found a strong role of topographic heterogeneity on exotic species richness patterns (Essl et al. 2019).

Islands have provided useful insights into the degree to which landmass characteristics can affect native and exotic species communities. Islands are the most severely invaded habitats on earth (van Kleunen et al. 2015; Essl et al. 2019). The exotic richness-area relationship is steeper on islands compared to continental regions (Pyšek et al. 2017). Darwin postulated that species assemblages on remote islands would have poor competitive abilities compared to continental species, and hence island ecosystems have lower biotic resistance (Sax and Gaines 2006). The Theory of Island Biogeography predicts that smaller and more remote areas should support fewer native species, meaning resources and space are less exploited by native species communities (Lloret et al. 2005). Indeed, islands that are further from other landmasses also support smaller native communities and higher numbers of exotic species for their environmental conditions and land area (Moser et al. 2018). Therefore, islands may be particularly invaded compared to continents of comparable environment gradients because resident taxa have a poor ability to repel invaders and/or there are more resources and space available that other species can exploit.

Predicting the potential distributions of exotic species is an uncertain business. While we can often reconstruct how exotic species were introduced and their current distributions, it is often difficult to forecast future spread and predict the potential number of exotic species that different areas could support (Ibáñez et al. 2009; Catford et al. 2011). Indeed, propagule pressure, human impacts, environmental gradients, land area and isolation all appear to explain some aspects of current exotic species richness patterns. However, it is challenging to use these variables to predict likely changes in exotic species richness through space and time. One issue is validating the accuracy of predictions of species' distributions (Mack and D'Antonio 1998). For example, comparing predicted and observed distributions is a common tool for validating predictions of native species' distributions (e.g. Guisan and Thuiller 2005). Many exotic species may not have achieved the full extent of their potential distribution in new regions because they have not had sufficient time to spread (Duncan 2021). Chronic dispersal limitation reduces the accuracy of comparing predicting and current exotic spices' distributions because patterns of exotic species richness in their invaded ranges may be biased to locations of human introduction and may not reflect their wider environmental tolerances (Sofaer and Jarnevich 2017).

One way to account for dispersal limitation is to use a species' distribution in its native range to predict its potential distribution in a new area (Broennimann and Guisan 2008). There is mixed support for this methodology (Duncan et al. 2009). Many studies on groups of species suggest environmental gradients explain species distributions similarly within native and exotic ranges (Thuiller et al. 2006; Ibáñez et al. 2009; Liu et al. 2020*a*). Other studies show that exotic species have different associations within their native and exotic ranges (Gallagher et al. 2010, 2013; Liu et al. 2020*b*). For example, Atwater and Barney (2021) showed that 815 exotic species had largely different associations with environmental conditions in their introduced ranges.

There is an urgent need to better resolve the relative strengths human activity, environment, and location on exotic species richness. With the current number of exotic plant species (at least 16,926), and the fact that numbers are rising (Seebens et al. 2017 onwards), we urgently need a global consensus of the factors that influence large-scale exotic plant assemblages. These factors should, ideally, come with some predictive power, enabling us to forecast the potential for different areas to support higher numbers of exotic species. A way forward is to develop a methodology that aims to estimate potential exotic species richness, and a way to determine the relative importance of different factors on exotic species richness patterns.

1.2 Native species richness as a template for potential exotic species richness

Comparing native and exotic richness patterns could inform us whether species assembly rules are strongly conserved between old (native) and new (exotic) species assemblages, and whether there is potential for using native species richness patterns as a template for potential exotic species richness patterns. Evidence from many plant species assemblages from around the globe suggests that where native and exotic plant species co-occur, at large spatial scales (> 1,000 m^2) native-exotic richness is generally positively correlated (mean Pearson's *r* value = 0.63; Table 1.1). These findings imply that in areas where native and exotic species co-occur, areas with high native richness tend to support high exotic richness. This suggests that patterns in native species richness could be used to inform the potential of exotic species to invade different areas (Stohlgren et al. 2003). Areas that are environmentally suitable but have low levels of human impacts may be locations where exotic species are dispersal-limited but have the potential to

invade further. Locations most at risk of invasion by the most exotic species could be identified as areas with high native richness and proportionately lower exotic richness.

Table 1.1 Native and exotic richness and their correlation at moderate-to-large spatial scales within different landscapes. Data taken from Tomasetto et al. (2019).

Native-exotic correlation (r)	Mean native richness	Mean exotic richness	Scale (km^2)	Region	Reference
0.85	125	20.9	1	Europe	Ricotta (2010)
0.84	685.7	34.6	500	Africa	Stadler (2000)
0.79	504.5	211.2	100	Europe	de Alburquerque (2011)
0.78	104.7	7	1	Europe	Godefroid (2003)
0.78	72	18.2	30	Europe	Kuhn (2003)
0.77	441	50.4	32	Europe	Deutschewitz (2003)
0.77	8.9	3.3	657	S-Africa	Richardson (2005)
0.76	8.3	2.6	10	Pacific islands	Chown (2005)
0.74	441	69	32	Europe	Deutschewitz (2003)
0.74	8.1	3	657	S-Africa	Richardson (2005)
0.72	7.9	2	657	S-Africa	Richardson (2005)
0.69	9	3.4	657	S-Africa	Richardson (2005)
0.69	8.4	3.7	657	S-Africa	Richardson (2005)
0.68	687.7	67.7	10	Europe	Bartomeus et al. (2012)
0.66	801	36	37.5	Europe	Marini (2009)
0.60	762.2	13.4	10	Europe	Bartomeus et al. (2012)
0.58	39.9	24.3	0.25	Europe	Jauni (2012)
0.57	591.4	45.9	10	Europe	Bartomeus et al. (2012)
0.54	5.5	2.2	657	S-Africa	Richardson (2005)
0.54	6.9	2.9	2	N-America	Seabloom (2006)
0.52	753.8	37.5	10	Europe	Bartomeus et al. (2012)
0.35	6.6	3.4	130	Europe	Kuhn (2003)
0.26	73	5.5	35	Europe	Carboni (2016)
-0.01	136	8.3	3.75	Europe	Renöfält (2005)

The strength of the positive correlation between native and exotic richness varies widely (Table 1.1). While there is a generally positive relationship between native and exotic richness at larger spatial scales, areas can vary widely, e.g. r = -0.01 and 0.85 (Table 1.1). In a meta-analysis by Pouteau and colleagues (2019), scale explained the most variation in native-exotic correlation values. There are also author and study design effects, such as nested plots and using data which were not initially collected for the purpose of native-exotic richness comparison (Pouteau et al. 2019). However, a key insight from this study was that the strength of the correlation values was stronger in studies that measured native and exotic richness at larger scales, meaning that at sufficiently large spatial scales, there is a reasonable expectation that native and exotic species richness is generally higher in similar areas.

The degree to which native and exotic species richness patterns are correlated at large scales, and their respective associations with environmental gradients and the impacts from human activities may provide us with a better understanding of the factors that structure plant assemblages. The native richness template methodology would only be expected to be useful when native and exotic species respond in similar ways to the same environmental gradients. Native and exotic species richness has been shown to have similar associations with climatic, resource and topographic gradients (Byers and Noonburg 2003; Davies et al. 2005; Fridley and Sax 2014). Comparing closely related native and exotic species may provide the best test for the native richness template because related species tend to have more similar physiologies and hence respond in similar ways to environmental factors (Crisp et al. 2009).

Moreover, the degree to which native and exotic richness patterns differ could inform us about the relative importance of different influences on native and exotic species assemblages. In many locations, native and exotic species have been shown to respond differently to climatic gradients and factors relating to human impact (Tomasetto et al. 2013; Pouteau et al. 2015). Additionally, if current native species richness patterns are the result of historic processes (e.g. dispersal barriers), then exotic species richness patterns might not follow native richness patterns. The effect of biogeographic processes is particularly relevant for islands, which are the most invaded habitat types (Pyšek et al. 2017) but have high proportions of endemic species (Kier et al. 2009). For example, many taxa that are poor long-distance dispersers are present on mainlands but absent from islands (e.g. Keppel et al. 2009). Exotic species have overcome these historic dispersal barriers through human-mediated transport, and so the phylogenetic make-up of native and exotic species assemblages on islands may be quite different.

1.2.1 Impacts of exotic species

The ultimate goal of forecasting exotic species' distributions is reducing their potential impacts in the areas they are likely to invade. The impact of exotic species on plant assemblages can be defined as the reduction in resident performance or biomass (Jeschke et al. 2014). Exotic species can impact communities by competing for shared resources such as establishment sites, light and nutrients (Seabloom et al. 2003) and can lead to sustained losses of species and functional diversity in native communities (Ceballos et al. 2010; Galera et al. 2017; Tordoni et al. 2019). Not all species access the same resources, nor need to access resources at the same time. The impact of exotic species has been shown to be greatest when exotic species compete with native species for the same resources (Davis and Pelsor 2001). This would explain why native

communities tend to experience greater impacts from exotic species when exposed to a greater diversity of invaders which are also more abundant (Levine et al. 2004).

In areas where they are present, the abundance of many exotic species varies over relatively small spatial and temporal scales, meaning impacts on native species assemblages can also vary locally. Three factors explain how an area becomes invaded: available resources, the propagule pressure of potential invaders, and the competitive abilities of the invader and resident community (Lonsdale 1999). Propagule pressure and the competitive ability of resident native species is assumed to be equal between areas at relatively fine spatial scales. But resources can vary strongly at fine spatial scales, and may be an important predictor of density of exotic species (Davis et al. 2000). Exotic impacts are high when native and exotic species share fluctuating and limited resources (Davis and Pelsor 2001). Successful invaders may have traits that allow them to pre-emptively sequester limited resources (Reich 2014). However, conservative traits allow for persistence through periods of poor resource levels (Mathakutha et al. 2019). From this point of view, the impacts of exotic species could be greatest where there are abundant resources, but low during resource-poor periods, even in otherwise highly invaded areas. If we can better understand what promotes invader abundance within their invaded ranges, we may be better equipped to forecast where in the landscape exotic impacts will be greatest (Vilà et al. 2015). For example, by identifying critical resources or periods with critical resource-levels that many exotic species respond to, this could be used to maximise conservation outcomes for given management effort in areas that are already invaded.

1.2.2 Species inventory data

Data on the composition and size of species assemblages is critical for addressing ecological challenges. The digitisation of herbarium records and the popularity of citizen science projects have massively increased data on where species occur (Lavoie 2013). Harnessing species occurrence records for ecological applications requires cleaning and verifying records to ensure that they are 'fit for purpose' (Meyer et al. 2016). Herbarium records, for example, are the result of unstructured sampling, meaning records are concentrated in areas with high levels of human activities, such as cities and roads, and are depauperate in remote locations (Dodd et al. 2016; Daru et al. 2017). Species richness tends to increase with the number of records, particularly in high-diversity communities or across large areas, which can confound the use of species richness for ecological applications (Chao and Lee 1992; Gotelli and Colwell 2001). For example, the presence of under-sampled communities can skew species richness-environment

associations and mis-identify species richness hotspots (Schmidt-Lebuhn et al. 2012; Sofaer and Jarnevich 2017). Thus, estimates of community diversity using online records must account for differences in sampling effort (Chao 1987).

Many statistical methods have been developed to correct for differences in sample effort between different communities to better estimate species richness (Colwell and Coddington 1994; Colwell et al. 2012). One such method is sampling completeness, which estimates a relationship between species richness and the number of records in an area, and then scales different areas to a pre-defined proportion of richness-records along that curve (Chao and Jost 2012). For instance, areas that are well-sampled have their species richness interpolated down the curve, and those areas that are under-sampled have their richness extrapolated up the curve. This has been shown to be effective at removing sampling bias in estimates of species richness among different areas (Chao et al. 2014).

Accounting for spatial bias in exotic species records is even more challenging than for native species records because exotic species are inextricably linked with human activities. However, comparing exotic species richness patterns to native species richness patterns may provide a useful template for the degree of persisting spatial bias in species records. That is, the strength of the association between native species richness and human impact could be used as an estimate of the residual spatial bias in the records. Exotic species richness that is more strongly associated with human impacts compared to native species richness might suggest that exotic species may be limited in their capacity to spread outside of areas characterised by human populations and their activities. On the other hand, both native and exotic species richness may have similar associations with human impacts, suggesting that exotic species are not more strongly associated with humans that any other taxa.

1.3 Model systems

1.3.1 Grasses as model taxa

Grasses (Poaceae) are a globally dominant plant family. To illustrate, Antarctica hosts only four flowering plants, three of which are grasses. Of the three, only one is native (*Deschampsia antarctica*) and the other two grasses are exotic and invasive (Galera et al. 2017; Pertierra et al. 2017). Across the globe, there are about 12,000 grass species, and grasses are the second largest

exotic family by species (Vorontsova et al. 2015; Pyšek et al. 2017), making them an ideal group to study and compare native and exotic species richness patterns.

The composition of grass species assemblages and their species richness patterns varies strongly with environmental gradients (Liu et al. 2009; Edwards and Smith 2010; Bocksberger et al. 2016). Much of the variation in grass assemblages is linked to the prevalence of species with C3 or C4 photosynthetic pathways (Hattersley 1983). Nearly 40% of the grass family have C4 photosynthesis (~5,000 species), the vast majority of the remaining 7,000 species have C3 photosynthesis, and the remaining minority have an indeterminate C3-C4 pathway or are undescribed (Sage 2016). C3 and C4 grasses have strong associations with climatic gradients, often in different directions (Hattersley 1983).

Grasses also have strong historical and contemporary ties with human activities (De Wet 1981; Saha and Butler 2017). Grasses have been introduced into many locations and have managed to thumb a lift into many other regions. For example, they are major food crops, pasture species, and provide services such as lawns for parks and properties (Wolfe 2009; da Silveira Pontes et al. 2015). Grasses are also passengers of human-induced changes, having strong associations with disturbed areas (HilleRisLambers et al. 2010; Preece et al. 2010).

1.3.2 Australia as a model continental landmass

Australia incurs significant ecological and economic costs from exotic species (Sinden et al. 2004). Australia currently has about 3,207 exotic plant species in 120 plant families (The Australian Weed Strategy, 2017). Australia's exotic grasses are particularly problematic. As well as being Australia's largest exotic plant family, exotic grasses constitute a disproportionately high proportion of Australia's problematic plant species (Lonsdale 1994; Daehler 1998; van Klinken and Friedel 2013) and are a serious threat to native communities throughout Australia (Morgan 1998; Rossiter et al. 2003; Grice 2004; McLaren et al. 2004).

An overview of the potential for exotic grasses to colonise new regions of Australia is lacking, and it is of general interest to understand what influences the potential distribution of exotic grasses. Many exotic grass species are already widely distributed across the continent and have strong impacts on native species (Grice and CSIRO 2000; Downey et al. 2010*a*). Noxious examples include *Andropogon gayanus* Kunth. (gamba grass) (Rossiter et al. 2003), *Eragrostis curvula* (African lovegrass) (Firn 2009), *Cenchrus ciliaris* L. (buffel grass) (Jackson 2005;

Martin et al. 2015), *Themeda quadrivalvis* (grader grass) (Keir and Vogler 2006), and *Nasella neesiana* (Chilean needle grass) (Bourdôt et al. 2012). The potential for species to spread may be based on the availability of suitable habitat. Under current climates, some problematic exotic grass species appear to have mostly filled, suggesting limit spread potential of some problematic grass species (Gallagher et al. 2013).

Australia has a history of biological surveys and has infrastructure that has enabled the digitisation of millions of herbarium specimens, along with recent citizen science programs that are contributing new records (Dodd et al. 2016). These available records suggests that plant communities are relatively-well sampled at large spatial scales (Haque et al. 2017). Therefore, Australia is a useful study system to understand how big data can be used to link native and exotic richness patterns to environmental conditions. Grasses present an opportunity to test these ideas, and Australia's other common exotic plant families provide opportunities to further refine these ideas.

The composition of Australia's grassland communities are influenced by water availability (Knapp et al. 2002; Petrie and Brunsell 2008; Medlyn 2011; Gibson-Forty et al. 2016). Thus, water availability may be a critical resource affecting exotic grass performance and likely impacts on native communities (Bolger et al. 2005). However, many regions of Australia have limited water availability, either seasonally or annually, suggesting that exotic grasses in Australia might have varying distributions or impacts related to water availability (Cocks 1994; Mackey et al. 2008). Hence Australia's native grasses may be useful system to test whether water availability is a critical component of exotic species impact in invaded communities.

1.4 Thesis objectives

I address four broad questions in this thesis:

(i) Does native grass species richness provide a template for the invasion potential of exotic grasses in Australia?
(ii) Which taxonomic, environmental or spatial factors might native species richness be useful as a template for the invasion potential of exotic species?
(iii) Do species richness–environment gradient relationships in one region predict similar richness relationships in other regions?

(iv) Do the competitive impacts of exotic grass species on a native grass community vary as a function of water availability?

My first question aims to determine whether native species richness could be used as a template to forecast the potential distributions of related exotic species, using C3 and C4 grass species in Australia. I develop models linking native and exotic species richness patterns across Australia using herbarium and verified citizen science records at a large (100 × 100 km) spatial scale. I test whether combinations of native and exotic C3 and C4 grass species richness are (i) positively correlated in areas they co-occur and (ii) whether native and exotic species have similar associations with environmental and human impact variables within Australia. Verifying (i) and (ii) implies that (iii) native species richness may provide a template for potential exotic species richness.

In my second question, I aim to determine whether the native richness template idea could work for other plant groups and in other locations. I do this by testing criteria (i), (ii) and (iii) on an additional 20 common native and exotic plant families within Australia. I also evaluate whether there are common characteristics among the plant families that can explain why criteria (i) and (ii) are met for some families but not others, to suggest instances when the template is likely to work for other groups of taxa in other locations.

In my third question, I test whether native and exotic richness in one location (Australia) can predict species richness in another location (New Zealand), again testing native and exotic C3 and C4 grass species richness at large (100 × 100 km) spatial scales. I compare native and exotic grasses of Australia and New Zealand because New Zealand is a smaller and more isolated landmass compared to Australia, and hence I may be able to determine the degree to which biogeographic factors affect its native species richness and the degree to which exotic species have overcome historical dispersal barriers via human-mediated dispersal.

Finally, I determine whether finer-scale variance in environmental conditions affects the performance of exotic species and in turn their impacts on a native community. I tested whether the impacts of successful invasive grasses on a community of three native grasses is a function of a key resource, the level of water availability, using glasshouse experimental set up. The results of which could indicate the locations in an area that are likely to sustain the greatest impacts from exotic species based on predicted resource levels.

1.5 Thesis outline

The four data chapters of this thesis have been prepared as standalone research articles, so there is some repetition in the Introductions and Methods among Chapters 2 – 4. Each research chapter is based on research I conducted at the University of Canberra between 2017 and 2021. Chapter 6 is a general discussion of the themes and implications of the four data chapters taken together.

Chapter 2 – Native species richness provides a template for the invasion potential of exotic grasses in Australia

2.1 Abstract

I evaluate whether native C3 and C4 grass (Poaceae) species richness can provide a template to forecast potential exotic C3 and C4 grass species richness across Australia, by testing if: (i) native and exotic richness are positively correlated where they co-occur at a landscape scale; and (ii) native and exotic richness have similar associations with environmental variables. If (i) and (ii) hold, this implies that areas with high native richness but currently low exotic richness have the potential to be invaded by a greater number of exotic species.

I estimated native and exotic C3 and C4 grass species richness in 1,104 100 × 100 km grid cells across Australia using 1,012,181 herbarium records. Species richness was modelled as a function of seven environmental variables and one human impact variable, and models were used to predict native richness across Australia scaled to values between 0 and 1. For each grid cell, exotic invasion potential was calculated as the difference between predicted scaled native richness and observed scaled exotic richness.

Where they co-occurred, native and exotic species richness were positively correlated, and native and exotic richness had similar associations with environmental variables for both C3 and C4 grasses. Native and exotic C3 richness was greatest in temperate regions in the southeast and west of Australia. The strong coincidence of native and exotic richness in these regions implied low invasion potential for C3 grasses across Australia. In contrast, native C4 richness was highest in warmer northern regions where exotic C4 richness was low, implying high invasion potential for C4 grasses across northern Australia.

For Australian grasses, native richness can provide a template for exotic richness and thus be used to estimate invasion potential, an approach that could be useful for forecasting exotic spread in other taxa and locations.

2.2 Introduction

Predicting the locations that appear particularly prone to invasion by multiple species is central to forecasting risk and managing invasions (Panetta et al. 1991; Carboneras et al. 2017; Adriaens et al. 2018). Species distribution models (SDMs) are commonly used to predict the potential spread of exotic species (Liu et al., 2020). Locations a species currently occupies are used to infer its environmental tolerances (Hirzel et al. 2002), which are then extrapolated across new regions to identify areas that are environmentally suitable for that species. Areas particularly prone to invasion can be identified by constructing SDMs for multiple exotic species, 'stacking' the resulting individual SDMs, and creating a map of predicted exotic species richness across the landscape (Ferrier and Guisan 2006; Schmitt et al. 2017). Areas with high predicted exotic richness are potential hotspots for future invasion (Bellard et al. 2013; Gallardo et al. 2015).

There are, however, some drawbacks associated with using stacked-SDMs for forecasting the locations of potential invaders, motivating the search for alternative methods. First, it can be time-consuming to construct individual SDMs for exotic species, since they require species-specific environmental data, and decisions about the modelling approach including model selection, fitting, and validation (Hao et al. 2019; Zurell et al. 2020). Second, it can be difficult to decide which species to include as potential invaders from an often large pool of candidates (Seebens et al. 2017) that may or may not be representative of potential future invaders. The aim of this Chapter is to evaluate an alternative method for identifying areas prone to invasion by exotic species: using native species richness as a template to predict potential exotic species richness.

Native species richness may predict potential exotic species richness if native and exotic species respond to major environmental gradients in similar ways, leading to a positive correlation between native and exotic richness across the landscape. There is strong evidence for this. Variation in plant species richness has been shown to correlate strongly with major environmental gradients, including temperature, water availability and topographic heterogeneity (Kreft and Jetz 2007; Jiménez et al. 2009; Stein et al. 2014). Both native and exotic species appear to respond similarly to climatic variation (de Albuquerque et al., 2011; Fridley and Sax, 2014; Gilbert and Lechowicz, 2005; Levine and D'Antonio, 1999; Peng et al., 2019), gradients in resource availability (Stohlgren et al. 1999; Byers and Noonburg 2003), and environmental heterogeneity (Davies et al. 2005; Brooks et al. 2013). Moreover, numerous

studies have documented a positive correlation between native and exotic species richness at large spatial scales (>1,000 m^2) (Stadler et al. 2000; Deutschewitz et al. 2003; Kuhn and Klotz 2003; Chown et al. 2005; Thuiller et al. 2005; Stohlgren et al. 2008; Seabloom et al. 2006; Stark et al. 2006; Stohlgren et al. 2006; Hulme 2008; Ricotta et al. 2010; Bartomeus et al. 2012). If native and exotic species richness vary in the same way along environmental gradients, then areas that support a greater number of native species should also support a greater number of exotic species (Fridley et al. 2007). Alternatively, those areas with other factors that also vary along environmental gradients (environmental covariates) that also predict high native and exotic richness are also expected to be invasion prone. Consequently, hotspots for future invasion should be those areas with high native richness but proportionally low exotic richness (Seabloom et al. 2006). While many studies have identified that areas of high native species richness are more likely to be invaded by exotic species (Stohlgren et al. 2003; Seabloom et al. 2006; Fridley and Sax 2014), I am not aware of any study that has used the observed positive correlation between native and exotic species richness to forecast invasion potential.

If native and exotic richness are highly correlated across a landscape, this could suggest that exotic species have already spread to the locations they could potentially occupy (Figure 2.1a, b). Native species richness may provide a more useful template for forecasting exotic invasion in situations where exotic species are currently restricted in distribution because they have not yet spread to occupy all suitable habitats (Figure 2.1c). If some locations currently have few or no exotic species due to dispersal limitation rather than unsuitable environmental conditions, I might still expect native and exotic richness to be positively correlated in areas where native and exotic species co-occur, but the correlation could be weakened by a directional bias: an excess of locations with relatively high native but low exotic richness would represent environmentally suitable areas yet to be invaded by exotic species (Figure 2.1c).

On the other hand, it is possible that native and exotic species richness are driven by different factors (Essl et al. 2019). Exotic species are more common in areas with high levels of human impacts, such as urban environments or modified agricultural lands (Preece et al. 2010; Catford et al. 2011; Tomasetto et al. 2013; Dainese et al. 2014; Mologni et al. 2021) whereas the opposite can be true for native species (Deutschewitz et al. 2003; Pouteau et al. 2015). If exotic species are more strongly associated with human impacts while the opposite holds for native species, then native richness may not provide a suitable template for identifying areas prone to invasion by exotic species. In these circumstances, I would expect native and exotic richness to

be either weakly or negatively correlated in areas where native and exotic species co-occur, and for exotic richness to be more strongly associated with levels of human impact than other environmental variables (Figure 2.1d).

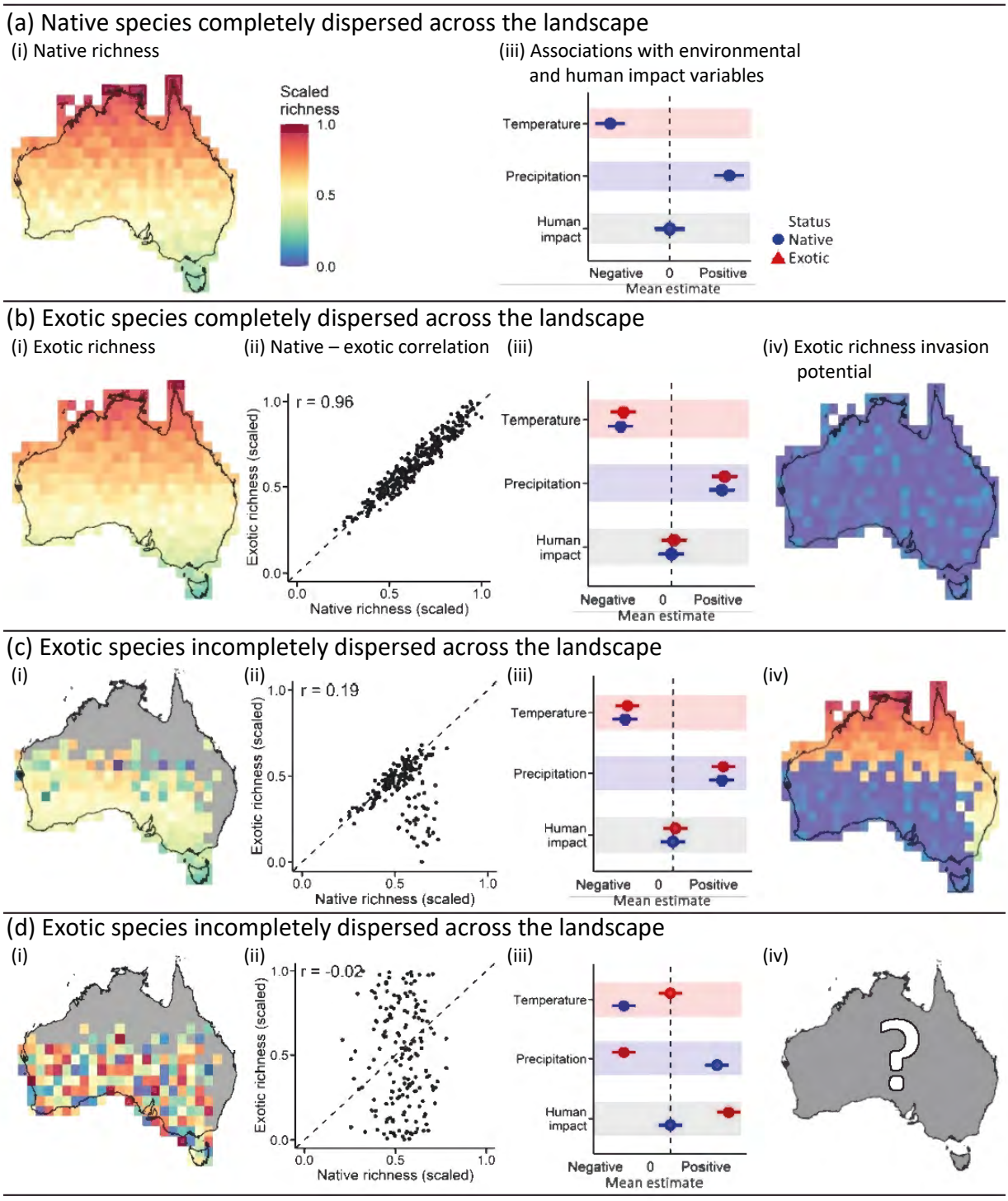

Figure 2.1 Conceptual scenarios of native species richness as a template for potential exotic richness at large spatial scales. Panel (a) (i) native species richness in gridded cells across the landscape, with hot colours (red-orange) indicating high species richness and cooler colours (blue-yellow) indicating low richness (with richness scaled to between 0 and 1). (ii) In this case,

variation in native richness is strongly associated with environmental gradients in temperature and precipitation. Panel (b) (i) exotic species richness assuming exotic richness responds to environmental gradients in a similar way to native richness and that exotic species have had the opportunity to spread to all locations. (ii) In this case, I expect native and exotic richness to be strongly positively correlated in cells where they co-occur. (iii) I further expect scaled native and exotic richness to show similar associations with the same environmental variables. (iv) Exotic invasion potential (the difference between scaled native and exotic richness) is low because exotic species fully occupy the landscape. Panel (c) (i) exotic species richness assuming exotic richness responds to environmental gradients in a similar way to native richness but that exotic species have not yet spread to all locations. (ii) In this case, I expect a positive correlation between scaled native and exotic species richness in areas where both co-occur, although some cells are expected to have high native richness and low exotic richness where exotic species have not fully occupied those areas. (iii) I expect scaled native and exotic richness to show similar associations with the same environmental variables. (iv) Areas currently lacking exotic species but that are suitable for native species are identified as having high invasion potential (calculated as the difference between scaled native and exotic richness). Panel (d) (i) exotic species richness assuming that exotic species' distributions are strongly associated with different factors to native species. (ii) In this case, I expect a weakly positive or no correlation between scaled native and exotic species richness in areas where they co-occur. (iii) I further expect richness of native and exotic species to show different associations with environmental and human impact variables. (iv) Under these circumstances, native species richness does not provide a useful template to forecast exotic richness and estimate invasion potential.

Here, I aim to test whether gradients in native species richness can provide a useful template for identifying areas particularly prone to invasion by exotic species by examining the alternative scenarios described above (and see Figure 2.1) using data on the distribution of Australia's native and exotic grasses (Poaceae). Australia's native grasses are a useful study taxa because they are speciose, widely distributed across the continent, and grass species richness is known to respond to large-scale environmental gradients (Hattersley 1983). Exotic grasses are also among the most problematic invaders of agricultural lands and native ecosystems in Australia (Rossiter et al. 2003; Grice 2004; Keir and Vogler 2006; Watt et al. 2011; Grice et al. 2013; van Klinken and Friedel 2013). Grasses include species with different photosynthetic pathways (C3 and C4, see Table 2.1) that differ in their distribution along environmental gradients associated with temperature and rainfall (Bocksberger et al., 2016; Edwards and Smith, 2010; Edwards and Still, 2008; Linder et al., 2017; Liu et al., 2009) resulting in distinct gradients in native C3 and C4 grass species richness across Australia (Hattersley 1983). This provides an opportunity to examine the potential for native species

richness to provide a template for exotic richness in two physiologically distinct groups of grasses that differ in their environmental responses.

I use location data for 1,012,181 Poaceae records in Australia, along with data for seven major environmental variables and one human impact variable, to address three questions:

(i) Where they overlap, are native and exotic grass species richness positively correlated?
(ii) Is variation in native and exotic richness related to environmental and human impact variables in a similar way?
(iii) Do the results of (i) and (ii) suggest higher invasion potential of exotic Poaceae species in Australia than currently realised?

2.3 Methods

2.3.1 Species and photosynthetic trait data

I downloaded all 2,175,967 Poaceae records available from the Atlas of Living Australia (dataset: https://doi.ala.org.au/doi/10.26197/5c78c275549a5 downloaded on 3 January 2020). The Atlas of Living Australia is a repository for information from the Australasian Virtual Herbarium (AVH), a database of vouchered herbarium specimens amalgamated from Australia's major herbaria and taxonomic-verified occurrence observations (CHAH 2018). I downloaded the records in R (R version 4.0.0) (R Core Team 2020) using the package ALA4R (v1.8.0), and cleaned the records using R in five steps.

First, I verified the taxonomy for each record to species-level using the Australian Plant Census (APC) (CHAH 2018). The APC provides an updated list of accepted names for Australian plant species, which I paired with ALA species names. I removed hybrid taxa and records with no matching name and assigned subspecies their species level name. Second, I excluded records that were missing either the year of collection or the coordinates of the collection location, records with coordinates located outside mainland Australia, nearshore islands, and Tasmania, and records with a reported accuracy of >10 km. Third, I identified potential duplicate records, which I defined as records with matching species, year, and location (rounded to the nearest kilometre), and combined duplicates into a single record. Fourth, I assigned each species a status as either native or exotic to Australia using the APC. The APC assigns the status 'native' or 'naturalised' to records at the state and territory level. I considered any species identified as

'native' in at least one Australian state or territory to be a native species, and any species identified as 'naturalised' (exotic and having a self-sustaining, wild population; APC; Richardson et al. 2000; Randall et al. 2007) in all states or territories where it was recorded as exotic.

Finally, I assigned each species to either C3 or C4 photosynthetic pathway by genus using Watson et al. (1992 onwards) and Osborne et al. (2014), except for the genus *Panicum*, which was assigned at the species level using Osborne et al. (2014). Ten species in three genera (*Alloteropsis*, *Neurachne*, and *Steinchisma*) were identified as having intermediate C3-C4 photosynthetic pathways, and I excluded these from the study. Six species in the genus *Panicum* (*P. capillare, P. hillmanii, P. luzonense, P. racemosum, P. simile, and P. trichoides*) had no recorded pathway and were also removed. I recognised *Megathyrsus maximus* as a synonym for *Panicum maximum* and assigned it a photosynthetic pathway from Osborne et al. (2014).

After data cleaning, I retained a total of 1,012,181 records for 1,348 native and exotic *Poaceae* species in Australia (Table 2.1).

Table 2.1 The total number of native and exotic Poaceae herbarium records and species included in this study, and the number of records and species grouped by photosynthetic pathway (C3 or C4). The herbarium records were downloaded from the Atlas of Living Australia (Atlas of Living Australia 2020).

Photosynthetic pathway	Number of species			Number of records		
	Native	Exotic	Total	Native	Exotic	Total
C3	384	183	567	353,746	257,941	611,687
C4	628	151	779	330,726	69,768	400,494
Total	1,012	334	1,346	684,472	327,709	1,012,181

2.3.2 Estimating species richness

I estimated species richness for native and exotic C3 and C4 grasses in 1,157 100 × 100 km grid cells across Australia. I chose a 100 × 100 km cell size for this study to ensure sufficient records in enough cells to reliably estimate species richness whilst providing sufficient resolution to capture landscape-level variation in species richness (Table A.1).

I used a cut off value of 15 records in a cell as the minimum number needed to reliably calculate cell species richness (see below for the calculation method and justification of this choice). There were then large differences in the total number of herbarium records per grid cell among those cells with ≥15 records (range: 15 – 33,410, Table A.1). Spatially biased sampling in

herbarium collections is common because records are the result of unstructured sampling effort, resulting in some areas being more heavily sampled than others (Boakes et al. 2010). In Australia, cells covering urban centres or those with major roads tend to have more records than cells covering harder to access areas (Dodd et al. 2016; Daru et al. 2017). When estimating species richness from herbarium collections, it is important to account for differences in sampling effort because species richness increases as a function of collection effort, potentially confounding associations between species richness and other factors (Schmidt-Lebuhn et al. 2012).

I used a species richness estimator that accounts for sampling effort by standardising all cells to an equal sample coverage. Sample coverage is a measure of how completely a cell has been sampled, defined as "the proportion of the total number of individuals in a community that belong to the species represented in the sample" (Chao and Jost 2012). In practical terms, a sample coverage of 0.8 means that, if a new record is collected from a cell, there is an 80% chance the new record belongs to a species already collected from that cell and a 20% chance it belongs to a new species. Standardising all cells to an equal sample coverage ensures that species richness estimated at that sample coverage is standardised to account for differences in the numbers of records per cell.

Estimating species richness for each cell at the same sample coverage involves deriving a species-accumulation curve for each cell, estimating sample coverage along each curve, and then taking species richness estimates at the point for each curve where the record number provides the desired sample coverage (Chao and Jost 2012). If the number of records in a cell exceeds the desired sample coverage, the number of records is interpolated backwards along the species-accumulation curve until the desired sample coverage is reached. If there are too few records in a cell to meet the desired sample coverage, the number of records is extrapolated forwards along the species-accumulation curve until the desired sample coverage is reached.

Ideally, I would estimate species richness using a sample coverage of 1, meaning I would estimate the total species richness of each cell. However, extrapolating forward from relatively few records can result in large uncertainties in species richness estimates. Simulations show that species richness cannot be reliably estimated when extrapolating beyond two times the number of records in a cell (Chao et al. 2014), which would be the case for most cells if I chose a sample coverage of 1. In this situation, where there is high variability in sampling effort among cells, it is recommended to aim for a sample coverage of at least 0.7 (Chao and Lee

1992). I chose to estimate species richness at a sample coverage of 0.8, which is the coverage used in comparable studies (Soberón et al. 2007; Daru et al. 2017; Haque et al. 2017).

I estimated species richness in each grid cell to a sample coverage of 0.8 for native and exotic C3, C4 and total Poaceae species in R, using the function *EstimateD* in the *iNEXT* package (version 2.0.19) (Hsieh et al. 2016). I did not estimate richness for cells with fewer than 15 records due to the large uncertainties associated with extrapolating species richness from few records. I also excluded estimates of species richness when these required extrapolation beyond two times the number of records in a cell, again due to the large uncertainties in these estimates (Chao et al. 2014). Cells where species richness was not estimated were given a missing value.

I log-transformed and scaled species richness estimates prior to input into linear regression models. Species richness was log-transformed to fit linear associations with environmental and human activity variables and to ensure homogenous variance, and scaled between 0 and 1, with 1 being the maximum richness observed in a grid cell, to estimate potential exotic richness. (See the next sections for details.)

2.3.3 Environmental and human impact variables

I used multiple linear regression to examine the associations between environmental and human impact variables and the species richness of native and exotic C3 and C4 and total Poaceae species in grid cells across Australia. We initially chose 28 environmental variables, representing the major climatic gradients and landscape features hypothesised to explain large-scale variation in plant species richness, including temperature, water availability and topographic heterogeneity (Kreft and Jetz 2007; Jiménez et al. 2009; Stein et al. 2014) (for the full list of variables and their sources see Table S2.2). Patterns in exotic species richness may be driven by both propagule and habitat availability linked to human activities (Mack and D'Antonio 1998; Catford et al. 2011). As measure of human impact, I used the Human Influence Index, which is an single measure of human impacts derived from data on population, road and building density, and land use (Sanderson et al. 2002).

I aimed to obtain a value for each of the 28 variables in each of the 1,157 100 × 100 km cells across Australia using R (R version 4.0.0) (R Core Team 2020). Twenty-eight of the variables were available as spatial grids that had different scales, extents, and coordinate projections relative to the 100 × 100 km grid cells I used to estimate species richness (Table A.2). (Creation

of the twenty-ninth variable, topographic heterogeneity, is explained below.) I transformed the 28 variables to the same extent, coordinate projection and spatial scale using the following steps. I converted all variables to a 1 × 1 km grid size to assign them the same coordinate projection using the *SP* (version 1.4-2) (Pebesma and Bivand 2005) and *raster* (version 3.1-5) (Hijmans 2020) packages in R. The cells of 24 variables were already at this size and their original data values were retained. The cells of five variables were 25 × 25 km. For these variables, I converted the cell data to a 1 × 1 km grid cell size using the same data values as the original larger cells. From this common cell size, I cropped all 28 variables to the same extent using the Australian boundary from the *raster* package. I combined the remaining 1 × 1 km cell values to obtain a single average value for each 100 × 100 km cell: I used the mean of the 1 × 1 km cells for the 28 variables, and I used the standard deviation of elevation to create a measure of topographic heterogeneity at a 100 × 100 km cell resolution (Ruifrok et al. 2014).

Of the 1,157 100 × 100 km cells, fifty-three coastal and near offshore island cells were missing data for some variables and I excluded these cells from further analysis, meaning I had 1,104 cells to compare environmental and human impact variables against native and exotic C3, C4 and total species richness. Other coastal and island cells had partial land coverage. Because species richness scales positively with sample area (Palmer and White 1994), I accounted for the effect of land coverage on species richness by including proportion of land cover in a cell (0 – 1) as a covariate in the regression models. To compare parameter estimates in the regression models, I standardised all variables by subtracting the mean and dividing by the standard deviation.

Including multiple predictor variables in a model when these are highly correlated is problematic for multivariate linear regression. Strong covariation among predictor variables increases the variances around parameter estimates, leading to inaccurate interpretations of parameter estimate importance (Dormann et al. 2012). I addressed the issue of covariation among the 29 variables by creating a correlation matrix using Pearson's *r* and identifying highly correlated variables as those where the absolute value of *r* exceeded 0.7 (Dormann et al. 2012) (Table A.3; Figure A.1). I then identified a subset of variables where this threshold was violated as few times as possible but that nevertheless captured the different components of environmental variation hypothesised to explain large scale plant species richness (Table A.4; Figure A.2). From this variable selection process, I retained seven environmental variables

measuring temperature, precipitation, interactions between temperature and precipitation, landscape heterogeneity, and human impact (Table 2.2).

Table 2.2 Environmental, human impact variables and proportion cover and spatial autocorrelation covariates used as predictors in multiple linear regressions. The seven environmental variables capture gradients that have previously been shown to correlate with plant species richness at large spatial scales. The human impact variable is an amalgamation of different aspects of human modifications of the environment. The covariates account for spatial autocorrelation and for cells without full land coverage. See Methods for details.

Category	Name	Description	Source
Temperature	Annual mean temperature	Annual mean temperature	Fick and Hijmans (2017)
	Temperature seasonality	Temperature seasonality	Fick and Hijmans (2017)
Precipitation	Summer rainfall	Precipitation of the warmest quarter	Fick and Hijmans (2017)
	Winter rainfall	Precipitation of the coldest quarter	Fick and Hijmans (2017)
Temperature-precipitation interaction	Aridity	Ratio of the mean annual precipitation to mean annual potential evapotranspiration	Zomer et al. (2008)
Landscape features	Topographic heterogeneity	The standard deviation of 1 × 1 km cells values of elevation at 100 × 100 km	Fischer et al. (2008)
	Plant extractable soil-water	Water availability to plants based on soil texture, organic matter content and depth	Dunne et al. (2000)
Human impact	Human impact	Human influence index: extent by which the landscape has been modified by human activities, calculated as an index of data layers on road and human density, artificial lights, and land use	(Sanderson et al. 2002)
Covariates	Proportion cover	Proportion of the 1 × 1 km cells of each 100 × 100 km cell that included land cover	
	Spatial autocorrelation structure	One of four structures was included, exponential, gaussian, ratio, or spherical	

2.3.4 Model building

Spatial data, such as that derived from gridded cells, can be spatially autocorrelated meaning that cells closer together in space are more likely to have similar values than cells chosen at

random (Dormann et al. 2012). In statistical models, this can result in fewer independent observations than indicated by the total number of cells due to nearby cells contributing similar information to the analysis. Failing to account for this autocorrelation can lead to underestimates of the uncertainty associated with parameters estimated in the model, potentially inflating the importance of explanatory variables included in the analysis.

I identified and accounted for spatial autocorrelation in the statistical models using the following steps. First, I tested the species richness for native and exotic C3, C4 and total Poaceae species for spatial autocorrelation using the Moran's I test implemented in the function *Moran.I* from the package *ape* (version 5.3) (Paradis and Schliep 2018) and found significant spatial autocorrelation within all six species richness groups (Table A.5). Second, I accounted for spatial autocorrelation by constructing multiple linear regression models with native and exotic C3, C4 and total Poaceae species richness as the response variable and nine explanatory variables (seven environmental variables, one human impact variable and proportion of land cover) with a spatial autocorrelation term using generalised least squares (GLS) implemented in the function *gls* from the R package *nlme* (version 3.1-147) (Pinheiro et al. 2020). Spatial autocorrelation can be accounted for using different correlation structures. I had no *a priori* reason to select a particular structure for this data, so I tested four different correlation structures for each species richness model, selecting the correlation structure for each species model with smallest value of the small-sample version of Akaike's Information Criterion Index (AICc) using the *model.sel* function in the package *MuMIn* (version 1.43.17) (Barton 2020) (Table A.6). Finally, for each selected model, I calculated 95% confidence intervals for each parameter using the *intervals* function in the *nlme* package.

I assessed the fit of the models to the data by first calculating predicted richness for native and exotic C3, C4 and total Poaceae species from the models using the *predict* function in R. I then regressed predicted values against cells with observed richness, calculated the associated adjusted R^2 value and used this as a measure of model fit (Table A.7). I compared observed exotic richness in each cell to both predicted native and predicted exotic richness to assess how well the native template (predicted native richness, see below) could predict current exotic richness. If current exotic species richness is better predicted by a model describing the distribution of native species richness than by a model describing exotic richness, this would provide strong support for the native template.

2.3.5 Estimating exotic invasion potential

I used predicted native species richness derived from the models as the native template. I did this because it provided estimates of native species richness in all grid cells, including those that lacked sufficient herbarium records. Moreover, using predicted native species richness derived from associations with environmental and human impact variables should further assist in removing local variation in species richness arising from patchy sampling effort.

One issue with quantifying potential exotic species richness using native species richness is that the size of the native and exotic species pools differ (Table 2.1) and the exotic pool has the potential to increase if new grass species establish and spread in Australia. To allow for differences in the size of the native and exotic species pools, I compared native and exotic richness on a relative scale. For each combination of native, exotic C3, C4 and total species, I scaled log-transformed species richness estimates to between 0 and 1, with 1 being the maximum richness observed in a grid cell. If native and exotic richness were perfectly correlated then, regardless of the size of the two species pools, the grid cells with maximum relative richness should coincide. To estimate potential exotic richness in each grid cell, I used the difference in predicted native species richness (the native template) and observed exotic species richness (both on the relative scale), assuming that exotics could eventually disperse to those grid cells. A large positive value means a grid cell has lower exotic richness relative to native richness, implying there is potential for more exotic species to occupy that cell. I used this difference as a measure of invasion potential and, by mapping invasion potential, could identify areas where exotic species are currently under-represented and there is high invasion potential. When grid cells had higher exotic richness than predicted from relative native richness, I set the invasion potential to zero.

2.4 Results

2.4.1 Total Poaceae species

For Poaceae species in Australia, total native and exotic species richness was only weakly correlated (Spearman rank correlation r = 0.25, n = 425) and variation in native richness was not well explained by the environmental or human impact variables (adjusted $R^2 = 0.23$) (Figure A.3). These findings for native species richness reflect exotic richness patterns that are not linked to climatic gradients in scenario (d) in Figure 2.1. In this case, predicted native richness

is not expected to be a useful template for potential exotic richness (Figure A.3). I therefore focus on the results for C3 and C4 grass species richness to address the three aims of this study.

2.4.2 Where they overlap, is native and exotic grass species richness positively correlated?

Observed native C3 richness and observed exotic C3 richness were strongly positively correlated in cells with native and exotic richness estimates (Spearman rank correlation r = 0.69, n = 266) but the correlation was weaker between observed native C4 richness and observed exotic C4 richness (r = 0.40, n = 310, Figure 2.2ai, bi). The weaker correlation for C4 species appeared due to many cells where native C4 richness was much higher than exotic richness. This directional bias is expected if exotic species have not yet dispersed to cells they are environmentally suited to occupy, resulting in cells with high native but low or no exotic richness.

2.4.3 Is variation in native and exotic richness related to environmental and human impact variables in a similar way?

For both C3 and C4 species, native and exotic richness had similar associations with environmental variables and native richness had moderate amounts of variation explained by the environmental variables, with adjusted R^2 values from regressions of observed versus predicted richness of 0.58 and 0.60, respectively (Figure 2.2aii, bii). For native C3 species, richness was lower in areas with higher mean annual temperature, higher aridity, and less seasonal temperature variation, and higher in areas with greater human impact and topographic heterogeneity (Figure 2.2aii). Exotic C3 richness showed very similar patterns but was more strongly associated with higher winter rainfall, greater temperature seasonality and lower aridity (Figure 2.2aii). Both native and exotic C3 grasses had highest species richness in southern and eastern regions of Australia (Figure 2.2aiii, iv).

For native C4 species, richness was higher in areas with higher mean annual temperature, summer rainfall, topographic heterogeneity, and human impact, and lower in areas with greater aridity and higher winter rainfall (Figure 2.2bii). Exotic richness showed similar patterns but was less strongly associated with higher annual mean temperature, and more strongly associated with higher winter rainfall, topographic heterogeneity and human impact, and lower temperature seasonality (Figure 2.2bii). Native C4 species richness was highest in northern

Australia, corresponding to locations with high mean temperature and summer rainfall, whereas exotic C4 grasses had highest richness along the north-eastern coastline, which is characterised by high human impact and low temperature seasonality (Figure 2.2biii, iv).

2.4.4 Do the results of (i) and (ii) suggest higher invasion potential of Poaceae species in Australia than currently realised?

Where they co-occurred, native and exotic C3 richness and C4 richness had similar associations with environmental variables (Figure 2.2a, b panel ii) and native richness was positively correlated with exotic richness (Figure 2.2ai, bi). These outcomes imply native species richness should provide a useful template for predicting exotic richness.

For C3 species, the template approach indicated low invasion potential across most of Australia (Figure 2.2av). Species richness of native and exotic C3 grasses were quite strongly correlated, with species richness in both groups having similar geographical extents and similar spatial gradients (Figure 2.2ai), such that there were few areas with high scaled native richness that had correspondingly low exotic richness (Figure 2.2av). Those parts of Australia that currently have low exotic C3 richness, notably the central and northern regions, also have low native C3 richness, suggesting these areas are less environmentally suited to colonisation by C3 grasses.

In contrast, the native template indicated moderate to high exotic C4 invasion potential across much of northern Australia (Figure 2.2bv). Native and exotic C4 richness were positively correlated and species richness of native and exotic C4 grasses showed similar north-south spatial gradients (2bi, iii, iv). However, native and exotic C4 richness had markedly different geographic extents, with many areas of moderate-to-high native C4 richness having low exotic C4 richness. Thus, there appears to be large areas of northern Australia that are environmentally suitable for C4 grasses where exotic C4 species are absent or are in low numbers, meaning that there are many areas that have the potential to support much higher numbers of C4 grasses (Figure 2.2bv).

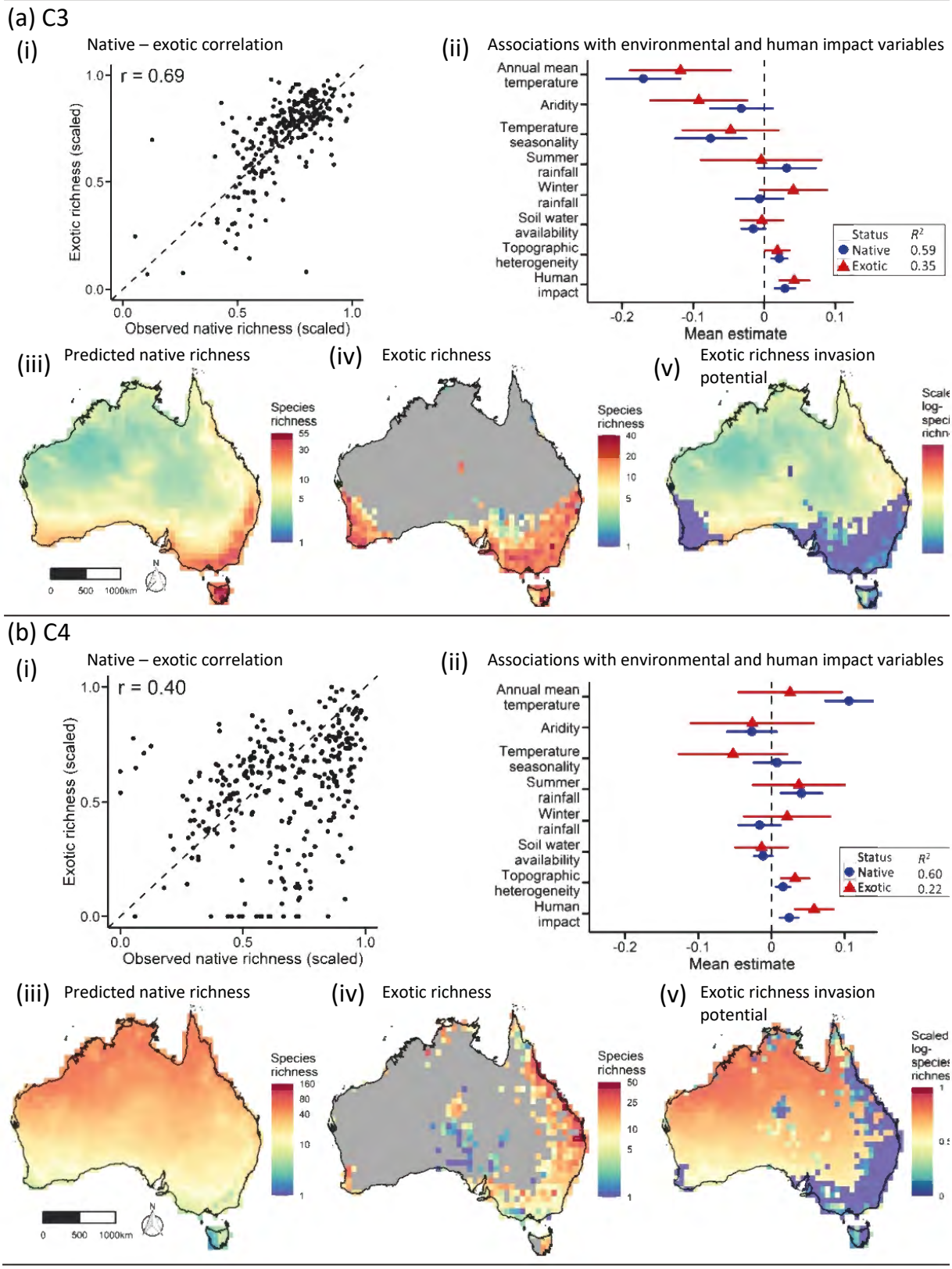

Figure 2.2 Native C3 and C4 Poaceae species richness as a template for exotic C3 and C4 Poaceae species richness at large spatial scales across Australia. Panel (a) C3 Poaceae species richness, (b) C4 Poaceae species richness. (i) Observed native richness (x axis) and observed exotic richness (y axis) scaled to between zero and one. Each point represents a 100 × 100 km gridded cell across Australia with both a both a native and exotic richness estimate. (ii) Mean

estimates of native (blue) and exotic (red) log-transformed and scaled species richness compared to seven environmental variables and a single human impact variable using multiple linear regression. Error bars represent 95% confidence intervals of the mean, which are significant ($P < 0.05$) if they exclude zero (vertical dashed line). The explanatory variables were scaled prior to modelling to compare estimate values. The mean estimates of two variables (proportion of land cover and a spatial autocorrelation term) were excluded from plots. (iii) Native species richness predicted across all areas of Australia using mean estimates from (ii). Note that species richness was modelled in log-transformed and scaled units but is displayed in raw species richness to indicate the large difference in the number of species represented by cells with hot colours (red-orange) and cool colours (blue-yellow). (iv) Exotic species richness observed across Australia. Grey zones contain cells that did not meet criteria to estimate species richness and were not analysed. (v) Exotic invasion potential across all areas of Australia, calculated for each cell as the difference between scaled and log-transformed predicted native richness and scaled and log-transformed observed exotic richness. Negative invasion potential values were set to zero. Maps were projected in the Australian Albers equal area projection.

2.5 Discussion

2.5.1 Exotic C3 and C4 invasion potential across Australian

I showed that native species richness provides a useful template for forecasting exotic species richness at a landscape scale using 100 × 100 km grid cells across Australia for C3 and C4 grass (Poaceae) species. The template worked because, where they overlapped at this scale, the richness of native and exotic grass species in both groups (C3 and C4) were positively correlated, meaning areas with high native richness tended to have high exotic richness. This positive correlation appeared to due to native and exotic species richness in both groups having broadly similar associations with environmental variables, implying that environmental conditions that favoured high native richness also favoured high exotic richness. I could then identify areas that appeared most vulnerable to invasion by greater numbers of exotic species as locations with the greatest relative difference between native and exotic richness.

For C3 grasses, native and exotic richness was strongly correlated in cells with sufficient records to estimate exotic richness (Figure 2.2ai). Moreover, cells with too few records to estimate exotic C3 richness were cells where native C3 richness was generally low (Figure 2.2aiii, iv). Together, these results suggest that over much of Australia where native C3 grass richness is low there is little potential for exotic C3 grasses to invade because conditions at these sites appear relatively unsuitable for C3 grasses (Figure 2.2v). In contrast, there were many cells with high native C4 richness but low exotic C4 richness (Figure 2.2bi), and many

cells with high native C4 richness where there were too few records to estimate exotic C4 richness (Figure 2.2biii-iv). This implies there is high invasion potential for exotic C4 grasses across large areas of Australia: there are many cells with environmental conditions suited to high C4 richness that currently have relatively low exotic C4 richness (Figure 2.2bv).

Exotic C3 invasion potential could be generally low across much of Australia because C3 grasses are better suited to cool, temperate environments, likely reflecting physiological constraints with C3 photosynthesis (Bremond et al., 2012; Liu et al., 2009). Regions with high C3 richness are also those subject to more intense human disturbance through urban and agricultural development (Hodgkin and Hamilton 1993; Dorrough et al. 2004; Johnson et al. 2007; Hogan and Phillips 2011). The abundance of exotic C3 grasses in these areas may partly reflect the widespread use of C3 grasses as pasture species in cool temperate regions (Cook and Dias 2006), contributing to their spread across the landscape such that they now occupy most regions suitable for establishment.

Exotic C4 grasses are mostly restricted to southern and eastern coastal regions (Figure 2.2biv). The reduced distribution of exotic C4 grasses compared to native C4 grasses may reflect the coincidence of environments suited to C4 grasses and areas of more intensive human impact and agricultural development that are in higher rainfall and cooler regions along the east coast (Lonsdale, 1994; van Klinken et al., 2015). These results suggest that given the opportunity to spread outside of areas with high human impacts, there are large regions of northern Australia that could support higher exotic C4 grass richness. In California grasslands, for example, exotic grasses are strongly associated with human activities, but also appear to be spreading into environmentally suitable habitats ahead of human habitat modification (Seabloom et al. 2006). Proposals to develop parts of northern Australian more intensively for agriculture may open up these areas to widespread introduction and further invasion by new C4 grasses (Preece et al. 2010).

It is important to recognise that cells classed as having low invasion potential because they had both high native and high exotic richness could still be prone to further invasion. The native richness template method used scaled richness to identify areas of relatively high and low native and exotic richness, allowing for differences in the size of the species pools. The large spatial scale used in this study does not reflect what happens as local scales where invasion plays out. The total exotic species pool could increase further in size if new exotic species establish and spread (Dodd et al. 2015). In these circumstances, I would predict that newly established exotic

grass species would be more likely to occupy cells most suited to C3 and C4 grasses, i.e. those that have higher native C3 and C4 grass species richness.

2.5.2 Native richness template general use and recommendations

I have demonstrated for Australian grasses that native species richness can provide a useful template for predicting the richness and invasion potential of exotic species, suggesting it could be usefully applied to other regions and plant groups. For the template to be generally useful, I identified two features that need to hold: (i) where they co-occur native and exotic species richness should be positively correlated, and (ii) both native and exotic species richness should respond in similar ways to the same environmental gradients.

The major limitation for applying the native richness template elsewhere is that the method requires data for estimating native and exotic species richness, which may limit its application to regions where there has been extensive and widespread herbarium or plot-based data collection. Online repositories of species occurrence records are increasingly useful sources of biodiversity information (Lavoie 2013) but records are biased toward wealthy regions (Meyer et al. 2016; Ladouceur et al. 2019). This reduces the feasibility of applying the native template method to test (i) and (ii) in areas with high biodiversity but that are currently under-sampled, such as tropical regions (Engemann et al., 2015; Myers et al., 2000).

Even if data are available, the template method relies on the accumulation of all native species to respond to environmental gradients in a similar way to all current exotic species, such that there is a positive correlation between native and exotic richness. There are reasons why this might not hold. For example, if exotic species distributions are primarily associated with human activities that modify the landscape (Gallardo et al., 2015; Peng et al., 2019) then areas of high native richness may not necessarily coincide with high exotic richness. Further, the method worked for C3 and C4 grasses but not for total grass richness. This was most likely because grass species differ in their distributions along environmental gradients (Liu et al., 2009). Hence, the method relies on identifying groups of species that are likely to respond in similar ways along environmental gradients, which may limit its application.

If the native richness template is broadly applicable, there is potential to use this approach in conjunction with established SDM methods. I showed that the native richness template could identify areas vulnerable to further grass invasion at a large scale (100 × 100 km). The choice

of this scale was driven by data availability – at finer scales there were often too few records per cell to reliably estimate species richness. However, this taxonomic and spatial scale may be too large to inform targeted monitoring and control efforts within high-exotic richness regions. Hence, the native richness template could be used to identify areas at a broad scale where exotic species are likely to establish in the greatest numbers. Within these areas, individual SDMs could be used to forecast the distribution of potentially problematic exotic species, and multiple SDMs could be stacked to produce species richness maps at finer scales to inform monitoring and control of potential new invaders in susceptible regions.

2.5.3 Conclusion

I show that native richness can provide a template to forecast the potential distribution of exotic species at a broad-scale across the Australian landscape. I show that exotic C4 grasses have the potential to occur at higher richness in grid cells across the northern and central western regions of Australia, implying that many more species may be capable of spreading into this region. The utility of this approach could be tested for plant groups in other regions of the world. Where suitable, I recommend the method could be used in conjunction with established SDM models to aid in forecasting the potential spread of exotic species and for targeting monitoring and control efforts.

Chapter 3 – When to use native species richness as a template for the invasion potential of exotic species

3.1 Abstract

In Chapter 2, I showed that native species richness could be used as a template to forecast potential exotic species richness for C3 and C4 grass species in Australia. Here, I aim to determine if the native richness template can forecast the potential distributions of exotic species of plant families more generally, and to determine when it could be used for other plant groups and in other locations. I do this by testing the framework developed in Chapter 2 on 22 common plant families (including Poaceae grouped into C3 and C4 species) across Australia.

I estimated native and exotic species richness for each of the 22 plant families in 1,156 100 × 100 km grid cells across Australia using 4,611,321 herbarium records. For each family, I determined (i) whether native and exotic species richness were positively correlated, and (ii) if native and exotic richness had similar associations with six environmental variables and one human impact variable. The modelled associations were used to predict native richness across Australia. If (i) and (ii) were supported, this implied that areas with high native richness and low exotic richness could support higher exotic richness, calculated as the difference between scaled native and exotic species richness. I also determined whether family-level factors explained why (i) and/or (ii) were not supported.

Six of the 22 families met the conditions for both (i) and (ii). For these six families, exotic invasion potential tended to be greatest in northern Australia. Families that failed to meet the requirements generally had weak native-exotic correlations, with exotic richness greatest in areas highly impacted by human activities that had low native richness, and/or idiosyncratic patterns of native richness that were not linked to gradients in measured environmental variables. These results suggest that exotic dispersal limitations and probable effects from biogeographic factors (isolation and historical climatic processes) likely limit support for the native richness template for other plant groups and in other locations.

3.2 Introduction

A central goal in invasion ecology is to predict which parts of the landscape are most vulnerable to invaders (Dodd et al. 2016). This task has proven difficult and relatively few consistent predictors of invasion vulnerability have emerged (Kolar and Lodge 2001; Williamson 2006; Lockwood et al. 2009; Catford et al. 2011). However one pattern that has emerged and is of particular concern is that areas with the greatest numbers of native species appear to be invaded by the greatest numbers of exotic species (Levine 2000; Stohlgren et al. 2003). Numerous studies across the globe have found that, at broad spatial scales, the number of exotic plant species found in an area (exotic species richness) is positively correlated with native species richness (Stadler et al. 2000; Deutschewitz et al. 2003; Kuhn and Klotz 2003; Chown et al. 2005; Thuiller et al. 2005; Stohlgren et al. 2008; Seabloom et al. 2006; Stark et al. 2006; Stohlgren et al. 2006; Hulme 2008; Ricotta et al. 2010; Bartomeus et al. 2012). The impact of exotic species is linked to their richness and abundance (Vilà et al. 2011), meaning areas that supports the most native species may also be those areas that are subject to the greatest impacts from exotic species.

Native and exotic species richness may be positively correlated because they respond in a similar way to resource availability (Stohlgren et al. 1999; Byers and Noonburg 2003), climatic variation (Levine and D'Antonio 1999; Ouyang et al. 2019), or environmental heterogeneity (Davies et al. 2005; Brooks et al. 2013). However, positively correlated native and exotic richness also suggests that native species richness could provide a template for potential exotic species richness in areas exotic species have not yet spread to and impacted (Stohlgren et al. 2003; Seabloom et al. 2006; Fridley and Sax 2014).

In Chapter 2, I demonstrated that native species richness could provide a template for the potential distribution of exotic species richness across large scale areas of Australia using two groups of native and exotic species within the grass (Poaceae) family: species with C3 and C4 photosynthetic pathways. Native C3 and C4 grasses have distinct species richness patterns along temperature and rainfall gradients (Hattersley 1983; Liu et al. 2009; Bocksberger et al. 2016). Within C3 and C4 Poaceae groups, I showed that, where native and exotic species co-occurred, areas with high native richness also tended to support high exotic richness, and native and exotic species richness had similar associations with environmental variables. This implied that areas with proportionately

high native richness but low exotic richness should have the environmental suitability to support greater numbers of exotic species.

The native richness template provides a method for estimating potential exotic richness, meaning that it could be applied to other plant groups and in other locations. This Chapter determines the bounds for using the native richness template for other plant groups and in other locations in two ways. First, to determine how often the native template forecasts potential exotic species richness for common native and exotic plant families; and second, to identify family-level characteristics that might explain why exotic species richness maps closely to native species richness for some families but not others.

At large spatial scales, terrestrial angiosperm species richness is strongly associated with variation in climatic variables and topographic heterogeneity (Francis and Currie 2003; Hawkins et al. 2003; Field et al. 2009; Huang et al. 2021). Yet, I expect the native richness template to work better by comparing related native and exotic species at finer taxonomic resolutions. More closely related species tend to have more similar distributions because they have similar physiological tolerances to environmental conditions (Crisp et al. 2009; Burns and Strauss 2012). Comparing native and exotic species at a genus level would be ideal because native and exotic congeners would be expected to share similar traits and thus species richness patterns. For example, Ricklefs and Latham (1992) showed that many plant genera in temperate regions in Asia had similar geographic range sizes as the same genera in Northern America, attributing this to similar physiological limits on respective distributions. However, areas often lack the data to estimate species richness to a reasonable accuracy (Schmidt-Lebuhn et al. 2012; Engemann et al. 2015), which is exacerbated if we consider lower taxonomic levels, such as richness at the sub-family or genus level (Meyer et al. 2016; Daru et al. 2017). Therefore, I test whether the native richness template works at the family level and at large spatial scales to balance the available data with the expected similarity between related native and exotic species.

For 22 common native and exotic plant families in Australia, I test whether native richness is a useful template for forecasting potential exotic richness, which requires two criteria to be met (developed in Chapter 2): (i) in areas where native and exotic species co-occur, native and exotic richness should be positively correlated, and this positive correlation should arise when (ii) native and exotic richness have similar associations with environmental variables (Figure

3.1 panel A). Families that meet (i) and (ii) implies that exotic species richness patterns are following native species richness patterns, because native and exotic species have similar tolerances to environmental conditions. Thus, areas with proportionately low exotic richness but higher native richness should have environmental conditions suitable for supporting greater numbers of exotic species (Chapter 2).

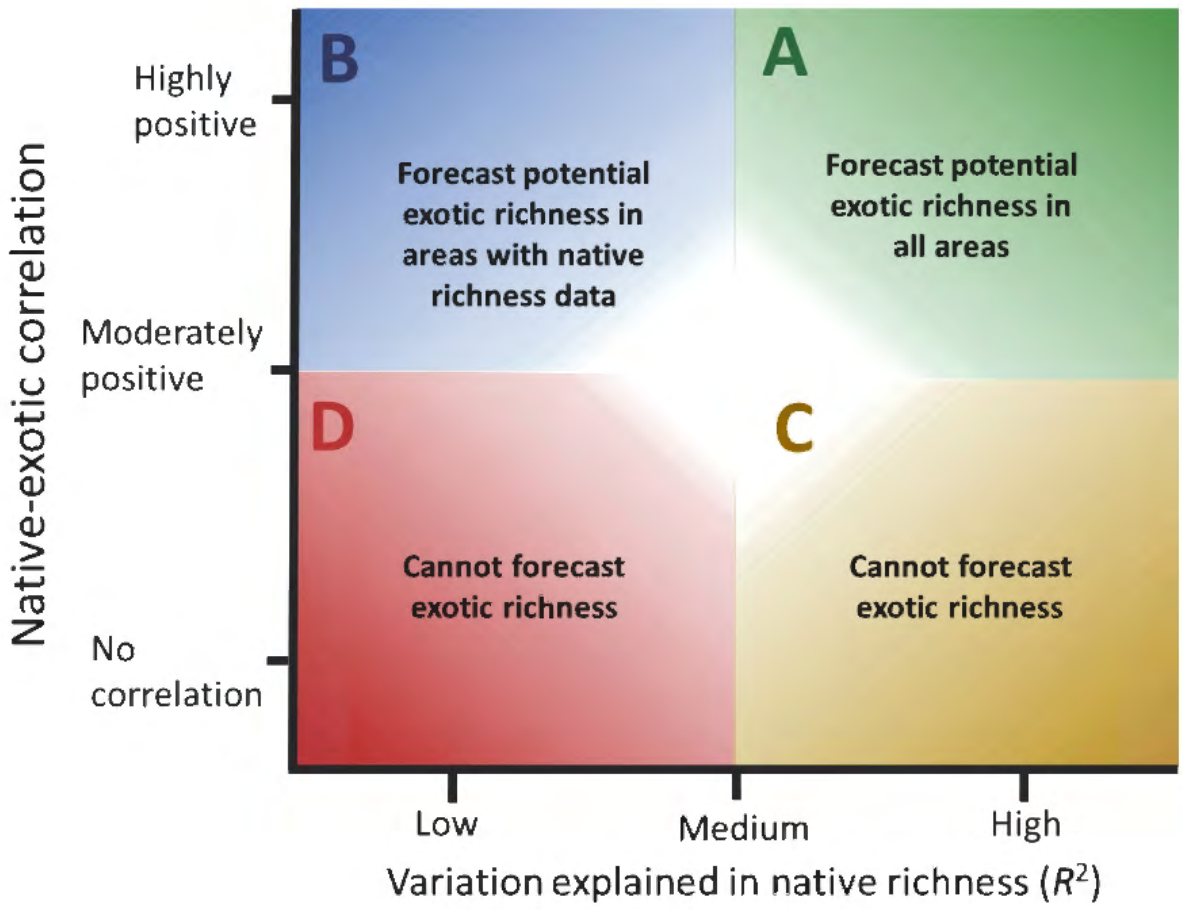

Figure 3.1. Conceptual framework for identifying when the native richness template is expected to be a useful template to forecast potential exotic species richness. X-axis: the amount of variation in family native species richness explained by associations with environmental and human impact variables (R^2). Y-axis: the correlation between native and exotic richness in areas they co-occur. Panel A: moderate-to-high amount of variation in native richness explained by gradients in environmental and human impact variables and moderate-to-strongly positive native-exotic correlation. Predicted native species richness across all areas of the landscape using native richness-environment relationships may be a template for potential exotic richness. Panel B: a low-to-moderate amount of variation in native richness explained by gradients in environmental and human impact variables and a moderately-to-strongly positive native-exotic correlation. Observed native species richness may be a template for potential exotic richness across areas of the landscape with native data. Panel C: a moderate-to-high amount of variation in native richness is explained by gradients in environmental and human impact variables and

a weakly positive or no native-exotic correlation. Predicted native richness may not be a useful template for potential exotic richness across all areas of the landscape. Panel D: a low-to-moderate amount of variation in native richness explained by gradients in environmental and human impact variables and a weakly positive or no native-exotic correlation. Observed native richness would not be a useful template for potential exotic richness across any areas of the landscape.

There are situations when the native richness template is expected to be partially or not at all useful for forecasting potential exotic species richness (Figure 3.1 panels B, C, D). Native and exotic richness could be strongly positively correlated but native and exotic richness patterns could be poorly explained by environmental variables (Figure 3.1 panel B). In this situation, the use of the native richness template may be limited because native richness cannot be reliably predicted across the landscape and hence we cannot reliably calculate exotic invasion potential from predicted patterns of native richness, using the native richness-environment relationships. This situation could arise if native species richness patterns are strong associated with unmeasured variables (Araújo and Luoto 2007; Wisz et al. 2013), there are complex interactions between climatic variables that are difficult to estimate (Francis and Currie 2003; Kreft and Jetz 2007), or native richness is not strongly associated with environmental gradients. For example, in Chapter 2 I found that total native and exotic Poaceae species richness was positively correlated but richness patterns were weakly associated with environmental variables. This was because species with C3 and C4 photosynthetic pathways have strong but opposing associations with mean annual temperature and rainfall patterns, such that total Poaceae species richness was not strongly associated with climate gradients across Australia. In situations where native and exotic richness are strongly positively correlated but not strongly associated with environmental gradients, native species richness may provide a template for potential exotic richness in areas with current native richness data (Figure 3.1 panel B).

The native template is not expected to work when native and exotic richness are weakly correlated (Figure 3.1 panels C, D). This could occur when native and exotic species respond differently to environmental factors. For example, native species could be dispersal-limited or excluded from suitable areas because of historical dispersal barriers, meaning richness patterns are somewhat independent of climatic gradients (Albert et al. 2017). Similarly, exotic species richness patterns could be influenced by different large-scale factors compared to native species. Human activities can alter conditions so they are more suitable for exotic species than native species (Catford et al. 2011; Tomasetto et al. 2013; Dainese et al. 2014). For example, exotic species assemblages can be compromised of species that are adapted to disturbed and

nutrient-rich conditions, whereas native species assemblages have wider tolerances to local environmental conditions, and thus native and exotic species have distinct species richness patterns across areas where they co-occur (Pouteau et al. 2015). Data limits could also confound observing a strongly positive native-exotic correlation. Native species may occur predominantly in areas that are hard to access, meaning they are poorly sampled (e.g. Schmidt-Lebuhn et al. 2012), or exotic species may not have spread into a representative range of their potential distributions from introduction sites (Boakes et al. 2010).

I investigated support for criteria (i) and (ii) and whether there are family-level characteristics which may explain why (i) and (ii) are not supported using 4,611,321 verified plant species for 22 plant families across Australia. The 22 families includes the Poaceae family grouped C3 and C4 photosynthetic pathways (Table 3.1). I test native and exotic species richness within each of the 22 families against six environmental variables hypothesised to strongly determine differences in plant species richness at large spatial scales (Kreft and Jetz 2007; Jiménez et al. 2009; Huang et al. 2021) and that have been previously found to be strongly associated with C3 and C4 grass species richness in Australia (Chapter 2), along with one human impact variable, which indexes human activities, disturbances, and land use change. With these data I ask the following questions:

(i) Does the native richness template work consistently for common native and exotic plant families?
(ii) Are there are family-level biogeographical or physiological characteristics that might affect the associations between native and exotic richness and environmental variables?
(iii) Does a strong association with human impact confound a positive correlation between native and exotic richness in some families?

3.3 Methods

All analyses were conducted in R (v4.0.2) (R Core Team 2020), using the packages ALA4R (v1.8.0), *raster* (version 3.1-5) (Hijmans 2020), *SP* (version 1.4-2) (Pebesma and Bivand 2005), *iNEXT* (version 2.0.19, Hsieh et al. 2016), *ape* (version 5.3) (Paradis and Schliep 2018), *nlme* (version 3.1-147) (Pinheiro et al. 2020), and *MuMIn* (version 1.43.17) (Barton 2020).

3.3.1 Species occurrence data

I downloaded all higher terrestrial plant records from the Atlas of Living Australia (ALA). The ALA is a database of vouchered herbarium specimens from Australia's major herbaria and well as a collection of verified records form citizen science initiatives (Atlas of Living Australia 2020). This data set had a total of 19,650,629 records for 656 plant families and can be accessed via https://biocache.ala.org.au/biocache-download/9353dd2f-aab4-3793-a82a-888e85a40d01/1578616694494/data.zip, which I downloaded January 10, 2020.

I filtered all records so they were fit for purpose by assessing their spatial, temporal, and taxonomic accuracy through several cleaning steps. First, I verified record spatial and temporal accuracy by removing records with missing, inaccurate (≤ 0 m), or large (> 10,000 m) location uncertainties, and records missing a collection year or when year of collection was zero. I removed records that were located outside of mainland Australia, Tasmania and nearshore islands using the *raster* package's *getData* function. Next, I used the Australian Plant Census (Australian Plant Census (APC) 2018) to check if records had accepted species-level taxonomy and to assign 'native' or 'exotic' origin. The APC is an updated list of accepted taxonomy and origin of Australia's plants. If ALA species records did not have a matching APC name they were discarded. The APC determines the origin of species by state and territory using 'native' and 'naturalised' tags. Native species can be identified 'naturalised' in states or territories outside of what is considered their native range, so I categorised native species as species in the ALA record list tagged in the APC as 'native' in at least one state or territory of Australia, and I defined exotic species as species solely tagged as 'naturalised.' Species with a different or no origin were excluded. I then set records identified to subspecies to relevant species-level rank, such that I was left with just native and exotic ranked species. Records that shared the same species, year, and had the same latitude and longitude rounded to the nearest 2 decimal places (~1km) were considered potential duplicates and combined into a single record.

3.3.2 Assigning C3 and C4 photosynthetic pathway to Poaceae

I assigned each Poaceae species a C3 or C4 photosynthetic pathway by genus using Watson et al. (1992 onwards) and Osborne et al. (2014), except for the genus *Panicum* which was assigned at the species level using Osborne et al. (2014). This process excluded eighteen species across five genera. *Alloteropsis* and *Steinchisma* were removed because they are labelled with 'intermediate' C3-C4 pathways and the genus *Cynochloris* and six species in the genus

Panicum (*P. capillare*, *P. hillmanii, P. luzonense, P. racemosum, P. simile, and P. trichoides*) had no recorded pathway and were also removed. I recognised *Megathyrsus maximus* as a synonym for *Panicum maximum* and assigned it a photosynthetic pathway from Osborne et al. (2014).

3.3.3 Family selection

Following record cleaning, I retained 8,563,459 records for 360 families (including Poaceae split into C3 and C4 pathways) containing 19,264 native and 2,755 exotic species. From these 360 families, I identified those with enough native and exotic records and species to compare species richness patterns and to model richness in relation to environmental and human impact variables across the Australian landscape. To do this, I excluded families that had fewer than 50 native and 20 exotic species and fewer than 20,000 native records. This left me with 4,611,321 records for 8,871 native and 1,634 exotic species across 22 families (including the C3 and C4 Poaceae species) (Table 3.1). There are complex phylogenetic relationships between two families, Chenopodiaceae and Amaranthaceae (Kadereit et al. 2003), with Chenopodiaceae now recognised as a subfamily within Amaranthaceae (The Angiosperm Phylogeny Group 1998). For consistency with APC's taxonomic treatment of these taxa, I treat them as separate families. For each family, I determined the total number of worldwide genera, species and proportion of C4 species using Christenhusz and Byng (2016), except for C4 Poaceae and Chenopodiaceae which I used Sage (2016) and Hernández-Ledesma et al. (2015), respectively (Table 3.1).

3.3.4 Estimating native and exotic family species richness

I estimated native and exotic species richness for each of the 22 families in 1,156 100 × 100 km gridded cells across Australia. I corrected for differences in sampling intensity by estimating species richness to a universal sample coverage using the *iNEXT* package's *estimateD* function. Sample coverage is a measure of how well a community has been sampled, defined as "the proportion of the total number of individuals in a community that belong to the species represented in the sample" (Chao and Jost, 2014). I estimated species richness to a sample coverage of 0.8. I excluded cells with fewer than fifteen records and estimates of species richness when these required extrapolation beyond two times the number of records in a cell due to the large uncertainties in these estimates (Chao et al. 2014). Cells where species richness was not estimated were given a missing value.

I log-transformed and scaled species richness estimates prior to input into linear regression models. Species richness was log-transformed to fit linear associations with environmental and human activity variables and to ensure that there was homogenous variance.

3.3.5 Environmental and human impact variables

I compared native and exotic species richness of the 22 plant families to six environmental variables and one human impact variable (Table 3.3). The six environmental variables represent the major climatic gradients and landscape features hypothesised to explain large-scale variation in plant species richness, including mean annual temperature and seasonal variability, water availability and topographic heterogeneity (Kreft and Jetz 2007; Stein et al. 2014; Huang et al. 2021). For a single measure of human impact, I used the Human Influence Index, which is a composite of data layers on population, road, and building density and land use (Sanderson et al. 2002).

I applied the following steps to obtain a single value in each of the 100 × 100 grid cells for the seven variables. Six of the seven variables had 1 × 1 km grid cell resolutions and different coordinate projections and global extents; the seventh variable, topographic heterogeneity, was created from another variable at the final stage of preparation (see below for details). First, I transformed the six variables to the same coordinate projection as the species richness estimates, and cropped the variables to an Australia boarder, using the *raster package*. Second, I transformed the 1 × 1 km resolution of each variable to 100 × 100 km by combining the 1 × 1 km cell values to a single 100 × 100 km value. For six variables, I used the mean of the 1 × 1 km cells to generate each 100 × 100 km cell and I used the standard deviation of elevation to create a measure of topographic heterogeneity (Ruifrok et al. 2014). This provided me with 1,156 100 × 100 km grid cells with data for all seven variables across Australia.

Coastal and island cells had only partial land cover and species richness positively scales with sample area (Palmer and White 1994) so I included proportion of land cover (0 – 1) for each cell as a covariate. To compare the size of parameter estimates within each linear regression model (see section below), I standardised all variables by subtracting the mean and dividing by the standard deviation.

Table 3.1 Environmental, human impact variables and proportion cover and spatial autocorrelation covariates used as predictors in multivariate linear regressions. The six environmental variables capture gradients that have previously been shown to correlate with

plant species richness at large spatial scales. The human impact variable is an amalgamation of different aspects of human modifications of the environment. The covariates account for spatial autocorrelation and for cells without full land coverage.

Category	Name	Description	Source
Temperature	Annual mean temperature	Annual mean temperature	Fick and Hijmans (2017)
	Temperature seasonality	Temperature seasonality	Fick and Hijmans (2017)
Precipitation	Summer rainfall	Precipitation of the warmest quarter	Fick and Hijmans (2017)
	Winter rainfall	Precipitation of the coldest quarter	Fick and Hijmans (2017)
Temperature-precipitation interaction	Aridity	Aridity index: ratio of the mean annual precipitation to mean annual potential evapotranspiration	Zomer et al. (2008)
Landscape features	Topographic heterogeneity	The standard deviation of 1 × 1 km cells values of elevation at 100 × 100 km	Fischer et al. (2008)
Human impact	Human impact	Human influence index: extent by which the landscape has been modified by human activities, calculated as an index of data layers on road and human density, artificial lights and land use	Sanderson et al. (2002)
Covariates	Land cover	Proportion of the 1 × 1 km cells of each 100 × 100 km cell that included land cover	
	Spatial autocorrelation structure	One of four spatial structures was included, exponential, gaussian, ratio, or spherical	

Table 3.2 The number of native and exotic family records and species selected for inclusion in this study, with Poaceae grouped by photosynthetic pathway (C3 or C4). Australian species and record data taken from the Atlas of Living Australia (https://biocache.ALA.org.au/), worldwide data were taken from Christenhusz and Byng (2016), Sage (2016), and Hernández-Ledesma et al. (2015).

Family	Australian species			Australian records			Worldwide taxa	
	Native	Exotic	Total	Native	Exotic	Total	Species	C4 species
Amaranthaceae	159	29	188	41,597	5,113	46,710	2,040	257
Apiaceae	106	31	137	63,411	8,606	72,017	3,575	0
Apocynaceae	162	21	183	43,289	9,325	52,614	5,100	0
Asparagaceae	159	38	197	180,199	16,314	196,513	2,900	0
Asteraceae	986	270	1,256	512,119	246,570	758,689	24,700	0
Boraginaceae	125	36	161	23,445	25,779	49,224	2,535	130
Brassicaceae	104	82	186	20,559	45,352	65,911	3,628	0
Chenopodiaceae	296	24	320	234,545	5,664	240,209	1,600	558
Convolvulaceae	99	28	127	55,849	4,185	60,034	1,660	0
Cyperaceae	641	56	697	278,563	10,080	288,643	5,500	0
Ericaceae	436	28	464	193,521	2,582	196,103	4,250	0
Euphorbiaceae	239	46	285	48,075	7,595	55,670	6,252	350
Fabaceae	2,466	290	2,756	791,447	96,930	888,377	19,500	0
Juncaceae	61	27	88	69,234	9,896	79,130	464	0
Lamiaceae	425	74	499	68,825	28,685	97,510	7,530	0
Malvaceae	537	43	580	91,658	10,710	102,368	4,225	0
Plantaginaceae	86	45	131	53,224	33,129	86,353	1,900	0
Poaceae C3	386	183	569	364,428	264,209	628,637	6,956	NA
Poaceae C4	629	150	779	305,959	72,110	378,069	5,044	5,044
Rubiaceae	315	32	347	102,633	11,157	113,790	13,620	0
Scrophulariaceae	250	24	274	62,719	5,247	67,966	1,830	4
Solanaceae	204	77	281	48,685	38,099	86,784	2,600	0
Grand total	8,871	1,634	10,505	3,653,984	957,337	4,611,321	125,809	7,943

3.3.6 Model building

I used multiple linear regression to examine the associations between eight variables (six environmental variables, one human impact variable, and proportion of land cover; Table 3.2) and species richness of each of the 44 groups of families (i.e. 22 native and 22 exotic groups). The gridded structure of the 100 × 100 km cells can violate the assumption of independence for linear regression. In my case, neighbouring cells could have environmental values that are more similar to one another than expected from randomly selecting cells from the total pool, which is assumed by the model. If so, the effective cell sample size is smaller than what independent information is provided by each cell. Unchecked, such spatial autocorrelation can conflate the degree of certainty around parameter estimates (Dormann et al. 2012).

I accounted for the possibility of spatially autocorrelated residuals in the statistical models (i.e. species richness as the response variable and eight explanatory variables) using the following steps. Before I constructed the models, I first tested species richness of the 44 native and exotic family groups for spatial autocorrelation using Moran's I test, using the ape package's *Moran.I* function. I found significant spatial autocorrelation within all 22 native family groups and 19 of the 22 exotic groups (Table B.1). I accounted for spatial autocorrelation for each of the affected family groups by adding a spatial autocorrelation term into their respective models. I tested four different autocorrelation structure terms for each group using generalised least squares (GLS), using the function *gls* from the package *nlme*. I selected a single correlation structure for each model that had the smallest AICc value, using the *MuMIn* package's *model.sel* function (Table B.2). For each of the 22 native and 19 exotic family models, I calculated 95% confidence intervals for each term using the *intervals* function from the *nlme* package. For the other three exotic families, I constructed linear regression models with species richness as the response variable and eight explanatory variables, calculating the mean effect size of each term and their confidence intervals using the *lm* and *confint* functions from base R.

I allowed for the possibility of non-linear associations between species richness and the six environmental variables and single human impact variable by adding quadratic terms for these variables into each of the 22 native family models. I retained the same spatial autocorrelation structure as the native family models with solely linear terms. As previously, I calculated 95% confidence intervals for each term in the GLS models using the *intervals* function in the *nlme* package. Adding variables into models increases the amount of variation explained but can lead

to overfitting the model to the data, which is an issue when using the model predict values using new data (Ginzburg and Jensen 2004). Therefore, for each of the 22 native family models, I removed non-significant quadratic terms (i.e. 95% confidence intervals that included zero) but retained all linear terms.

For each native family, I selected between the model with quadratic terms and the model with solely linear terms using a AICc threshold. Typically, models that have AICc values that are within 4 have similar fit to the data for their complexities, but differences in AICc values greater than 10 strongly suggests that the model with the lower AICc value is better fit to the data for its complexity (Burnham and Anderson 2004). For each native family, I selected the model with quadratic terms only if its AICc value was ≤ 10 compared the model with solely linear terms. Six of the 22 native families met these conditions and were modelled with quadratic terms (Table B.3).

I modelled exotic family richness using the same set of environmental and human impact variables as respective native family richness but retained the original exotic spatial autocorrelation structure if required. For the exotic family GLS models, I calculated 95% confidence intervals for each term using the *intervals* function in the *nlme* package. For the exotic family models without spatial autocorrelation structures, I used *lm* and *confint* functions from base R to estimate the mean effect sizes of each term and their confidence intervals.

Finally, I assessed model fit for the 44 selected native and exotic family models by predicting species richness across Australia from the models using the *predict* function. I then compared predicted richness to observed richness in all cells with estimated species richness from the ALA data and calculated the associated adjusted R^2 value (Table B.4).

3.3.7 Estimating exotic invasion potential

Predicted native richness patterns should provide a template for potential exotic richness, assuming exotic species can spread to the same areas, when (i) areas that have high exotic richness have high native richness and (ii) native and exotic species have similar richness-environment associations. For each family that meets these two criteria, the potential for areas to support more exotic species can be calculated as the difference between scaled predicted native and scaled observed exotic richness in each cell. Comparing native and exotic richness on a relative scale allows for differences in the size of the native and exotic species pools (Table

3.1). Using predicted native species richness derived from the models as the template provides estimates of native species richness in all grid cells, including those that lacked sufficient ALA records, and herbarium collections are the result of unstructured sampling and so species richness estimates of neighbouring areas can be highly heterogeneous.

For each family, I scaled log-transformed native and exotic species richness estimates to between 0 and 1, with 1 being the maximum native or exotic richness observed in a grid cell. I then used the difference between scaled predicted native and scaled observed exotic richness in each cell as indication of the cell's suitability to being invaded by many species, which I defined as 'invasion potential.' A large positive value means a grid cell has lower exotic richness relative to native richness, implying there is potential for more exotic species to occupy that cell. By mapping invasion potential across all areas of Australia, I identified areas where exotic species are currently under-represented and there is high invasion potential. When grid cells had higher exotic richness than predicted from relative native richness, I set the invasion potential to zero.

3.3.8 Testing Fabaceae species richness without *Acacia*

Of the 2,466 native Australian species in the Fabaceae family, 1,455 belong to the endemic Australian genus *Acacia* (Carruthers and Robin 2010; Table B.6). As there cannot be any recorded exotic *Acacia* species, I sought to determine whether a native Fabaceae species richness template without the *Acacia* genus could be a better fit to map potential exotic Fabaceae species richness. I applied the same steps to estimate native Fabaceae species richness without *Acacia* as the other 22 native families, and to determine associations with environmental and human impact variables. I report the results in Figure B.5.

3.3.9 Other factors that could confound the native template

The crux of the native richness template is whether native and exotic richness are positively correlated in areas they co-occur. I test whether the 22 native-exotic family correlation values were predictable from other factors that represent some of the hypothesised influences on native and exotic richness. Variation in native richness patterns explained by environmental and human impact gradients (i.e. [adjusted] native R^2) may be a predictor of the native-exotic correlation (Table 3.1). under this hypothesis, higher native adjusted R^2 values should have higher native-exotic correlations. The total number of world-wide species and C4 species may

predict native-exotic correlation. Larger families may have species with wider environmental tolerances and hence have native species richness pattens that do not strongly with respect to environmental gradients, meaning there may not be a strong signal of high-to-low native and exotic richness to generate a strong positive correlation value. Families with a higher proportions of C4 species could also produce a similar outcome, having lower amounts of variation explained in native richness patterns due to C3 (and/or or CAM) and C4 species having differences in responses to environmental gradients, such as Poaceae species in Australia (Hattersley 1983; Chapter 2).

Dispersal limitation also appears to affect native-exotic correlations when many exotic species appear to not have spread into locations that are environmentally suitable (Chapter 2). I tested possible dispersal limitation in three ways: the ratio of the number of cells occupied by native species and exotic species, expecting ratio to be inversely related to native-exotic correlation value; number of exotic records, predicting that fewer exotic records should have lower native-exotic correlation values; and mean year of first occurrence of exotic species, with 'younger' exotic families expected to have lower native-exotic correlation values. I report the results of this model in Table B.7.

3.4 Results

3.4.1 Does the native richness template work consistently for common native and exotic plant families?

Six of the 22 families met the assumptions of the native richness template, Cyperaceae Apocynaceae, C3 Poaceae, Rubiaceae, C4 Poaceae and Convolvulaceae (Figure 3.2 box a; Figure B.1). Evaluating native and exotic richness for each family by two criteria consistently identified the families for which the template was expected to work: (i) the correlation value between native and exotic richness in areas they co-occurred and (ii) the amount of variation explained in native richness patterns (group A in Figure 3.3; see Table B.5 for values).

For criterion (i), I found that a native-exotic richness correlation value of at least 0.30 suggested that areas that support high exotic richness also tended to support high native richness (Figure 3.2a; Figure B.1, Table B.5). Families which had native-exotic correlation values above 0.3 had native and exotic richness estimates that were consistently similar in areas they co-occurred (Figure 3.2a, b panel i; Figure B.1, B.3 panel i). Whereas native-exotic correlation values below

0.3 did not consistently indicate that areas that had higher native richness also tended to have higher exotic richness (Figure 3.4a, b panel i; Figure B.2, B.4 panel i). For the six families that showed strong support for using the native template (Figure 3.3 group A), many cells had proportionately low exotic richness and moderate-to-high native richness (Figure 3.2ai; Figure B.1a-e panel i). A deviation in the native-exotic correlation in this direction was expected if many exotic species have not yet dispersed to areas that they are otherwise capable of occupying, resulting in areas with low exotic richness and high native richness.

For criterion (ii), I identified that at least 40% of the variation explained in native species richness patterns was necessary to determine whether native and exotic richness had similar associations with environmental variables and to predict native richness patterns across Australia with reasonable accuracy (Figures 2a, 4a; Figures B.1, B.3). Families which had less than 40% variation explained had poorly-resolved predictions of native species richness across Australia (Figures 3.2b. 3.4b; Figures B.2, B.4). All six families that had a native-exotic correlation value above 0.30 and greater than 40% of the variation explained in native species richness patterns (i.e. Figure 3.3 group A) also had similar native and exotic richness associations with environmental variables (Figure 3.2aii; Figure B.1a-f panel ii).

The results for the six families that met criteria (i) and (ii) implied that patterns of predicted native species richness may provide a template for potential exotic species richness across Australia. For five of the six families, northern regions of Australia had the greatest difference between scaled native and exotic richness, indicating a large capacity to support much greater numbers of exotic species (Figure 3.2avi; Figure B.1a, b, d-f panel vi). For all six families, south-east and eastern coast regions had relatively high exotic richness, indicating these regions support the greatest numbers of exotic species and hence have a low invasion potential by new species, compared to areas with relatively high native richness but with currently low exotic richness. Cyperaceae Apocynaceae, C3 Poaceae, Rubiaceae, and Convolvulaceae had large regions across Australia had low predicted native richness (< 10 native species), suggesting a low environmental suitability for establishment of exotic species.

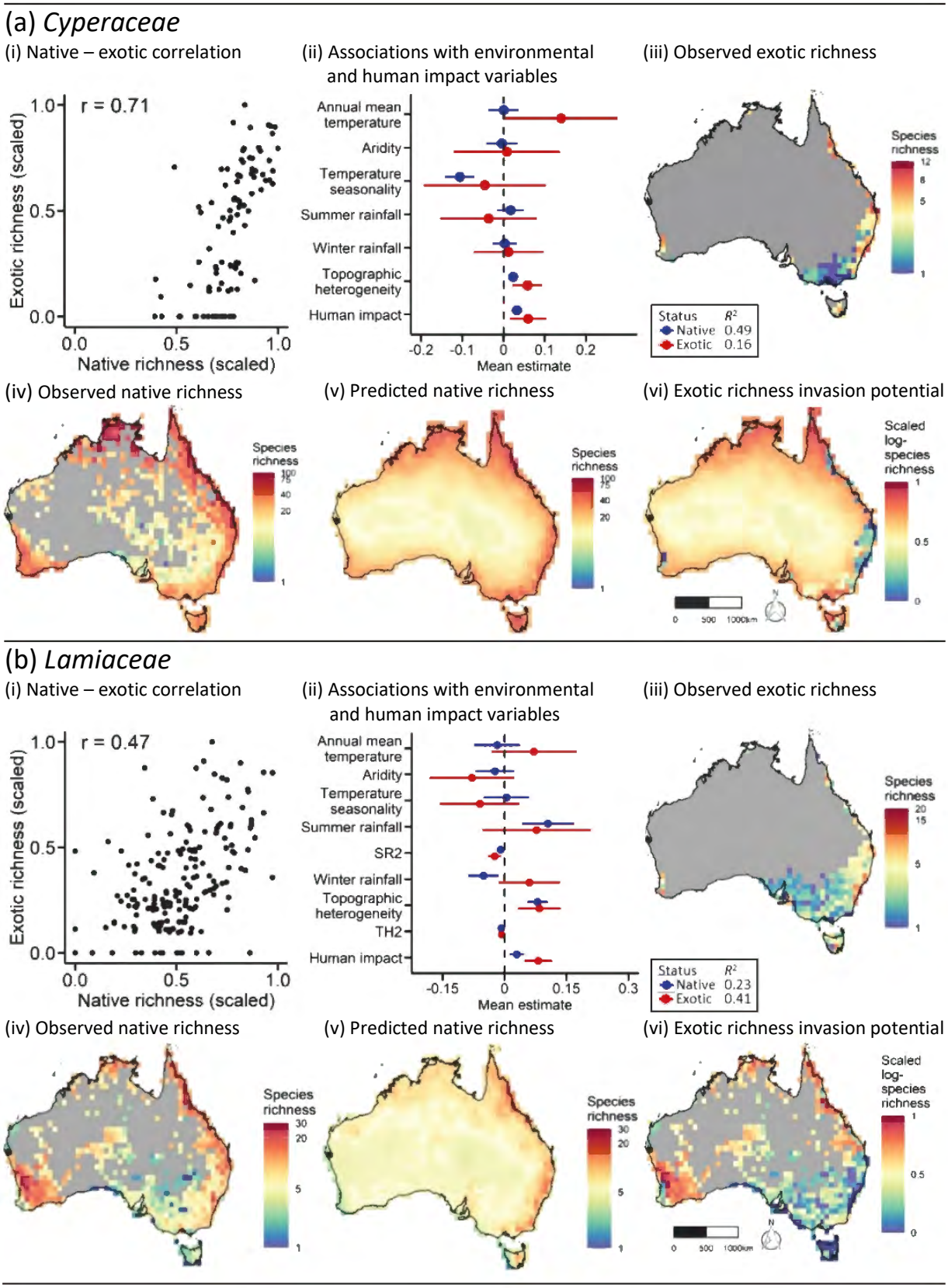

Figure 3.2 Native Cyperaceae (Box a) and Lamiaceae (Box b) species richness as templates for potential exotic Cyperaceae and Lamiaceae species richness at large spatial scales across Australia. (i) Observed native richness (x-axis) and observed exotic richness (y-axis) scaled to between zero and one. Each point represents a 100 × 100 km cell across Australia with both a

both a native and exotic richness estimate. (ii) Mean estimates of native (blue) and exotic (red) log-transformed species richness compared to six environmental variables and a single human impact variable using multiple linear regression. Error bars represent 95% confidence intervals of the mean, which are significant ($P < 0.05$) if they exclude zero (vertical dashed line). The explanatory variables were scaled prior to modelling to compare mean estimate values. SR2 = (summer rainfall)^2 and TH2 = (topographic heterogeneity)^2. (iii) Observed exotic, (iv) observed native, and (vi) predicted native species richness across Australia. Note that predicted species richness was modelled in log-transformed units but is displayed with raw species richness to indicate the large difference in the number of species represented by cells with hot colours (red-orange) and cool colours (blue-yellow). Grey zones did not meet criteria to estimate species richness and were not analysed. (vi) Exotic invasion potential across Australia, calculated for each area as the difference between log-transformed native richness and log-transformed observed exotic richness both scaled to values between 0 and 1. For (a) predicted native richness were used. For (b) observed native richness values were used and invasion potential was not calculated for areas missing observed native species richness values. Negative invasion potential values were truncated to zero. Results for Apocynaceae, Poaceae C3, Rubiaceae, Poaceae C4 and Convolvulaceae were quantitatively similar to Cyperaceae (Box a) and are shown in Appendix B.1a-d, respectively. Results for Euphorbiaceae, Fabaceae, Solanaceae, Apiaceae, and Juncaceae were quantitatively similar to Lamiaceae (Box b) and are shown in Figure B.2a-e, respectively.

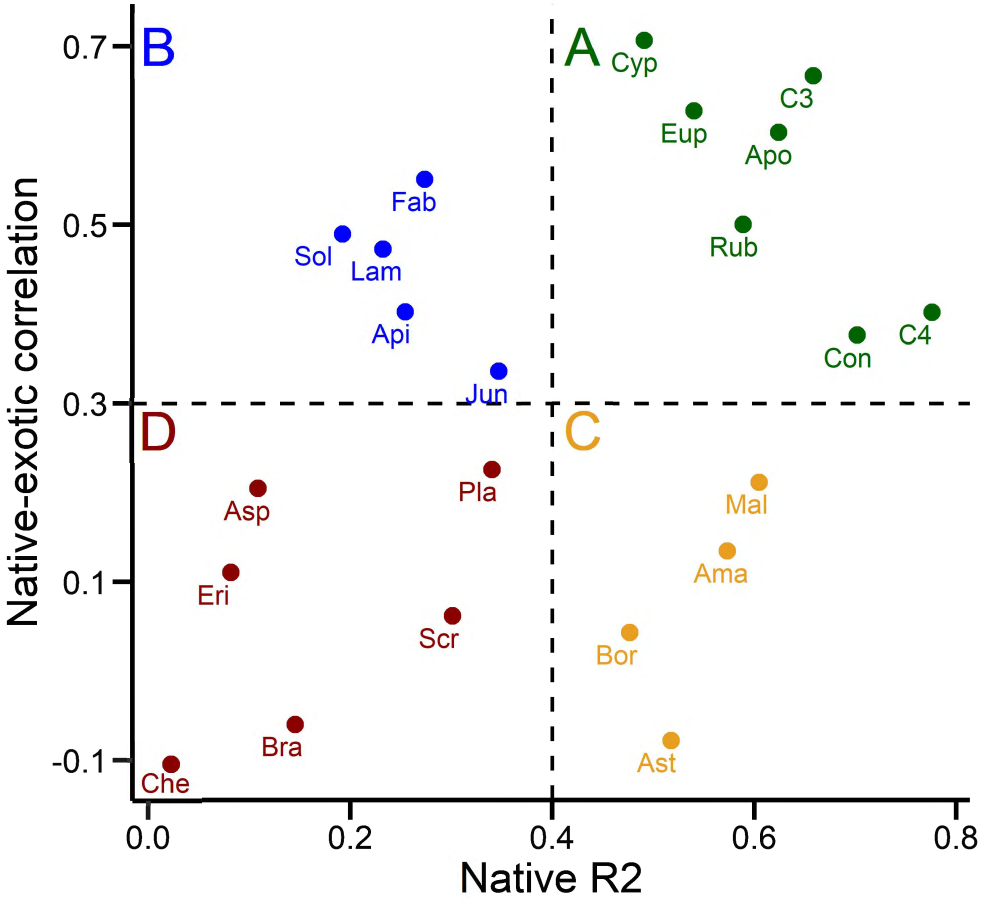

Figure 3.3 Determining support for using native species richness as a template for potential exotic species richness using two criteria. (i) The correlation value between native and exotic richness in cells they co-occur (y-axis), and (ii) the amount of variation in family native richness explained by associations with environmental and human impact variables (native R^2) (x-axis). Correlation values above 0.30 indicated that, in cells where native and exotic richness co-occurred, cells with high exotic richness tended to support high native richness and a native richness R^2 value of 40% or more was enough to reliably compare native and exotic richness associations with environmental and human impact variables (Figures 2, 4; Figures B.1-4). Panel A: six families fulfilled both (i) and (ii) and the native richness appeared to work for these families (see Figure 3.2a; Figure B.1). Panel B: six families fulfilled (i) but not (ii) and the native richness worked for these families in areas with native species richness estimates (see Figure 3.2b; Figure B.2). Panel C: four families fulfilled (ii) but not (i), suggesting that native richness may not be a useful template for potential exotic richness (see Figure 3.4a; Figure B.3). Panel D: six families did not fulfill either (i) or (ii), strongly suggesting that native richness also may not be useful a template for potential exotic richness (see Figure 3.4b; Figure B.4). Ama = Amaranthaceae, Api = Apiaceae, Apo = Apocynaceae, Asp = Asparagaceae, Ast = Asteraceae, Bor = Boraginaceae, Bra = Brassicaceae, C3 = Poaceae C3, C4 = Poaceae C4, Che = Chenopodiaceae, Con = Convolvulaceae, Cyp = Cyperaceae, Eri = Ericaceae, Eup = Euphorbiaceae, Fab = Fabaceae, Jun = Juncaceae, Lam = Lamiaceae, Mal = Malvaceae, Pla = Plantaginaceae, Rub = Rubiaceae, Scr = Scrophulariaceae, Sol = Solanaceae.

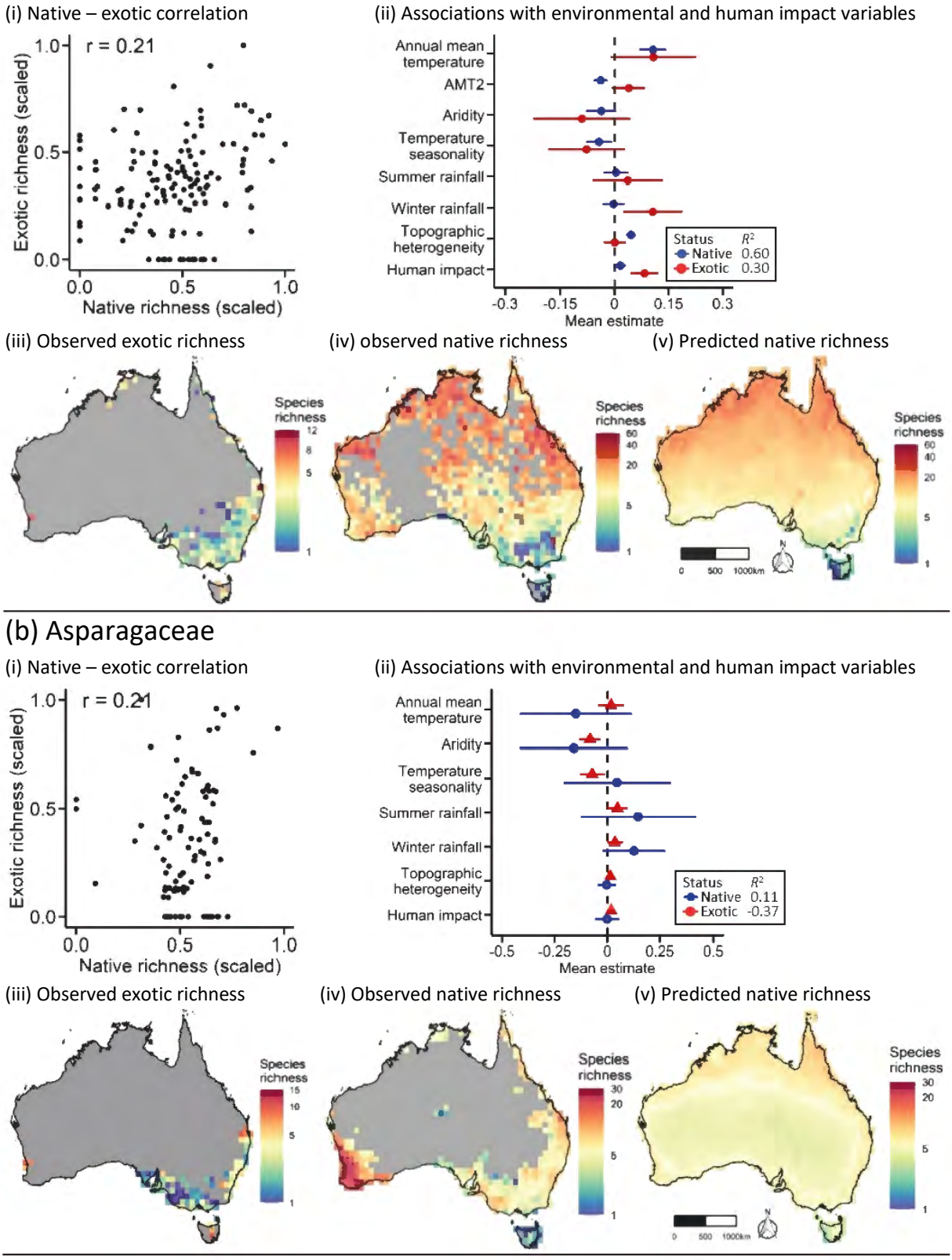

Figure 3.4 Native Malvaceae and Asparagaceae species richness as poor templates for potential exotic Malvaceae and Asparagaceae species richness at large spatial scales across Australia. Box (a) Malvaceae species richness, (b) Asparagaceae species richness. (i) Observed native richness (x-axis) and observed exotic richness (y-axis) scaled to between zero and one. Each

point represents a 100 × 100 km gridded cell across Australia with both a both a native and exotic richness estimate. (ii) Mean estimates of native (blue) and exotic (red) log-transformed species richness compared to six environmental variables and a single human impact variable using multiple linear regression. Error bars represent 95% confidence intervals of the mean, which are significant (P <0.05) if they exclude zero (vertical dashed line). The explanatory variables were scaled prior to modelling to compare estimate values. The mean estimates of two variables (proportion of land cover and a spatial autocorrelation term) were excluded from plots. AMT2 = (annual mean temperature)2. (iii) Observed exotic and (iv) observed native species richness across Australia. Note that species richness was modelled in log-transformed units but is displayed with raw species richness to indicate the large difference in the number of species represented by cells with hot colours (red-orange) and cool colours (blue-yellow). Grey zones did not meet criteria to estimate species richness and were not analysed. (v) Native species richness predicted across all areas of Australia using mean estimates from (ii). Results for Amaranthaceae, Boraginaceae, and Asteraceae were quantitatively similar to Malvaceae (Box a) and are shown in Figure Appendix B.3a-c, respectively. Results for Plantaginaceae, Ericaceae, Scrophulariaceae, Brassicaceae, and Chenopodiaceae were quantitatively similar to Asparagaceae (Box b) and are shown in Figure B.4a-e, respectively.

3.4.2 Does a strong association with human impact confound a positive correlation between native and exotic richness?

Of the ten families that had a native-exotic richness correlation value below 0.30 (Figure 3.3 groups C, D), two had exotic richness that was more strongly associated with human impact compared to native richness (Figure 3.4a, b panel ii; Figures B.3a-c, B.4a-d panel ii). However, for all families that the native richness template was identified to work for (Figure 3.3 group A), exotic richness was also more strongly associated with human impacts compared to native richness (Figure 3.2aii; Figure B.1a-d panel ii).

Five of the ten of families with poorly correlated native-exotic values had exotic richness that were concentrated in south-eastern Australia and low native richness values in this region (Figure 3.4a, b panel iii; Figures B.3a, b, B.4c panel iii). For all families, the south-eastern region of Australia had cells with enough records to estimate exotic species richness (Figures 2, b, 4a, b panel iii; Figures B.1-4 panel iii). Native richness values for ten families were typically low in south-eastern Australia, suggesting native species in these families may be poorly suited to environmental conditions in this region (Figures 2a, 4a, b panel v; Figures B.1a, d-e panel v; B.3a-c, B.4c panel iv). Hence, observing a strongly positive native-exotic correlation may have been confounded when exotic richness estimates were predominately in areas with low native richness.

Four of the remaining five families that had a poor native-exotic richness correlation had many cells with low exotic richness and high native richness (Figures B.3c, B.4a, b, d panel i). Proportionately lower exotic richness could be due to many exotic species being dispersal-limited from areas that are otherwise suitable for colonisation, resulting in cells with low exotic richness and high native richness. This occurred in large families, with many cells having co-occurring native and exotic species, and in small families with few cells. For instance, both Asteraceae and Ericaceae had moderate-to-high native richness and low exotic richness despite large differences in their cell sample sizes (n = 376 and n = 21, respectively) (Figure B.3ci), which potentially confounded observing a strong positive native-exotic correlation.

Only one of the 22 families had strongly differing native and exotic richness patterns which could be due to exotic species having comparatively stronger species richness associations with human impact (Brassicaceae, Figure B.4d).

3.4.3 Are there are family-level biogeographic or physiological characteristics that might affect native-exotic correlation or native species richness associations with environmental variables?

Twelve families had native richness patterns that were poorly explained by gradients in environmental and human impact variables (Figure 3.3 groups B, D). Five of these families had particularly high native species richness in the south-western region of Australia (Lamiaceae, Asparagaceae, Fabaceae, Solanaceae, Apiaceae, and Ericaceae) (Figures 2b, 4b panels iv, v; Figures B.2b-d, B.4b panels iv, v). High native richness in the south-west was also apparent in four families with native richness patterns that were well explained by environmental and human impact variables, with underpredicted native richness estimates in in this region (Cyperaceae, Malvaceae, Amaranthaceae, and Asteraceae) (Figures 2a, 4a panels iv, v; Figure B.3a, c panels iv, v).

Native richness patterns that were not linked to environmental gradients did not confound observing a positive native-exotic correlation (i.e. Pearson's $r > 0.3$). Four of the five families that had a south-western native richness hotspot also had native-exotic correlation values above 0.30 (Figures 2b, 4b panel i; Figure B.2b-d panel i). The results of six families that were positively correlated had richness patterns were not linked to environmental gradients (Figure 3.3 group B). In these cases, native richness may provide a template for potential exotic richness when restricted to areas with current estimates of native richness. Areas with the greatest

differences between observed native and exotic richness varied among the six families: south-west Australia (four families), northern Australia (three families), central Australia (two families), south-east Australia (one family) and Tasmania (one family) (Figure 3.4bvi; Figure B.3a-e panel vi).

I tested whether removing a large endemic genus, Acacia, increased support for the native richness template for Fabaceae (Table B.6). Removing *Acacia* did not appear to substantially alter the richness patterns of native Fabaceae species and the south-western richness hotspot persisted (Figure B.5iv). Removing *Acacia* resulted in a negligible change in the correlation between native and exotic Fabaceae species richness: Spearman's rank r = 0.56 without *Acacia* (Figure B.5i) compared to r = 0.55 for the entire native family (Figure B.2bi). The R^2 value derived from removing *Acacia* did not significantly improve native richness associations with environmental and human impact variables compared to the entire family (0.353 versus 0.2273, respectively) (Table B.4) presumably because of the south-western hotspot. Therefore, species richness of Fabaceae without *Acacia* could not be predicted across all areas of Australia, meaning estimates of potential exotic Fabaceae richness without *Acacia* were still limited to areas with current native richness data. Invasion estimates for the two Fabaceae groups were similar (Figure B.5vi).

The degree to which native and exotic family richness was correlated was not related to any of the six factors (native R^2, log-transformed total family size, log-transformed total number of C4 species, log-transformed number of exotic records, mean year of first exotic species' occurrence, proportion of the number of cells with native and exotic richness estimates) hypothesised to affect it (overall ANOVA *P* value = 0.6363, adjusted R^2 = -0.090, F = 0.726, df = 14) (Table B.7).

3.5 Discussion

3.5.1 Was there general support for the native richness template?

Six out of 22 common native and exotic plant families in Australia met the assumptions of the native template (Figure 3.2 box a; Figure B.1). For these six families, in areas where native and exotic species co-occurred, native and exotic richness was positively correlated, showing that areas that tend to support high native richness also tend to support high exotic richness (Figure 3.2ai; Figure B.1i). Variation in native and exotic richness also showed similar associations

with environmental gradients (Figures 3.2a, 3.4a panel ii; Figures B.1 and B.3 panel ii), suggesting that areas that have environmental conditions suitable for supporting high native richness may also be suitable for supporting high exotic richness. For these six families, areas with the capacity to support the greatest numbers of new exotic species were identified as those areas with the greatest difference between predicted native richness and observed exotic richness (Figure 3.2avi; Figure B.1vi). For Cyperaceae C4 Poaceae, Rubiaceae, and Convolvulaceae, northern regions support high native species richness and currently have low exotic species, implying high invasion potential in these regions. For all six families, southern and eastern regions characterised by high levels of human impact appeared to be already well-invaded, suggesting low invasion potential in these regions.

3.5.2 Use of the native richness template for other plant groups and in other locations

The results of this Chapter confirm that the native richness template should be applicable to other plant taxa and locations using two criteria developed in Chapter 2: (1) the correlation value between native and exotic richness in areas they co-occur and (2) the amount of variation explained in native species richness patterns by gradients in environmental and human impact variables (Figure 3.3, Table B.5). Here, I judged that a correlation value > 0.30 in areas where native and exotic species co-occurred was sufficient to suggest that areas that support high native richness also tend to support high exotic richness (Figure 3.2a, b panel i; Figures B.1, B.2 panel i). Where they co-occur, native and exotic species richness are generally correlated at large spatial scale in regions globally (see meta-analyses by Peng et al. 2019; Tomasetto et al. 2019). Consistent with global patterns, I found that at least 40% of the variation explained in native richness patterns provided accurate predictions of native richness across all areas of Australia (Figures 3.2a, 3.4a panel ii; Figures B.1, B.3 panel ii). Importantly, in all instances of when there was > 0.30 native-exotic correlation values and > 0.40 native richness R^2, native and exotic species richness had similar associations with environmental variables (Figure 3.3 panel A). These results suggest that assessing families by criteria (i) and (ii) can consistently and relatively easily determine the level of support for using the native richness template as a means of forecasting potential exotic richness.

Use of the native richness template was supported when exotic richness estimates occurred in cells with a range of native richness values and when native richness estimates varied along environmental gradients. Meeting this requirement did not require lots of areas with native or exotic records, suggesting that the native richness template could be applied to small families,

or large sub-families and genera. Moreover, the native richness template may be useful for taxa which appear to have many exotic species that have not yet spread much from their areas of introduction, if exotic richness estimates occur in a range of areas with high, moderate and low native richness (e.g. Cyperaceae, Figure 3.2a; Apocynaceae, Figure B1a). Predicting the potential spread of exotic species that are in the early stages of invasion may be particularly useful in pre-empting their impacts (Panetta et al. 1991; Jeschke and Strayer 2008). For instance, Europe's 1,485 species are predicted to occupy only an average of 4.2% of their potential global ranges (Pouteau et al. 2021) and the number of new species listed as exotic is continuing to increase at a consistent rate (Seebens et al. 2018)

3.5.3 What family-level characteristics explained situations when the assumptions of the native richness template were not met?

Most families met only one or neither of criteria (i) and (ii) (Figure 3.3 groups B-D). Families that met (i) implied partial support for the native richness template because areas that supported high native richness tended to also support high exotic richness (Figure 3b; Figure B.2). But for families that just met (ii), or neither (i) or (ii), there was no support for the native richness template (Figure 4a, b; Figures B.3, B.4). None of the factors I looked at were statistically significant indicators that could explain support for template (Table B.7). However, I found likely effects of human impacts, biogeographic factors and phylogenetic factors within the families in groups B-D which could explain why the template worked for some families but not others.

3.5.3.1 Human impacts

I expected that richness patterns in families with weak native-exotic richness correlations might be explained by strong exotic richness associations with human impacts, but this expectation was not supported (Table B.4). For all 22 families, cells with enough records to estimate exotic richness were concentrated in south-eastern Australia, whether or not there was particularly high exotic richness in this region. South-eastern Australia contains ports that are potential entry points for exotic species, high-density human population centres, and heavily human modified landscapes (e.g. urbanisation) which are often strong predictors of exotic species richness (Hulme 2009; Preece et al. 2010; Mologni et al. 2021). However, no families had particularly high exotic richness in all areas with high levels of human impact, suggesting that, at least in part, a role for environmental factors in exotic species richness patterns. Indeed, families where

exotic richness was strongly associated with human impacts often also had strong associations with environmental gradients, and often in similar ways as respective native family richness (e.g. Figures 3.2a, b, 3.3a panel ii; Figures B.2a-e, B.2b, e, B.3c panel ii). This suggests that families which been subject to large introduction efforts by humans may more closely match environmental gradients because they are at saturation within many areas of the landscape.

A strong link between exotic species richness with both human impacts and environmental gradients has been found in other studies (Seabloom et al. 2006; Kier et al. 2009; Pyšek et al. 2010; Essl et al. 2019; Liu et al. 2020*a*; Mologni et al. 2021; Pouteau et al. 2021; Wohlwend et al. 2021). Together, these results and the ones presented in this Chapter suggest that human activities are an important means of exotic dispersal but are not necessarily the areas where we expect to find future exotic hotspots. Thus, to varying degrees, potential exotic richness hotspots are likely to be environmentally determined.

Human impacts influence how dispersal-limited exotic species are (Thuiller et al. 2006; Pouteau et al. 2021) which affected support for the native richness template. Recent dispersal limitation estimates of Europe's 1,385 recorded exotic species suggest that, on average, they only occupy around 4% of their potential global distributions, and are strongly represented in areas characterised by high levels of human activity (Pouteau et al. 2021). I found that many families which had weakly correlated native and exotic richness ($r < 0.3$) also had low native richness in South-eastern Australia but had exotic richness estimates were constrained to this region (e.g. Amaranthaceae, Figure B.3a). South-eastern Australia is cooler, wetter and has more stable temperatures compared to Central and Northern regions of Australia. Native species in many families were poorly suited to the environmental conditions in Southeast Australia (Figures 3.2b, 3.4a panel v; B.1e, B.3a, b panel v, B.2a, B.4c, e panel iv). Like Australia, global human activities are greatest in particular climatic conditions, favouring coastal regions and cooler climates (Xu et al. 2020). Therefore, I anticipate that support for the native richness template will be reduced for families which are particularly suited to warmer, arid and inland regions where exotic species have likely yet to be introduced or spread to.

Additionally, I also observed exotic dispersal limitation in areas with both native and exotic richness estimates. Fifteen families had many areas that had proportionately low exotic richness relative to native richness (Figures 3.2a, b, 3.4a, b panel i; B.1d, B.2b, c, e, B.3a-c, B.4a-c panel i), which was expected to be a result of exotic species not yet had the opportunity to disperse into suitable locations. Thus, I recommend treating instances when there is a weak correlation

between native and exotic richness with caution. More related species tend to have more similar traits and geographic range sizes (Ricklefs and Latham 1992; Crisp et al. 2009). Phylogenetic conservatism is the idea that more related species tend to share more similar ecological characteristics, including environmental tolerances (Wiens and Graham 2005). Phylogenetic conservatism has been used to determine the potential distributions of related species and inform the relative importance of variables among related native and exotic species (Crisp et al. 2009; Buckley and Catford 2016). If enough variation in native richness is explained by environmental gradients ($R^2 > 0.40$, found here), current associations between native and exotic richness with environmental variables could be used as a broad diagnostic tool for the potential distribution of exotic species, even when there is a weak correlation between native and exotic richness (i.e. Figure 3.3 group C). The exotic species in their home range could also be modelled to determine whether they appear to have the capability to spread further in their invaded ranges (Broennimann et al. 2007; Broennimann and Guisan 2008; Gallagher et al. 2010).

Additionally, dispersal limitation will affect some taxa more than others. Dispersal time for some life-forms is much less than for others, e.g. grasses and herbaceous leguminous Fabaceae have traits associated with long-distance dispersal and quick reproduction times (Seabloom et al. 2006; Mologni et al. 2021), whereas trees had significant invasion time-lags (Duncan 2021). Taking into account the locations of introduction and dispersal rate are important invasion predictors, although no factors used to represent these features were significant in this study (Table B.7).

3.5.3.2 Biogeographic factors

Many families had particularly high native species richness in South-western Australia which was not linked with environmental gradients. Half the families whose native species richness was poorly explained by gradients in environmental and human impact variables had particularly high native richness in the Southwest (Figures 3.2b, 3.4a panels iv, v; Figure B.3a, c panels iv, v). To a lesser extent, many families whose native richness patterns were otherwise well-explained also had high richness in the Southwest, with underpredicted native richness in this region (Figures 3.2a, 3.4b panels iv, v; Figures B.2b-d, B.4b panels iv, v). South-western Australia is known for high species richness and proportion of endemic species (Myers et al. 2000), a pattern thought to have occurred because the Southwest is surrounded by ocean and desert which isolate it from the rest of Australia and other potential propagule sources (Hopper 1979). As such, the Southwest appears to have high levels of endemism due to vicariance and

in situ radiative speciation from infrequent long-distance dispersal events (Crisp et al. 2001; Rix et al. 2014; Gioia and Hopper 2017). As a result, environmental gradients did not explain patterns of species richness well for families with high richness in the Southwest.

The effects of isolation and long-term climate change on species richness appear to influence species richness patterns of many groups of plants in many locations (e.g. Myers et al. 2000; Niet and Johnson 2009; Visser et al. 2012; Mairal et al. 2015; Veron et al. 2019). Therefore, the effects of biogeographic factors on native species richness are expected to be an issue for applying the native richness template in other locations and for other plant taxa.

Curiously, exotic species richness in many families was also particularly high in Southwest Western Australia. This phenomenon is not likely due to the same historical processes postulated to have caused high native species richness in this region (i.e. isolation and *in situ* speciation). Yet many families which had particularly high native richness in the Southwest also had particularly high exotic richness. This trend suggests that exotic species may be responding to different but co-varying factors compared to native species that were not measured in this study. Or that there are local-scale factors that promote high species richness in this area independent of species native/exotic origin. The causes of this phenomenon warrant further investigation because of the impacts of exotic species in areas with particularly high native species richness and endemism (Stohlgren et al. 2003; Seabloom et al. 2006).

I applied a conservative modelling framework due to the taxonomic breadth of the families included in this study. Species richness can have complex non-linear associations with environmental gradients (e.g. Francis and Currie, 2003), which I included as quadratic relationships to environmental and human impact variables. However, plant species richness may respond to interactions between variables, such temperature and rainfall, that I did not include (Francis and Currie 2003; Hawkins et al. 2003). I did not account for possible interactions between variables (e.g. mean annual temperature × summer rainfall) that could have had improved model fit for some families compared to the models I selected. I also chose a conservative model selection threshold. For example, the poor amount of variation explained in native Chenopodiaceae richness (adjusted R^2 value = 0.02) increased when modelled with quadratic terms (adjusted R^2 value = 0.64) (Table B.5) but the model with quadratic terms did not meet the AICc score difference I applied in this study.

To attain the most accurate estimates of potential exotic richness, it is advisable to model fewer target taxa (families/genera) and test a larger range of models. Here, models with a range of quadratic relationships and interaction terms could be compared using AICc values for each of the families (e.g. Francis and Currie 2003).

3.5.3.3 Phylogenetic characteristics

Knowing the number of native and exotic species globally and in the region of interest is important for applying the native richness template. For example, Myrtaceae and Proteaceae are among Australia's largest native families but together had less than 10 exotic species (data not shown). On the other hand, *Rosaceae*, *Iridaceae*, and *Caryophyllaceae* are among the top 10 most common exotic families by species (Pyšek et al. 2017) but did not have enough native species to resolve native-exotic correlations and environmental associations (data not shown).

Larger families tended to have many cells with high native species richness estimates relative to the total pool of cells with species richness estimates, but few cells with low native richness, which was not ideal for correlating gradients in native and exotic species richness to each other or to environmental variables (e.g. Asteraceae, Fabaceae). Due to the generality of criteria (i) and (ii) to determine support for the native richness template, larger families could be split up into common genera, subfamilies or by functional traits. For instance, Poaceae poorly met criteria (i) and (ii) (Chapter 2) but grouping species by photosynthetic pathway (C3/C4 photosynthesis) was useful because species with these pathways have differential responses to climatic gradients (Edwards and Still 2008). Additionally, some genera have traits that predispose species belonging to them to become exotic (Rejmánek and Richardson 1996). I tried this indirectly with Fabaceae by removing *Acacia*, the dominant genus in Australia that has no recorded exotic species in Australia (Table B.6; Figure B.5). But its removal, however, did not alter the support of the native richness template. However, identifying the dominant exotic genera of Asteraceae may be useful because Australian Asteraceae species are typically poor dispersers, belonging to a phylogenetically distinct lineages relative to other regions of the globe (Schmidt-Lebuhn et al. 2012) (but see Schmidt-Lebuhn et al. 2020), while exotic Asteraceae typically have high dispersal rates and are represented by a few conserved genera (Martín-Forés et al. 2018).

3.5.4 Future directions

This study suggests that species assembled from different origins (native/exotic) largely conserve their environmental tolerances, also suggested by other studies (Stohlgren et al. 2005; de Albuquerque et al. 2011), implying that native species richness-environment associations in one location could be used to predict native and/or exotic richness patterns in other locations. That is, native richness from one location could be used as a template in other locations. Islands, however present a challenge because of the pervasive influence of landmass and isolation on community size and phylogenetic composition (MacArthur and Wilson 1963; Kier et al. 2009). However, islands are also the most invaded systems (Moser et al. 2018), meaning assessing support for this tool in isolated landmasses would be a useful future goal.

3.5.5 Conclusions

Using 22 common native and exotic plant families in Australia, I show that native species richness can be used as a template for potential exotic species richness at large spatial scales when native and exotic species richness (i) are positively corelated in areas they co-occur and (ii) a moderate amount of variation is explained in native richness patterns. The native richness template method should be useful for other groups of plant taxa and in other locations when native and exotic species meet these two criteria. Key to meeting (i) and (ii) was having native species richness that varied along environmental gradients and exotic richness estimates that were not concentrated in areas that had environmental conditions that were poorly suited to native species. Families that did not meet criteria (i) or (ii) suggested that use of template may be restricted when native species richness are influenced by non-environmental factors and when exotic species are strongly dispersal-limited. A useful future direction is to determine whether species richness-environment associations are consistent among other plant taxa, including smaller taxonomic groups and plant functional groups; and whether native richness in one location can forecast native and potential exotic richness patterns in other locations.

Chapter 4 – Environmental gradients predict similar species richness between isolated old- and newly-assembled grass assemblages

4.1 Abstract

Here, I evaluate how variation in species richness in old (native) and newly assembled (exotic) C3 and C4 grass species assemblages are linked to environmental gradients, and whether these links are consistent between isolated landmasses, suggesting that species richness in one location could be used to predict species in others.

I estimated native and exotic C3 and C4 grass species richness in 100 × 100 km grid cells across Australia and NZ using 1,024,676 herbarium records. Species richness was modelled as a function of six environmental variables and one human impact variable. I used the models developed in Australia to predict and compare native and exotic richness patterns across NZ.

Environmental conditions in NZ predicted relatively high native Australian-origin and NZ-origin C3 grass richness in similar locations. Within NZ, average Australian-origin C3 richness was 15% higher than average NZ-origin C3 richness. There were too few records of native C4 grasses in NZ to estimate species richness. NZ's exotic C3 and C4 grasses are likely dispersal-limited, with richness estimates concentrated in areas with high levels of human impact. Exotic C3 grasses had similar environmental associations compared with native NZ C3 grasses, suggesting that predicted native NZ or Australian C3 richness could provide useful templates for potential exotic C3 spread. The same areas in NZ supported moderate-to-high exotic C4 richness and Australian-origin C4 richness, also suggesting Australian-origin C4 richness could be a broad template for potential exotic C4 richness.

Overall, these results show that old and new plant assemblages appear to have conserved associations with environmental gradients that predict similar numbers of species in the same areas. These results imply native species richness in one location could predict native and exotic species richness in other locations. Average species richness may be dependent on land area and geographic position, with fewer natives and more exotic species supported in a smaller and more isolated landmass.

4.2 Introduction

As early as 1850, von Humboldt proposed that species' distributions are limited by their ability to tolerate environmental conditions (Hawkins 2001). Terrestrial angiosperms (plants) are a mega-diverse kingdom of 304,419 currently described species (WFO 2021). The number of plant species in a given area (species richness) changes in different locations. Linking species richness patterns to other variables has helped test theories about how species assemblages are structured (Hillebrand 2004; Stein et al. 2014). Yet there are over thirty theories concerning how species assemblages arise, concerning many different factors (Hillebrand 2004). Teasing apart the roles of different factors on species richness is thus a useful endeavour.

There is strong empirical evidence that environmental gradients affect plant species distributions (Francis and Currie 2003; Kreft and Jetz 2007; Field et al. 2009; Ben-Hur and Kadmon 2020). Ambient temperatures, light and water levels vary considerably across earth's surface and are intimately linked with plant performance (Wu et al. 2011; Fick and Hijmans 2017). Equatorial regions, for example, are year-round warm and wet, and are thought to impose the fewest broad physiological limits on plant performance and hence support the greatest numbers of plant species (Francis and Currie 2003). Conversely, climatic conditions that tend be more variable (seasonal/diurnal), cooler, or drier (or have combinations of these conditions) should provide progressively stronger limits on the types of plant physiologies that can meet their basic needs (Nano and Pavey 2013; Chen et al. 2017). At large spatial scales, the relationship been species richness and environmental gradients has been used to predict global plant species richness patterns with reasonable accuracy (Kreft and Jetz 2007; Field et al. 2009; Huang et al. 2021).

There are other theories that have been put forward to explain differences in species richness, with also strong support. Macroevolutionary theory posits that at large spatial scales, species richness is a product of dispersal, speciation and extinction processes (Gaston 1998). The interpretation that plant physiology is the dominant driver of species richness presumes that dispersal, speciation and extinction rates are equal in different locations. However, MacArthur and Wilson's (1963) Theory of Island Biogeography (TIB) provided a predictive basis for why dispersal, speciation and extinction processes can vary. The Theory of Island Biogeography posits that smaller and more isolated landmasses are harder to disperse to. Areas with fewer immigrants should support fewer species (Veron et al. 2019). There have been additions to TIB. Smaller areas should also support smaller populations, leading to increased extinction risk,

which reduces the size of the species pool (Wiens and Donoghue 2004; Keppel et al. 2009). Additionally, larger areas may be able to support higher numbers of specialised species because species may be better able to escape competition for shared resources compared to smaller habitats (Gouveia et al. 2014). Consequently, with the same environmental conditions, smaller and more isolated landmasses are expected to support fewer species than larger and more connected landmasses.

Both environmental gradients and biogeographic factors (isolation and land area) appear to be important in structuring plant communities, but may provide differing scenarios for the number of species in a given area, and patterns of species richness across a landmass (Francis and Currie 2003; Albert et al. 2017). Determining the relative importance of factors on plant communities is critical for meeting conservation goals (Yates et al. 2018; Meyer and Pebesma 2020). For instance, many native richness 'hotspots' still remain poorly sampled, limiting the ability to identify areas that could receive the greatest benefits from protection and additional sampling effort (Myers et al. 2000; Engemann et al. 2015). Coupling species richness patterns with other factors, like environmental gradients, can overcome sampling constraints by using environmental factors to predict species richness into other areas (Jiménez et al. 2009). Predicting species richness patterns is particularly relevant on islands because islands host many unique species (Kier et al. 2009). When plant species richness patterns are impacted by isolation or smaller land area, however, it is less clear whether environmental gradients should be able to accurately predict species richness patterns (Kadmon and Allouche 2007; Albert et al. 2017).

Understanding the influences on plant species richness patterns could also help forecast the potential distributions of exotic species (Bellard et al. 2013; Gallardo et al. 2015). Globally, at least 16,926 plant species have established outside of their native ranges and the number of novel plant introductions continues to rise (Seebens et al. 2017 onwards). Exotic (i.e. introduced and established) plant species have significant economic and ecological impacts in the areas they invade, and impacts tend to be greater in areas that support greater numbers of exotic species (Pimentel et al. 2005; Vilà et al. 2011; Roy et al. 2018). The large effects and potential spread of exotic species has motivated determining the locations where the most exotic species can spread to (O'Donnell et al. 2012; Gallardo et al. 2015; Bellard et al. 2017).

The distributions of exotic species appears to be strongly linked with areas that have high levels of human activities and to environmental conditions (Pyšek et al. 2010). Exotic species richness

is associated with trade and transport hubs, human population centres, and modified land use (Lonsdale 1999; Taylor and Irwin 2004). However, exotic species richness patterns also follow environmental gradients. For example, Pouteau and colleagues (2021) found that 1,485 European plant species have species richness patterns in other locations that are strongly linked to key climatic variables, but on average have yet to spread into the vast majority (~96%) of their potential ranges. Importantly, the difference between observed and predicted exotic species richness was related to the degree of human impact, suggesting that human impacts may be important dispersal mechanisms for exotic species but the potential distributions of exotic species may be environmentally determined.

Exotic species following environmental gradients could imply that areas which are environmentally suitable for many native species may also be suited to support many exotic species. At large spatial scales, native and exotic species richness in many different locations and habitat types is positively correlated (Chapters 2 and 3; Seabloom et al. 2006; Stark et al. 2006; Stohlgren et al. 2006; Essl et al. 2019). A positive native-exotic correlation has been attributed to similar tolerances to climatic variation, resource levels and topographic heterogeneity (Davis et al. 2005; de Albuquerque et al. 2011; Fridley and Sax 2014). Moreover, more closely related species tend to have more similar tolerances to environmental conditions (Wiens 2004), suggesting that areas with high numbers of a particular group of native species should also be suitable for supporting related exotic species.

Comparing native (old) and exotic (new) continental and island plant species richness could help elucidate the relative importance of the factors that structure plant communities. If environmental gradients are general and strong influences on plant communities, then native and exotic species richness patterns should vary with environmental gradients in similar ways within a continent and island. If so, the associations that continental plant communities have with environmental gradients should predict similar species richness patterns on islands. This would suggest that community assembly rules are consistent between different locations and species of different origin.

For native plant communities, average island species richness in a given area is expected to be lower than average continental species richness because of the effects of isolation and land area. Conversely, an island may well support much higher exotic species richness in areas they have managed to invade compared to native island or continental richness (Moser et al. 2018; Essl et al. 2019). Possibly because humans activities have broken down the dispersal barriers that

have historically isolated geographically distinct plant communities (Duncan et al. 2019). Yet, native and exotic species richness patterns along environmental gradients are expected to be conserved, meaning areas with high native richness are also expected to support high exotic richness.

Grasses (Poaceae) are useful study taxa for assessing the effects of environmental gradients, biogeographic effects and species' origin. There are 12,000 grass species with representatives on every continent (Still et al. 2003; Vorontsova et al. 2015). The success of grasses is underpinned by a suite of functional and physiological traits. The grass family contains species with C3 or C4 photosynthetic pathways that have enabled grasses to colonise a broad range of environmental conditions (da Silveira Pontes et al. 2015). Ancestral grasses had C3 photosynthesis but C4 photosynthesis has evolved independently within the grass family at least twenty times and is now present in almost half of its species (Edwards and Smith 2010; Sage 2016). The different photosynthetic pathways provide advantages to C3 and C4 species under different conditions, resulting in the species richness of these two groups being predictable from environmental factors (Chapter 2; Bocksberger et al. 2016). C3 photosynthesis provides effective carbon-capture under relatively cool and wet conditions, and C3 grass richness is highest in temperate latitudes (Liu et al. 2009). C4 photosynthesis, in contrast, is advantageous in water-limited environments, such as regions with summer-dominated rainfall or arid regions (Edwards and Still 2008; Bocksberger et al. 2016). Consequently, C3 and C4 grasses have distinctive species richness patterns, providing an opportunity to evaluate the extent to which both native and exotic C3 and C4 grass species assemble in similar ways on different landmasses.

Grasses are one of the most common exotic families by species (Daehler 2003; Pyšek et al. 2017). Grasses have effective dispersal and competitive abilities, and cause and benefit from disturbances (Linder et al. 2017). Grasses are used by people for many ecosystem services (Cook and Dias 2006; Murray and Phillips 2012; O'Mara 2012). Impacts from human activities are also drivers for ancillary invaders, including grasses (Mack and Lonsdale 2001; Pyšek et al. 2010). Grasses can have large impacts on the ecosystems they invade (Rossiter et al. 2003; Pertierra et al. 2017) so understanding the potential spread of grasses is a useful endeavour.

Australia is a large continent and supports many native and exotic grass species (Table 4.1). Environmental gradients are important in structuring patterns of native and exotic C3 and C4 grass species richness in Australia (Chapters 2 and 3; Hattersley 1983). Native and exotic

Australian C3 grasses have similar associations with key environmental variables and are both strongly represented within the same temperate regions. Exotic C4 grasses have a much-reduced geographical extent compared to native C4 grasses, but both C4 groups have similar associations with environmental variables and similar richness patterns where they co-occur. These results suggest that environmental gradients are key in structuring patterns of diversity in both old (native) and newly assembled (exotic) grass communities, and appear to structure them in similar ways (Seabloom et al. 2006).

New Zealand provides a good opportunity to compare grass species richness, patterns, and environmental associations with Australia. New Zealand is 25 times smaller than Australia. Australia is New Zealand's nearest large neighbour, but the countries have been isolated for 80 million years. Currently, New Zealand shares the same latitudes as Australia's southern regions and consequently Australia and New Zealand have relatively high C3 grass diversity (Table 4.1). However, the majority of New Zealand's native plant species appear to have originated via long-distance dispersal and subsequent *in situ* speciation (Mcglone et al. 2011). Among its grasses, 15% of New Zealand's native species are also native in Australia (Table 4.1). As such, Australia and New Zealand's native grasses are somewhat independent examples of old plant assemblages.

Native Australian and New Zealand grass species richness patterns could vary due to their differing biogeographic histories. Prior to human arrival, New Zealand has been mostly forested with the exception of glacial periods, with pollen evidence suggesting grasses can be completely succeeded by New Zealand's woody species (Macphail and McQueen 1983; Ewers et al. 2006). Grasses are strongly adapted to frequent disturbances, particularly grazing and fire (Linder et al. 2017). While New Zealand vegetation is impacted by disturbances (Mcglone et al. 2014; Wyse et al. 2018), fire is not thought to be very frequent (Ogden et al. 1998) and New Zealand does not support any native ungulates. Thus, New Zealand grasses may have a long history of being outcompeted for suitable environments by wooded vegetation. Whereas in Australia, fire has probably facilitated grass dominance or persistence in many suitable habitats (Gill 1975). Consequently, while environmental gradients likely structure the distributions of New Zealand's grasses (Mcglone et al. 2011), native Australian and New Zealand grass species may have different associations with environmental gradients.

Unlike their native floras, the exotic floras of Australia and New Zealand have probably been assembled in similar ways. Eighty-five percent of the exotic grasses in New Zealand are also

exotic in Australia (Table 4.1). This may be a consequence of similar periods of intensive species introductions and human impacts from British and European colonisation. In both countries, native habitats have been extensively cleared, northern-hemispheric grasses introduced and spread (Charlton and Belgrave 1992; Cook and Dias 2006).

This Chapter aims to determine whether Australia's and New Zealand's native and exotic C3 and C4 grass species have similar richness-environment associations, and whether richness-environment associations in Australia predict similar richness patterns across New Zealand. Specifically, I aim to answer three questions:

(i) Do native Australian and New Zealand grass species richness patterns have the same associations with environmental variables, or do they show different patterns as a consequence of a different biogeographic histories and landscape features (i.e. small, isolated island versus large landmass)?

(ii) Do exotic Australian and New Zealand grass species richness patterns have similar associations with environmental gradients due to shared recent assembly histories?

(iii) As a consequence of the relationships in (i) and (ii), are patterns of grass species richness in New Zealand predictable from the patterns in Australia, suggesting that the assembly of native and/or exotic plant species in one region may be predictable from patterns in other regions.

4.3 Methods

4.3.1 Species and photosynthetic trait data

I obtained records of grasses for Australia and New Zealand by downloading all Poaceae records from the Atlas of Living Australia (ALA) (CHAH 2018) using the package ALA4R (v1.8.0) in R (v4.0.2; R Core Team, 2020). The ALA is a download portal for the Australasian Virtual Herbarium, a database of vouchered herbarium specimens amalgamated from Australia's and New Zealand's major herbaria (CHAH 2018), and contains records from citizen science projects that have gone through a verification process. The Poaceae data set had a total of 2,175,967 records and can be accessed via https://doi.ala.org.au/doi/10.26197/5c78c275549a5 and was downloaded on 3 January, 2020.

I determined whether the Australian and New Zealand records were fit for purpose by assessing their spatial, temporal, and taxonomic accuracy through several filtering steps. I assessed the spatial accuracy of the records by excluding records located outside of Australia and New Zealand defining the boundaries of each country using the *getData* function from the *raster* package in R (version 3.1-5; Hijmans, 2020). I also removed records with missing, no (≤ 0 m), or large (> 10,000 m) reported location uncertainties. At this stage of filtering, 94% of New Zealand records were missing location uncertainties so I chose to retain New Zealand records missing this information whilst still removing Australian records missing location uncertainties. I excluded records missing or with an incorrect year of collection (i.e. year = '0').

I checked if records had up to date species level taxonomy and assigned 'native' or 'exotic' status for Australia and New Zealand records using the Australian Plant Census (APC) (CHAH 2018) and the Checklist of the New Zealand Flora (CNZF) (Schonberger et al. 2018). Both the APC and CNZF are updated lists of accepted taxonomy and origins of Australia's and New Zealand's respective plant species. I discarded records that were not identified to species level and assigned subspecies ranked records to their relevant species rank. I removed records identified as 'forms' and 'varieties' because these records may be cultivated species which have not formed wild populations. ALA records that did not have respective matching APC or CNZF species names were discarded. I then assigned species as 'native' or 'exotic'. For Australian species, I categorised native species as species in the ALA record list tagged as 'native' origin in at least one state or territory and I defined exotic species as species tagged solely as 'naturalised'. Species with a different or no origin were excluded. Using the CNZF, I considered New Zealand ALA species as native if they were labelled as 'endemic' or 'non-endemic' and exotic if they were tagged as 'exotic'. Species labelled as 'extinct,' 'uncertain,' or missing origin were excluded. Records that shared the same species, year, and latitude and longitude rounded to the nearest 2 decimal places (~1km) were considered duplicates and combined into a single record.

Finally, I merged the Australian and New Zealand records and assigned each species a C3 or C4 photosynthetic pathway. I assigned photosynthetic pathway by genus using Watson et al. (1992 onwards) and Osborne et al. (2014), except for the genus *Panicum* which was assigned at the species level using Osborne et al. (2014). This process excluded seventeen species across five genera: Alloteropsis, Neurachne and Steinchisma were removed because they are labelled with 'intermediate' C3-C4 pathways and the genera *Connorochloa* and *Anemanthele* and six

species in the genus *Panicum* (*P. capillare*, *P. hillmanii*, *P. luzonense*, *P. racemosum*, *P. simile*, *and P. trichoides*) had no recorded pathway and were also removed. I recognised *Megathyrsus maximus* as a synonym for *Panicum maximum* and assigned it a photosynthetic pathway from Osborne et al. (2014).

After data cleaning, I retained at total of 1,024,676 records for 1,783 native and exotic C3 and C4 Poaceae species in Australia and New Zealand (Table 4.2).

Table 4.1. Native and exotic Poaceae genera and species in Australia and New Zealand. Shared taxa are present in both Australia and New Zealand expressed as a percentage of New Zealand taxa. Australian and New Zealand genera and species checklists and origin were sourced from the Australian plant Census (CHAH 2018) and the Checklist of the New Zealand Flora (Schonberger et al. 2018), respectively.

Country	Genera			Species		
	Native	Exotic	Total	Native	Exotic	Total
Australia	203	125	328	1151	353	1504
New Zealand	47	148	195	193	296	489
Shared*	63.8%	39.5%	48.6%	15.1%	84.8%	54.6%

*Percentage of New Zealand's taxa.

Table 4.2 The number of Australian and New Zealand Poaceae species and records for native and exotic Poaceae herbarium records and species included in this study, grouped by C3 and C4 photosynthetic pathway. The herbarium records were downloaded from the Atlas of Living Australia (https://biocache.ALA.org.au/). Native and exotic status were assigned using the Australian plant Census (APC) (CHAH, 2018) and the Checklist of the New Zealand Flora (Schönberger, 2018) and C3 and C4 data were taken from Watson et al. (1992 onwards) and Osborne et al. (2014).

Country	Photosynthetic pathway	Number of species			Number of records		
		Native	Exotic	Total	Native	Exotic	Total
Australia	C3	381	183	564	363,946	264,188	628,134
	C4	637	153	790	312,445	72,832	385,277
New Zealand	C3	166	174	340	5,857	3,932	9,789
	C4	5	84	89	118	1,358	1,476
Total		1,189	594	1,783	682,366	342,310	1,024,676

4.3.2 Grass groups analysed and compared within this study

I analysed five groups of grass species in this study. I used Australia's native C3 and C4 grass species richness to represent its native and exotic C3 and C4 grass species, because native and exotic species in these groups have similar richness-environment associations and more variation was explained in native richness patterns (Chapters 2 and 3). This provided me with

three groups of C3 grasses to compare: Australian C3, native New Zealand C3, and exotic New Zealand C3. I chose not to analyse native New Zealand C4 species and records due to the low incidence of this group (Table 4.2). This provided me two groups of C4 grasses to compare, Australian C4 and exotic New Zealand C4 species.

To compare the Australian and New Zealand grass species, I predicted Australian C3 and C4 species richness across New Zealand using Australian C3 and C4 grass richness associations with environmental and human impact variables (see Modelling Building). Predicted Australian grass species richness across New Zealand is termed 'Australian-origin' richness, and native New Zealand grass species richness predicted across New Zealand is termed 'New Zealand-origin' richness.

4.3.3 Estimating species richness

For each of the five groups of grasses, I aimed to derive species richness values in 100 × 100 km grid cells within Australia and New Zealand from the ALA records. Variation in sampling effort leads to large differences in the numbers of herbarium records in different areas (Daru et al. 2017). Not accounting for differences in sampling effort can lead to erroneous ecological inferences (Guerin et al. 2018). I adjusted raw species richness values within the 100 × 100 cells by using a species richness estimator that accounts for differences in sample coverage. Sample coverage is a measure of how well the species in an area have been sampled, which Chao and Jost (2012) define as "the proportion of the total number of individuals in a community that belong to the species represented in the sample". Here, sample coverage was the proportion of all plants in a 100 × 100 km cell that were represented by an ALA record in that cell.

I estimated species richness to a universal sample coverage of 0.8, using the *EstimateD* function from the *iNEXT* package in R (version 2.0.19, Hsieh et al. 2016). A 0.8 threshold has been used in comparable studies (Soberón et al. 2007; Daru et al. 2017; Haque et al. 2017). To attain a universal 0.8 sample coverage, cells which are well-sampled (sample coverage of >0.8) had down-weighted species richness and poorly sampled cells (sample coverage of <0.8) had an increased species richness. I did not estimate species richness for cells with fewer than fifteen records and I excluded estimates of species richness which required extrapolation beyond two times the number of records in a cell due to the large uncertainties in these estimates (Chao et al. 2014). Cells for which species richness was not estimated were given a missing value. I log-

transformed species richness estimates so they were approximately normally distributed and had homogeneous variances for fitting linear relationships with environmental and human impact variables.

4.3.4 Environmental and human impact variables

I used six environmental variables and one human impact variable (Table 4.3) to compare to species richness patterns for the five groups of grasses. The six environmental variables represent the major climatic gradients and landscape features hypothesised to explain large-scale variation in plant species richness, including mean annual temperature and seasonal variability, winter and summer water availability and topographic heterogeneity (Kreft and Jetz 2007; Jiménez et al. 2009; Stein et al. 2014; Huang et al. 2021). For a single measure of human impact, I used the Human Influence Index, which is a composite of data layers on population, road, and building density and land use (Sanderson et al. 2002).

To compare species richness to the seven environmental and human impact variables, I required a single value of each variable in each of the 100 × 100 km grid cells in Australia and New Zealand. The raw data layers that represented the seven variables had 1 × 1 km grid cell resolutions and different coordinate projections and global extents. I used the following steps in R using the *raster* package to obtain a single value in each of the 100 × 100 cells across within Australia and New Zealand.

First, I transformed the seven variables to the same coordinate projection as the species richness estimates, and cropped the variables' extents to Australia and New Zealand boundaries using the *getData* function. To transform the resolution of the variables to 100 × 100 km cells, I combined the 1 × 1 km cell values to a single value for each 100 × 100 km cell. I used the mean of the 1 × 1 km cells for mean annual temperature and seasonal variability, winter and summer rainfall, and aridity and human impact for each 100 × 100 km grid cell. And I used the standard deviation of elevation as an index of topographic heterogeneity (Ruifrok et al. 2014). These steps provided me with 1,156 100 × 100 km grid cells for Australia and 83 cells for New Zealand.

Coastal and island cells had only partial land cover and species richness positively scales with sample area (Palmer and White 1994) so I included proportion of land cover (0 – 1) for each cell as a covariate. To compare the size of parameter estimates within each multiple linear

regression model (see section below), I standardised the seven variables by subtracting the mean and dividing by the standard deviation pooling cell values across Australia and New Zealand.

Table 4. Environmental, human impact variables and proportion cover and spatial autocorrelation covariates used in multiple linear regression. The six environmental variables capture gradients that have previously been shown to correlate with plant species richness at large spatial scales. The human impact variable is an amalgamation of different aspects of human modifications of the environment. The covariates account for cells without full land coverage and spatial autocorrelation arising from gridded cells.

Category	Name	Description	Source
Temperature	Annual mean temperature	Annual mean temperature	Fick and Hijmans (2017)
	Temperature seasonality	Temperature seasonality	Fick and Hijmans (2017)
Precipitation	Summer rainfall	Precipitation of the warmest quarter	Fick and Hijmans (2017)
	Winter rainfall	Precipitation of the coldest quarter	Fick and Hijmans (2017)
Temperature-precipitation interaction	Aridity	Aridity index: ratio of the mean annual precipitation to mean annual potential evapotranspiration	Zomer et al. (2008)
Landscape features	Topographic heterogeneity	The standard deviation of 1 × 1 km cells values of elevation at 100 × 100 km	Fischer et al. (2008)
Human impact	Human impact	Human influence index: extent by which the landscape has been modified by human activities, calculated as an index of data layers on road and human density, artificial lights and land use	Sanderson et al. (2002)
Covariates	Land cover	Proportion of the 1 × 1 km cells of each 100 × 100 km cell that included land cover	
	Spatial autocorrelation structure	One of four spatial structures was included, exponential, gaussian, ratio, or spherical	

4.3.5 Model building

I used multiple linear regression to examine the linear associations between eight variables (six environmental variables, one human impact variable, and proportion of land cover) and species richness of each of the five grass groups. The gridded nature of the cells can violate the assumption of independence for multiple linear regression (Guélat and Kéry 2018). In my case,

neighbouring cells could have environmental values that are more similar than expected if they were randomly selected from the total pool of cells, which is assumed by the model. If so, the effective cell sample size is smaller than what independent information is provided by each cell. Unchecked, such spatial autocorrelation can conflate the degree of certainty surrounding parameter estimates (Algar et al. 2009).

I accounted for the possibility of spatially autocorrelated residuals in the linear regression models (species richness as the response variable and eight explanatory variables) using the following steps. I first tested the species richness of the five grass groups for spatial autocorrelation using Moran's I, implemented using the function *Moran.I* from the package *ape* (version 5.3) (Paradis and Schliep 2018) and found significant spatial autocorrelation within four of the five groups (Table C.1). I then accounted for spatial autocorrelation within the four groups by including a spatial autocorrelation term in the model for each group, using generalised least squares (GLS) implemented via the function *gls* from the R package *nlme* (version 3.1-147) (Pinheiro et al. 2020). I tested four different correlation structure terms for each of model, selecting a single correlation structure for each model that had the smallest AICc value, using the *model.sel* function in the package *MuMIn* (version 1.43.17) (Barton 2020) (Table C.2). Finally, for each model, I calculated 95% confidence intervals for each parameter estimate using the *intervals* function in the *nlme* package.

4.3.6 Model fit

I assessed model fit based on adjusted R^2 values, calculated by regressing predicted richness to observed richness in all cells with estimated species richness (Table 4.4). I first did this for each of the five grass groups using observed and predicted richness within their respective countries. To assess whether species richness-environment associations appear to be conserved between native (old) and exotic (new) grass assemblages, I also compared Australian-origin richness predicted across New Zealand to observed New Zealand-origin richness (Table C.3). If native or exotic New Zealand-origin richness is well predicted by native Australian-origin richness, this would provide strong support for the conservation of species richness-environment associations.

4.3.7 Native richness as a template for potential exotic richness

Native species richness is expected to be a useful template for potential exotic species richness when: (i) areas that have high exotic richness have high native richness and (ii) native and exotic species richness-environment associations are similar (Chapter 3). Provided these two criteria are met, predicted native richness patterns could provide a template for potential exotic richness, assuming exotic species can spread to all areas. I tested two native richness templates to forecast potential exotic C3 richness across New Zealand: predicted native Australian-origin C3 richness and predicted native New Zealand-origin C3 richness. To forecast potential exotic C4 richness, I only used predicted native Australian-origin C4 richness because of the paucity of native New Zealand C4 records (Table 4.2).

I used the difference between native and exotic richness in each cell as an indication of the cell's suitability to being invaded by many exotic species, which I defined as 'invasion potential.' Areas may already be severely invaded, indicated by a small difference between native and exotic species richness, and will have a low invasion potential. Areas with a large difference between native and exotic richness may be able to support greater numbers of exotic species, and hence will have a large invasion potential.

An issue with calculating invasion potential in this way is that the size of the native and exotic species pools differ (Table 4.1). The exotic pool has the potential to increase if new species establish and spread in New Zealand, and for the C3 grasses, I tested two different native templates, which may well suggest dissimilar invasion potentials. To account for differences in the sizes of the native and exotic pools, I compared native and exotic richness on a relative scale. I transformed native and exotic richness values to between 0 and 1, with 1 being the maximum richness in a grid cell. If native and exotic richness were perfectly correlated then, regardless of the size of the two species pools, the grid cells with maximum relative richness should coincide. When grid cells had higher exotic richness than predicted from relative native richness, I set the invasion potential to zero.

4.4 Results

4.4.1 (i) Do native C3 grasses of Australian-origin and New Zealand-origin have similar species richness associations with environmental variables?

A large proportion of native Australian C3 species richness was explained by gradients in environmental and human impact variables (R^2 = 0.613, Table 4.4). Cells with C3 species richness estimates in Australia showed that native C3 richness was highest in the Southeast and Tasmania, and low in inland and northern regions (Figure 4.1i). Australian C3 richness was higher in cooler and less arid areas that had more stable seasonal temperatures, higher topographic heterogeneity and higher levels of human impact (Figure 4.1iii).

A moderate amount of variation in native New Zealand C3 richness was explained by associations with environmental and human impact variables (adjusted R^2 = 0.518, Table 4.1). Native New Zealand C3 species had broadly similar richness-environment associations compared to Australian C3 grasses (Figure 4.1iv). Native New Zealand C3 richness was higher in drier and cooler areas, had no association with the level of human impact, and had weaker associations with annual and seasonal temperature variables. In New Zealand, most areas had enough records to estimate native C3 richness, and C3 richness was typically high in the South Island and moderate in the North Island (Figure 4.1ii).

Environmental conditions predicted similar patterns of native Australian-origin and New Zealand-origin C3 richness across New Zealand (Figure 4v, vi). Across New Zealand, predicted native Australian-origin and New Zealand-origin C3 species richness were highly positively correlated (Spearman rank correlation r = 0.88, n = 83), suggesting that the areas which have environmental conditions that are suitable for supporting high native New Zealand-origin C3 richness could also be suitable for supporting high Australian-origin C3 richness (Figure 4.1v). Within New Zealand, median predicted Australian-origin C3 richness was 15% higher than median predicted New Zealand-origin C3 richness (Table 4.4). Despite a strong positive association with level of human impact, predicted Australian-origin C3 richness across New Zealand did not appear to have particularly high richness in cells containing large human settlements (e.g. Auckland, Taranaki, Wellington, Figure 4.1v).

Predicted rather than observed native New Zealand-origin C3 richness was compared with Australian-origin C3 richness because of the moderate amount of variation in New Zealand-

origin C3 richness explained by associations with environmental and human impact variables and observed and predicted New Zealand-origin C3 richness were highly positively correlated (Spearman rank correlation r = 0.78, n = 40, Figure C.1).

Table 4.3 Adjusted R^2 values from regressions of observed versus predicted values for combinations of native and exotic Australian and New Zealand C3 and C4 Poaceae species richness. Median species richness predicted within New Zealand is based off species richness-environment and human impact models fitted to the group shown in the Status and origin column and predicted across New Zealand.

				Median species richness	
Photosynth-etic pathway	**Status and origin**	**Adjusted R^2**	**Number of cells (n)***	**Observed**	**Predicted within NZ**
C3	Native Australian	0.613	491	11.9	31.8
	Native New Zealand	0.518	55	32.5	27.7
	Exotic New Zealand	0.385	40	28.3	28.4
C4	Native Australian	0.633	770	34.4	4.4
	Exotic New Zealand	-0.148	23	20.4	16.6

*Number of cells which met the record criteria to estimate species richness.

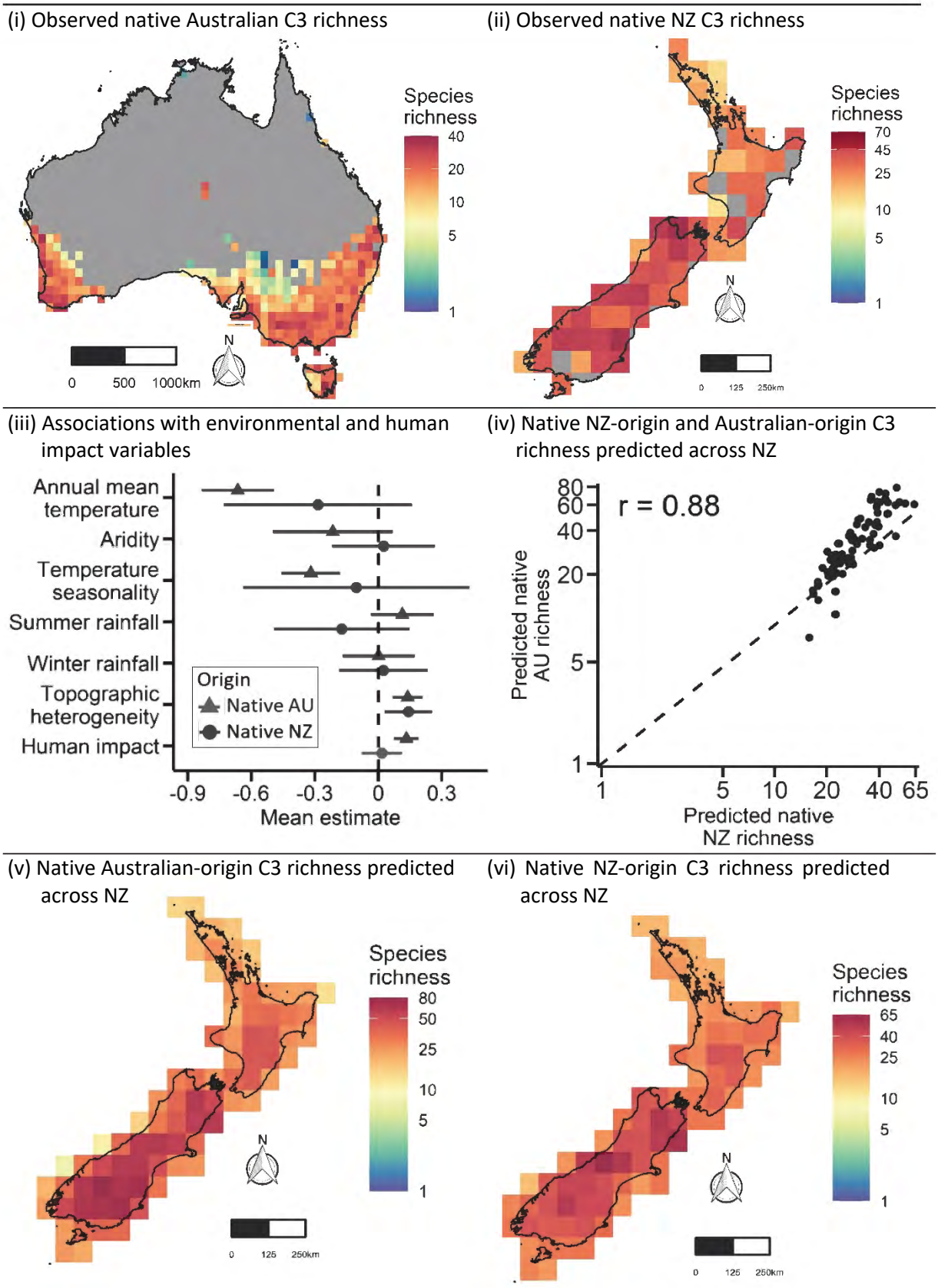

Figure 4.1 Native Australian-origin and New Zealand-origin (NZ) C3 Poaceae species richness predicted at large spatial scales across NZ using their associations with key environmental and human impact variables. (i) Observed native Australian C3 species richness in 100 × 100 km gridded cells across Australia. Note that species richness is displayed in raw species richness to

indicate the large difference in the number of species represented by cells with hot colours (red-orange) and cool colours (blue-yellow) using log-transformed species richness. Grey cells did not meet the record criteria to estimate species richness. (ii) Observed native NZ C3 species richness in 100 × 100 km gridded cells across NZ. (iii) Mean estimates of the associations between native Australian (triangle) and NZ (circle) log-transformed species richness and six environmental variables and one human impact variable, using multiple linear regression across their respective distributions in Australia and NZ. Error bars represent 95% confidence intervals of the mean, which are significant (P <0.05) if they exclude zero (vertical dashed line). The explanatory variables were scaled prior to modelling to compare estimate values. The mean estimates of two parameters (land cover and a spatial autocorrelation term) were excluded from plotting. (iv) Predicted NZ native richness (x-axis) and predicted Australian native richness (y-axis) across NZ using associations with environmental and human impact variables from (iv). Each point represents a 100 × 100 km grid cell across NZ with both a predicted Australian and NZ species richness estimate. The dashed line represents a 1:1 relationship between raw species richness. (v) Native Australian-origin species richness predicted in 100 × 100 km gridded cells across NZ using the associations with environmental and human impact variables from (iii). (vi) Native NZ-origin species richness predicted in 100 × 100 km gridded cells across NZ using the associations with environmental and human impact variables from (iii). The Australian map was projected in the Australian Albers equal area projection and NZ maps were projected in the New Zealand GD2000 Transverse Mercator projection.

4.4.2 (ii) Do exotic Australian and New Zealand grass species richness patterns have similar associations with environmental gradients due to shared recent assembly histories?

4.4.2.1 C3 grasses

Exotic C3 species in New Zealand had a moderate amount of variation in richness patterns explained by gradients in environmental and human impact variables (R^2 = 0.385, Table 4.4). Exotic C3 richness was higher in hotter, drier, and flatter areas characterised by high levels of human impacts (Figure 4.2ii). Exotic C3 richness estimates tended to be in cells which also contained human population centres (e.g. Auckland, Wellington, Christchurch, Dunedin, Figure 4.2i).

Exotic C3 grasses in New Zealand had distinct species richness-environment associations compared to Australian-origin C3 grass richness, while native New Zealand C3 associations were in the middle of Australian and exotic C3 mean estimates (Figure 4.2ii). Across New Zealand, predicted Australian-origin and native New Zealand-origin C3 richness were weakly negatively correlated with observed exotic New Zealand C3 richness (Spearman's rank r = -

0.05 and -0.13, n = 40 and 35, respectively; Figure 4.2i, ii). The weakly negative correlation values occurred because many cells had proportionately low exotic C3 richness and moderate-to-high Australian-origin or native New Zealand-origin C3 richness (Figure 4.2i, ii). Cells with proportionately low exotic species richness are expected to occur if many exotic species are dispersal-limited from areas that they are otherwise suited to occupy.

4.4.2.2 C4 grasses

Environmental and human impact variables explained a moderate amount of variation in native Australian C4 richness across Australia (R^2 = 0.633, Table 4.4) but a poor amount of variation in exotic C4 richness across New Zealand (R^2 = -0.148, Table 4.4). Australian C4 richness was higher in hotter areas that had higher summer rainfall and lower aridity (Figure 4.3ii). Across New Zealand, the associations between Australian-origin C4 species richness and environment and human impact variables predicted relatively high C4 richness in the North Island and along the eastern half of the South Island (Figure 4.3ii). Relative to Australia, suitable areas of New Zealand for C4 grasses were predicted to support much lower richness compared to suitable areas in Australia (Figure 4.3i, ii).

The low amount of variation explained in exotic C4 richness patterns in New Zealand could have been confounded by the small number of cells that met the record requirements to estimate species richness (n = 23, Table 4.4). Estimates of exotic C4 grass richness in New Zealand were also concentrated in cells containing human population centres (Figure 4.3iv)

Across New Zealand, scaled exotic New Zealand C4 richness was weakly correlated with scaled predicted Australian-origin C4 richness (Spearman rank r = 0.23, n = 23, Figure 4.3iii). In 22 of the 23 cells with both Australian-origin and exotic New Zealand C4 grass richness estimates, scaled Australian-origin and exotic New Zealand C4 richness were both moderate-to-high (0.5 – 1) (Figure 4.3iv). Across New Zealand, median exotic C4 richness was 6.5 times higher than median predicted Australian-origin C4 richness (Table 4.4).

4.4.3 (iii) Can steps (i) and (ii) be used to forecast potential exotic New Zealand species richness?

4.4.3.1 C3 grasses

Native and exotic New Zealand C3 grass species had similar associations with environmental variables and areas that had relatively high native richness tended to have relatively high exotic richness (Figure 4.2ii, iv), implying that predicted native New Zealand C3 richness patterns may provide a template for potential exotic C3 richness. The difference between predicted native and observed exotic C3 richness in cells across New Zealand suggests that coastal and central-southern areas of the South Island have the capacity to support much greater numbers of exotic C3 grasses (Figure 4.2vi).

Conversely, native Australian C3 richness had different associations with environmental variables compared to exotic New Zealand C3 richness (Figure 4.2vi), implying that predicted Australian-origin C3 richness across New Zealand may be not a suitable template for potential exotic C3 richness in New Zealand. However, predicted Australian-origin and native New Zealand-origin richness patterns were nearly identical and areas predicted to have relatively high Australian-origin richness also tended to have relatively high exotic richness (Figure 4.1v, vi; Figure 4.2iv). Thus, predicted Australian-origin and native New Zealand-origin richness patterns produced similar forecasts of exotic C3 invasion potential, both suggesting that coastal areas and some areas in southern South Island could support many more exotic C3 grass species (Figure 4.2v and vi).

4.4.3.2 C4 grasses

The large uncertainties around the associations between exotic C4 richness and environmental variables preclude determining whether exotic C4 grasses in New Zealand have similar responses to environmental conditions compared to native Australian C4 grasses (Figure 4.3v). Within New Zealand, predicted Australian-origin and observed exotic New Zealand C4 species richness were weakly positively correlated, suggesting that Australian-origin C4 richness could be used as a coarse template to forecast potential exotic C4 richness (Figure 4.3iv). Northern and central areas in the North Island and the south-eastern region of the South Island appear to be capable of supporting greater numbers of exotic C4 grass species (Figure 4.3vi).

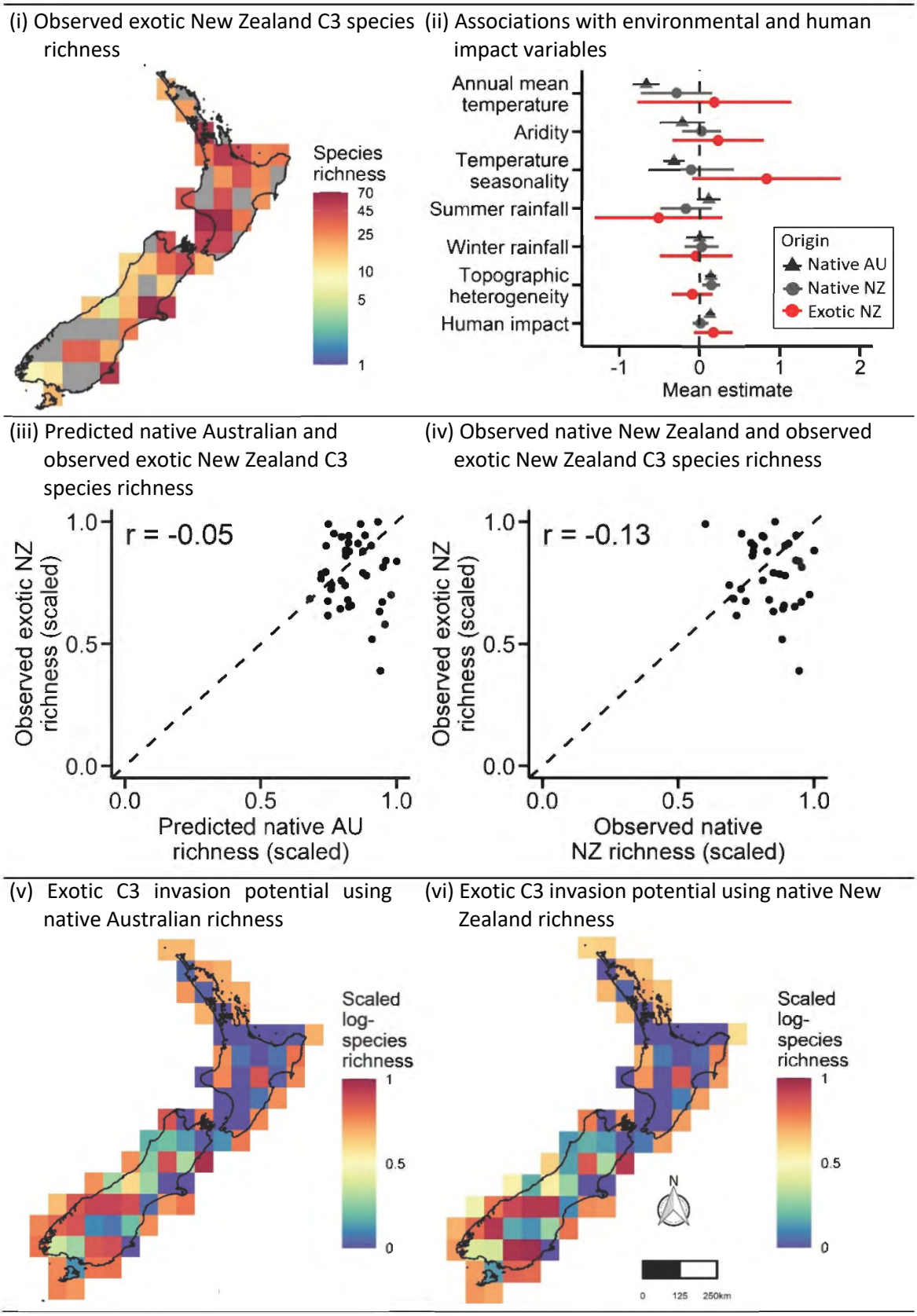

Figure 4.2 Native Australian-origin and New Zealand-origin (NZ) C3 Poaceae species richness as templates to forecast potential exotic NZ C3 species richness at large spatial scales across NZ. (i) Exotic NZ C3 species richness observed across NZ for cells with enough records to estimate species richness. Note that species richness is displayed in raw species richness to

indicate the large difference in the number of species represented by cells with hot colours (red-orange) and cool colours (blue-yellow) but was modelled using log-transformed species richness. (ii) Mean estimates of the associations between NZ (circle) and Australian (triangle) native (grey) and exotic (red) C3 log-transformed species richness and six environmental variables and one human impact variable, using multiple linear regression across their respective distributions in Australia and NZ. Error bars represent 95% confidence intervals of the mean, which are significant ($P < 0.05$) if they exclude zero (vertical dashed line). The explanatory variables were scaled prior to modelling to compare estimate values. The mean estimates of two parameters (land cover and a spatial autocorrelation term) were excluded from plotting. AU = Australia. (iii) Predicted Australian-origin C3 native richness across NZ using the associations between Australian-origin C3 richness and environmental and human impact variables from (ii) (x-axis) and observed exotic NZ C3 richness (y-axis). Each point represents a 100 × 100 km gridded cell across NZ with both a both a NZ and Australian species richness estimate. The diagonal dashed line represents a 1:1 relationship between scaled species richness. (iv) Predicted native NZ-origin richness (x-axis) and observed exotic C3 richness (y axis). (v) Exotic C3 invasion potential across all areas of NZ, calculated for each cell as the difference between log-transformed predicted native Australian-origin C3 richness and log-transformed observed exotic NZ C3 richness scaled to between 0 and 1. Negative invasion potential values were set to zero. (vi) Exotic C3 invasion potential across all areas of NZ, calculated for each cell as the difference between log-transformed predicted native NZ-origin C3 richness and log-transformed observed exotic NZ C3 richness scaled to between 0 and 1. The Australian map was projected in the Australian Albers equal area projection and NZ maps were projected in the New Zealand GD2000 Transverse Mercator projection.

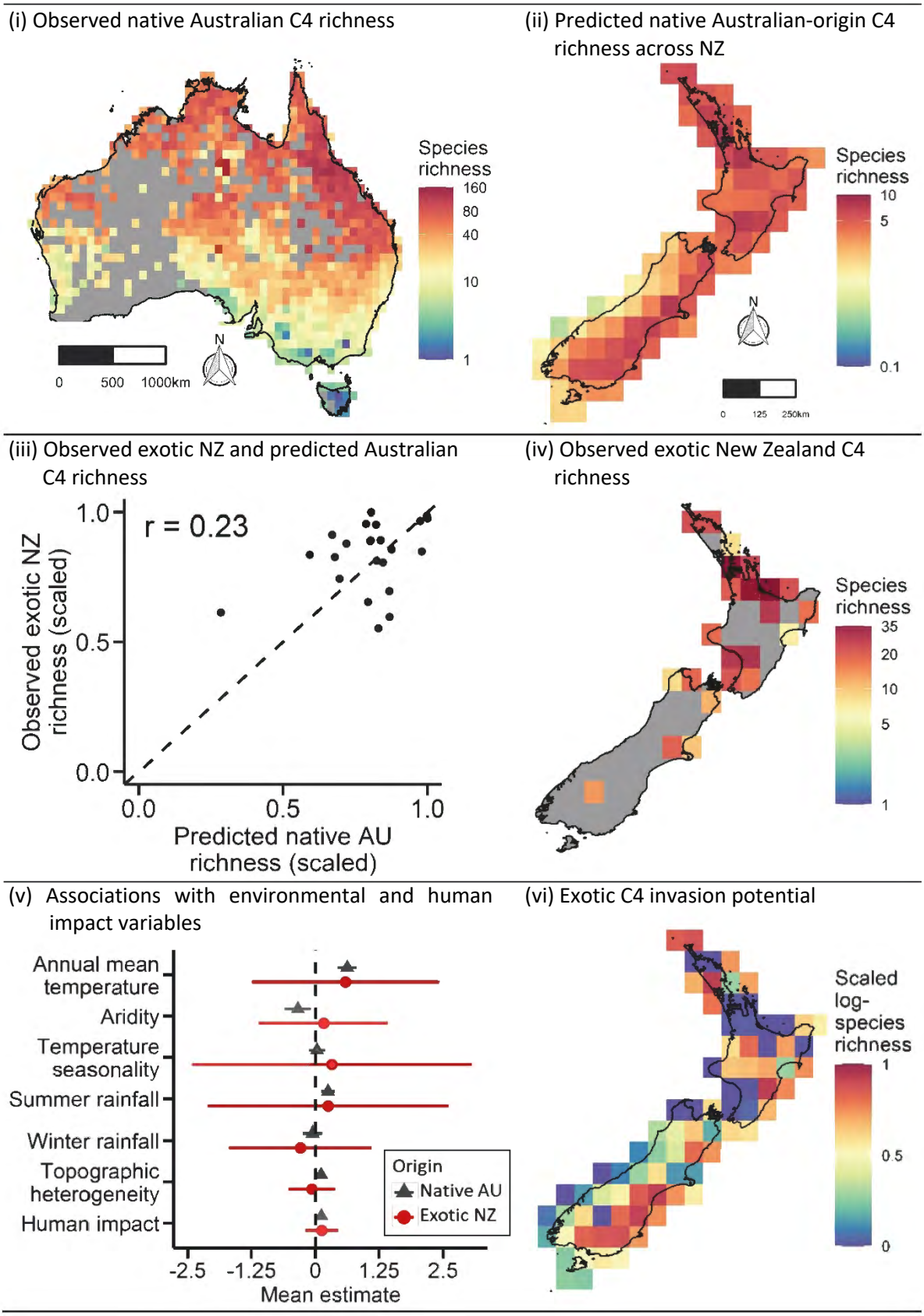

Figure 4.3 Native Australian-origin C4 Poaceae species richness predicted at large spatial scales across New Zealand (NZ) as a template to forecast potential exotic NZ C4 species richness. (i) Native Australian C4 species richness observed in 100 × 100 km grid cells with enough records to estimate specie richness. Note that species richness is displayed in raw

species richness to indicate the large difference in the number of species represented by cells with hot colours (red-orange) and cool colours (blue-yellow) using log-transformed species richness. (ii) Native Australian-origin C4 species richness predicted across NZ using the associations between Australian C4 richness and environmental and human impact variables from (v). (iii) Scaled predicted native Australian-origin C4 richness across NZ using the associations with environmental and human impact variables from (ii) (x-axis) and scaled observed exotic NZ C4 richness from (iv) (y-axis). Each point represents a 100 × 100 km grid cell across NZ with both a both a native and exotic species richness estimate. The diagonal dashed line represents a 1:1 relationship between scaled species richness. (iv) Exotic NZ C4 species richness observed across NZ for cells with enough records to estimate species richness. (v) Mean estimates of the associations between native Australian (grey triangle) and exotic NZ and exotic (red circle) C4 log-transformed species richness and six environmental variables and one single human impact variable, using multiple linear regression across their respective Australian and NZ distributions. Error bars represent 95% confidence intervals of the mean, which are significant ($P < 0.05$) if they exclude zero (vertical dashed line). The explanatory variables were scaled prior to modelling to compare estimate values. The mean estimates of two parameters (land cover and a spatial autocorrelation term) were excluded from plotting. (vi) Exotic C4 richness invasion potential across all areas of NZ, calculated for each cell as the difference between log-transformed predicted native Australian C4 richness and log-transformed observed exotic NZ C4 richness scaled to between 0 and 1. Negative invasion potential values were set to zero. The Australian map was projected in the Australian Albers equal area projection and NZ maps were projected in the New Zealand GD2000 Transverse Mercator projection

4.5 Discussion

4.5.1 The influence of environmental gradients and biogeographic factors on native species richness

At large spatial scales, environmental gradients are universal influences on terrestrial plant communities (Francis and Currie 2003; Kreft and Jetz 2007; Jiménez et al. 2009; Ben-Hur and Kadmon 2020) due to the physiological limits imposed by the prevailing climatic and landscape features (Hawkins 2001; Hawkins et al. 2003; Field et al. 2009). Here I showed that at a course resolution (100 × 100 km), environmental gradients were strong influences on native Australian and New Zealand C3 Poaceae species richness patterns (Table 4.4). Moreover, the associations that native Australian and New Zealand C3 richness had with environmental gradients predicted near identical Australian-origin and New Zealand-origin C3 richness patterns across New Zealand (Figure 4.1). Similar species richness-environmental associations from independently assembled communities results support the theory that plant communities have conserved

tolerances to environmental gradients that predict similar geographic distributions in different locations (Ricklefs and Latham 1992; Crisp et al. 2009).

Independent of environmental gradients, landmass and geographic connectivity are important influences on native species richness (Gaston 1998; Ricklefs 2004; Albert et al. 2017). In support of this view, I found that at a course resolution, species richness is lower New Zealand is lower in equivalent environmental conditions compared to Australia (Table 4.4, Figure 4.3; Appendix C). Lower native species richness in New Zealand compared to Australia is consistent with the expectations of the Theory of Island Biogeography (TIB) (MacArthur and Wilson 1963). New Zealand is much smaller and is more isolated than Australia, which TIB predicts makes it harder for species to disperse to, and constrains species' population sizes resulting in smaller species pools (Warren et al. 2015). Thus, lower average native New Zealand-origin C3 and C4 richness compared to Australian-origin C3 and C4 richness may be a consequence of the dispersal barriers and population limits set by New Zealand's relative isolation and total land area.

4.5.2 The influences of environmental gradients and human impacts on exotic species richness patterns

Regions of Australia and New Zealand support some of the greatest numbers of exotic plant species in the world (Pyšek et al. 2017). In particular, New Zealand supports a high number of exotic species relative to native species (Essl et al. 2019). These trends were reflected in the total native and exotic grass species New Zealand supports (Table 4.2) and New Zealand also supports many exotic C3 and C4 grasses in many large scale areas compared to how many native species were predicted to be supported from its environmental conditions (Figures 4.2, 4.3).

Exotic C3 and C4 richness patterns tended to be associated with areas that also contained human population centres, long-distance trade and transport hubs, and for C3 grasses, some areas that are used for intensive pasture practices (Figures 4.2, 4.3). For example, exotic C4 richness patterns were not explained by environmental gradients but exotic C4 richness was high (> 20) in cells that contained cities and modified land use (Figure 4.3iv, v), These results highlight how human activity is an important factor for the number and distribution patterns of exotic species (Pyšek et al. 2010). The large number of exotic species in New Zealand also suggests that human activities have overcome the dispersal barriers that have previously isolated native

plant communities to geographically distinct locations. Thus, the negative effects of smaller land area and isolation for average native richness may be positive predictors of exotic species (Moser et al. 2018; Essl et al. 2019; Wohlwend et al. 2021).

Exotic species do appear to be responding to environmental gradients and in similar ways compared to native species. Exotic C3 grasses in New Zealand had similar associations with environmental conditions as New Zealand's native C3 grasses, and in areas with relatively high exotic C4 richness tended to have relatively high predicted Australian-origin C4 (Figures 4.2ii, 4.3iii). These results imply that areas highly suitable for lots of native species may also be environmentally suitable for exotic species and that areas with high numbers of native species but currently low numbers of exotic species are most prone to being able to support the greatest numbers of spreading or newly introduced exotic species (Chapters 2 and 3). The potential spread of large numbers of C4 grasses in New Zealand is concerning because of the ability of some C4 grasses to alter fire regimes which can impact native species and benefit other invaders (D'Antonio and Vitousek 1992; Rossiter et al. 2003; van Klinken and Friedel 2013).

The distribution patterns of exotic C3 and C4 grass richness is patchy in New Zealand, whereas exotic C3 and C4 grass richness is more widely and contiguously distributed in Australia (Chapters 2 and 3). This difference likely reflects the difference between New Zealand's and Australia's agricultural practices and native vegetation structures. There are large tracts of low-intensity 'grazing lands' in Australia, with mixed native-exotic vegetation structures. For example, South-eastern Australia is one of the most invaded regions in the world (Pyšek et al. 2017) and has large areas of native temperate grasslands and mixed grassy-woodlands which have converted to exotic pasture lands relatively easily under European farming practices (Mack 1989; Lunt 2005; McIntyre and Lavorel 2007).

Historically, New Zealand was mostly forested, which is thought to have excluded the formation of grasslands in many otherwise suitable regions for grasses (Macphail and McQueen 1983; McGlone 1989). Thus, clearing of wooded structures in many regions is required to maintain exotic pastures, such as managed agricultural or urbanised areas. There are some suitable areas for exotic grasses that are not as forested, e.g. sub-alpine areas in the central North and South Island, which will likely support more exotic grasses in the future as they disperse from their current locations. But a third of New Zealand's total land area is also protected, which includes large areas of native forest with low levels of human disturbances (Molley 2015). As a consequence of low human disturbance and environmental protection, much of

New Zealand's forest cover remains (Molley 2015). Dense forest cover in New Zealand may be preventing the establishment of exotic C3 and C4 species in these otherwise suitable areas, and may be responsible the differences in exotic C3 and C4 invasion potentials between Australia and New Zealand (Chapter 2).

4.5.3 Predicting native and exotic richness between different locations

The methodology developed here could also predict native and exotic richness in other locations for other groups of species. At large spatial and taxonomic scales, environmental gradients appear to be strong and generally conserved influences on plant communities (Francis and Currie 2003; Jiménez et al. 2009; Ben-Hur and Kadmon 2020). Phylogenetic niche conservatism posits that more closely related species have more similar tolerances to environmental conditions, related groups of species may closely follow environmental gradients in different locations because of their similar physiological tolerances (Ricklefs and Latham 1992; Wiens 2004; Wiens and Graham 2005; Crisp et al. 2009). Grasses may be particularly useful species to test the roles of environmental influences on richness patterns because of the strong and distinct influences of C3 and C4 photosynthetic pathways on the tolerances of those species to large-scale environmental conditions (Hattersley 1983; Edwards and Still 2008; Bocksberger et al. 2016). However native and exotic species richness in other plant families also appear to be strongly influenced by environmental gradients and in similar ways (Chapter 3). Suggesting comparing related native and exotic species richness patterns and environmental conditions could be useful to predict the distributions of other plant taxa and in other locations. Noting that average native species richness should be expected to be lower in overall smaller and more isolated landmasses, while exotic richness can be much greater.

4.5.4 Conclusions

Here I showed that at large spatial scales, old (native) and newly assembled (exotic) grass species appear to have similar associations with environmental gradients that predict similar species richness gradients between Australia and New Zealand. These findings suggest that independently assembled island and continental plant groups appear to have strongly conserved associations with large-scale environmental conditions. Biogeographic factors have likely impacted the number of native C3 and C4 species New Zealand supports, with fewer species for its climatic conditions. On the other hand, New Zealand supports large numbers of exotic grass species and exotic grasses appear to have the capacity to spread into other areas. The

methodology in this study suggests that species richness in one location could be used to estimate native or potential exotic richness specie richness in other locations. The generality of the approach used in this study means that it could also be used for other native and exotic plant communities (e.g. Chapter 3) and in other locations.

Chapter 5 – Do the impacts of exotic species on a native community increase over a water availability gradient?

5.1 Abstract

Exotic species can impact native communities by supressing their biomass, abundance and diversity. Currently, it is challenging to predict when and where the greatest impacts from exotic species will occur. Theory and empirical evidence show that exotic plant species often more strongly compete and impact native species in conditions with higher resource levels. If exotic impacts are related to resource levels, management and control efforts could be prioritised to areas or during periods with high expected resource levels.

Here, I tested the competitive effects of three exotic grassland invaders (*Eragrostis curvula*, *Phalaris aquatica*, and *Dactylis glomerata*) on a community of three native grasses (*Bothriochloa macra*, *Chloris truncata*, and *Rytidosperma auriculatum*) that are common in temperate grasslands in South-eastern Australia across a gradient of water availability. By varying frequency of native and exotic individuals across 34 species-density combinations, I quantified both intracommunity (within the native community) and interspecific (native-exotic) competitive effects for each of the three exotic species relative to the three native species. Species treatments were placed in randomised blocks across three water treatments (low, medium and high), replicated four times, totalling 3,600 individual grasses across 408 pots. Species were grown for seven months and individual performance was assessed using aboveground biomass.

All six species had low biomass and high mortality across all the three water levels, suggesting that the experimental set-up in the glasshouse pots were consistently water-limiting. However, the three exotic species had similar or higher biomass and low mortality compared to the native community. Despite the overall poor performance of the grass species, *Dactylis glomerata* was strongly reduced native community biomass; all other competitive interactions were small, presumably because of the stressful glasshouse conditions. Overall, these findings suggest that common invaders can tolerate extended periods with low resources and can still compete and impact native species. Additionally, exotic species are not out-performed by native species during resource-poor conditions, implying that exotic species may resume growth and potential

impacts when conditions become favourable. Thus, prioritising management efforts to areas with high-resource levels may miss the impacts of exotic species in stressful conditions.

5.2 Introduction

Exotic species can have severe impacts on native communities by reducing native biomass, abundance, and local diversity (Pyšek et al. 2012, 2013; Foxcroft et al. 2017). Completely eradicating problematic invaders is often not possible (Schiffman 1997; Gardener et al. 2010). Exotic impacts on native communities are positively related to exotic abundance and diversity (Catford et al. 2011; Vilà et al. 2011), suggesting that management efforts applied to areas with the greatest numbers of exotic individuals could provide the greatest net benefit to native communities.

Within the landscapes they invade, the distributions of exotic species are heterogenous through time and space, making it difficult to predict where and when exotic species are likely to have the greatest impacts on native communities (Levine et al. 2003; Chytrý et al. 2008). The fluctuating resource hypothesis (Davis et al. 2000) has been used to explain why exotic species tend to have heterogeneous distributions. Species differ in their ability to acquire and tolerate varying resource levels (Grime 2006; Reich 2014). Fast-growing, high-biomass species are favoured under high resource conditions, where they often have a competitive advantage over other species (Adler et al. 2018). For example, during spring periods of high rainfall, which is limited during other periods of the year (Thapa et al. 2012; Hovenden et al. 2019). Conversely, species that have conservative habits, e.g. slow growth rate and lower biomass, may be able to persist through extended resource-poor periods when competitive interactions are less important than abiotic tolerance (Volaire 2018). The patchy distribution of exotic species may then reflect the patchy distribution of resources in a landscape: with exotic species having competitive dominance in areas (or during periods) with high resource levels, but not being able to persist in areas or periods with low resource levels.

Native and exotic species often differ in traits associated with resource acquisition and growth rate (Gioria and Osborne 2014; Sandel and Low 2019). Compared to native species, exotic species can have higher values in performance traits, such as growth rate, size, and leaf-area allocation (Van Kleunen et al. 2010). Differences in the growth rate and performance of native and exotic species can lead to exotic species attaining larger biomass compared to native species (Figure 5.1a). With increasing supply of resources, exotic species can competitively impact and

exclude native species (Thompson et al. 2001; Carboni et al. 2016). But the same exotic species may not be able to establish or persist during extended periods of low resource availability, whereas native species may be adapted to such conditions (Figure 5.1a). Hence the impact of exotic species may be resource-dependent. In this way, if we identify a critical resource in the landscape, we may be able to predict the level of invader impact from the level of resource availability across areas of a landscape.

Natural south-eastern Australian temperate grasslands have properties which lend themselves to understanding the impacts of exotic species. Remaining natural temperate grasslands have high species-level diversity but grasslands have been severely impacted by exotic species (McIntyre 1993; Morgan 1998). Many introduced pasture grasses have escaped and become problematic in native Australian grasslands (Cook and Dias 2006; van Klinken and Friedel 2013). In temperate grasslands, many exotic species are often restricted to wetter parts of the landscape, with impacts on native communities greatest in these areas (Charlton and Belgrave 1992; Lolicato 2000; Thapa et al. 2012). However, there is evidence that some 'super-invaders' do well under both high and low resource levels (Funk and Vitousek 2007; Han et al. 2012). But their impacts on native communities are not well enough understood to predict exotic impacts in resource-poor conditions (but see Mason et al. 2012).

Comparing any change in biomass for native and exotic species when grown together and separately across a resource gradient can help assess whether the impacts of exotic species are dependent on resource levels (Figure 5.1a). Exotic impact can be measured as the difference in native biomass when grown by itself (intraspecific competition) compared to when grown in the presence of an exotic species (interspecific competition). Yet, in natural field settings, native species exist in communities, such that there is a mixture of native species competing for the same resources and space (Levine et al. 2003). Therefore, a more useful measure of intraspecific competition is to grow multiple native species with each other (which I term 'intracommunal' competition). One could then compare intracommunal biomass to when the native community are grown in the presence of exotic species (interspecific competition). If the impacts of the exotic species are resource-dependent, exotic species may cause a greater reduction in native community biomass with increasing resources, such as increasing water availability in grasslands; i.e., stronger interspecific relative to intracommunal competition (Figure 5.1a). Changes in native-native and native-exotic densities confound estimating the competitive effect of exotic species, which can reduce the certainty of using experimental results in field settings (Freckleton and Watkinson 2000; Inouye 2001). Ideally, native-exotic species interactions are

compared across multiple densities and proportions of native-exotic individuals to determine the strength of exotic impact (Figure 5.1b). This experimental design allows competition estimates to be calculated for individuals or at the community-level accounting for variation in density (Inouye 2001). Estimates of intracommunal and interspecific competition could then be used to determine whether higher resource levels are associated with greater exotic impact.

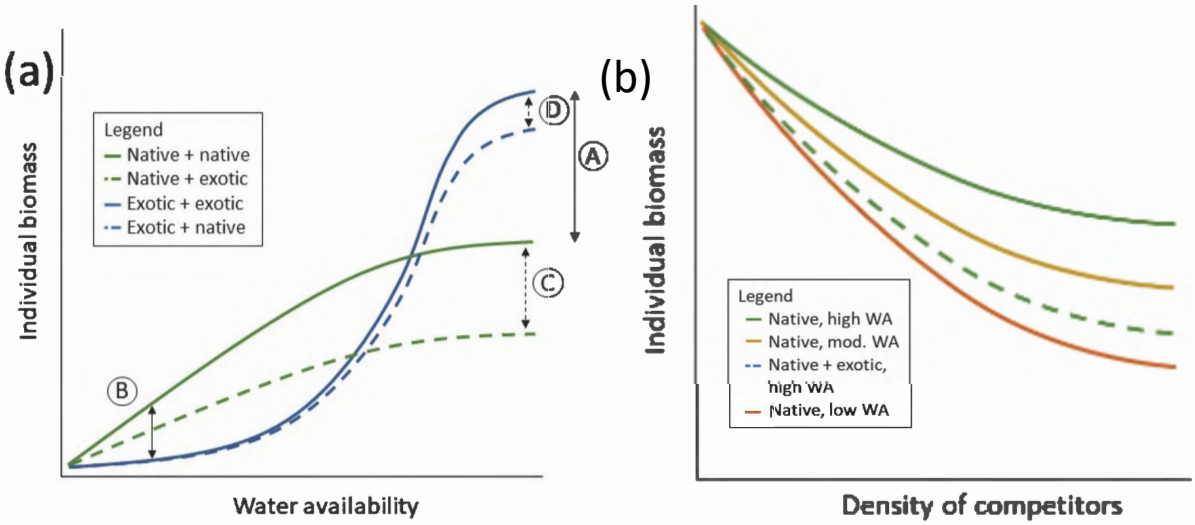

Figure 5.1 Individual native and exotic biomass as a function of increasing water availability and density of competitors. (a) The biomass of an individual native species (solid green line) and exotic species (solid blue line) grown in monoculture pairs are expected to increase with water availability to a point where biomass is limited by other factors and additional water has no further effect on biomass. At this end point, exotic species often have high biomass under high-resource conditions, meaning exotic biomass is expected to be much greater than native biomass (A). But at low water levels, this trend may reverse because native species have traits than may enable them to better utilise low levels of resources (B). When native and exotic individuals are grown together, it is expected that native biomass will be reduced compared to monoculture growth (C), as will exotic biomass (D), but this difference in biomass will be much greater in the native individual (C >> D) which is defined as high exotic impact. (b) Biomass of an individual native species in a community of other competitors (solid green line) is expected to be the greatest when grown in isolation and decrease with increasing density of competitors. Similarly, native biomass is expected to decline with decreasing water availability (WA) (high-to-medium-to-low). The effect of density may be greater at the highest level of water availability if the identity of the competing individual is changed from a native species to an exotic species (dashed green line) and may be comparable to the effect of low water availability (i.e. drought). Figure (b) adapted from Hart et al. (2018).

Here, I aim to test whether water availability can alter the outcomes of the competitive impact of three exotic grasses on a community of three native grasses. I grew the three native grasses

together with and without the presence of each of the three exotic species across a water availability gradient (high, medium and low levels) in pots within a glasshouse. I defined exotic impact on the native community as the difference in native community biomass between intraspecific (native community) treatments and interspecific competition (native community biomass in the presence of each exotic species) treatments. To quantify competitive effects, I used an experimental design that varied the density and proportions of native-exotic neighbours (Hart et al. 2018), allowing me to estimate the effects of intra- and interspecific competition on the native community allowing for variation in density. In addition, this enabled me to determine how competitive effects, and hence impact, varied across a water availability gradient.

I used biomass data from 3,600 individuals across 408 experimental units to test three hypotheses:

(i) Native community and exotic species biomass declines with decreasing water availability and this decline is greater for exotic species relative to native species.

(ii) Exotic species have stronger competitive impacts on native community biomass than native species have on themselves, and exotic biomass is less affected by competition from the native community compared to itself.

(iii) The competitive effect of exotic species on the native community is reduced under water stressed conditions, such that exotic species have a disproportionately low impact in dry conditions but a much greater impact in wet conditions.

5.3 Methods

5.3.1 Species selection

To make up the native community, I selected three common native perennial grasses that co-occur in temperate grasslands of south-eastern Australia, *Bothriochloa macra* (Steud.)*, Chrolis truncata* (R. Br.), and *Rytidosperma auriculatum* (Lindl.). These grasses have differing water use requirements during their growing periods (Sprague 1908; Wilson 1996; Weller et al. 2019), and I chose these species to represent some of the diversity in growth strategies in native temperate grassland communities. *B. macra* and *R. auriculatum* are C3 species (cool-season growth) and *C. truncata* is a C4 species (warm-season growth).

To test the competitive impact of exotic species on the native community, I selected three common exotic grasses: two perennial pasture grasses, *Phalaris aquatica* L. and *Dactylis glomerata* L., and a Weed of National Significance, *Eragrostis curvula* (Schrad.) (Thorp 2006). All three exotic grasses have been widely planted across south-eastern Australia (Firn 2009; Reed 2014) and have subsequently naturalised in natural temperate grasslands. These exotic grasses have different resource demands, enabling me to test how native-exotic competitive interactions could differ across a water gradient: *P. aquatica* is a water-demanding C3 grass (Lolicato 2000) and *D. glomerata* is a relatively drought-resistant C3 grass (Duru et al. 2004); and *E. curvula* is a drought-resistant C4 grass (Han et al. 2012).

5.3.2 Experimental design

The native community and the three exotic grasses were grown in 2 L pots in a glasshouse at the University of Canberra, ACT. There were a total of 34 competition treatments across the four densities of the native community, each of the three exotic species, and the native community-exotic mixtures (Figure 5.1; Table D.1). In the pots, I quantified intra- and interspecific competition across four densities (3, 6, 9 and 12 individuals) (Figure 5.2). All three native species were included in treatments that contained the native community, and so each native species contributed 1/3 of the total pot density, e.g. a native density of 3 meant that there was 1 individual of each species, while a native density of 9 comprised of 3 individuals of each species. The three exotic species were grown separately from one another to provide species-specific estimates of their competitive effect on native species. Consequently, the density of each exotic species matched the exotic species density of the pot (Table D.1).

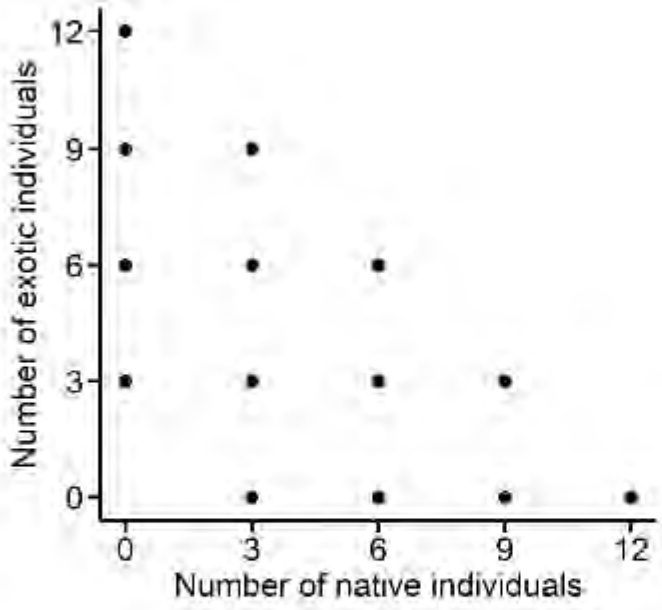

Figure 5.2 Density and identity of individuals from a native community (native individuals) and exotic species (exotic individuals). This design ensures that native and exotic individuals are grown in isolation to test for intraspecific competition (bottom row, left column), and together to test for interspecific competition (mixed native-exotic individuals), across different proportions and total densities (Jolliffe 2000).

The 34 competition treatments were replicated four times across the three levels of water availability (low, medium, high), totalling 3,600 individuals across 408 pots.

I used a blocked design to allocate pot positions within the glasshouse. I based the blocks on water availability replicates (12 blocks of 34 pots). I randomly allocated blocks across bench positions within the glasshouse, ensuring that neighbouring blocks were different levels of water availability.

5.3.3 Set up of experimental units

In 2019, I attained seeds of *P. aquatica* and *D. glomerata* from CleanSeeds Ltd. (Bungadore, NSW), and *B. macra*, *C. truncata* and *R. auriculatum* from Foreshore Plants (Batemans Bay, NSW), and *E. curvula* on site at the University of Canberra (S 35°23’47.8”, E 149°08’44.8”). *Bothriochloa macra* was obtained pre-sowed June 13 (because of limited availability of native seed stock), and I sowed the other five species July 22 in seed raising trays containing a coir mix (Bunnings, Belconnen, ACT).

I transplanted the seedlings beginning August 4 over a two-week period. I randomly selected the order of potting up by replicate (block), and each block was completed in a single day. The native community and the three exotic grasses were grown in 2.0 L pots in soil consisting of 60% pine bark, 25% sand and 15% vermiculite (Australian Growing Solutions, Tyabb, VIC). During the potting up period, all pots and seed raising trays were watered twice daily to saturation. There were differences in the sizes of the seedlings between and within each species, so seedlings of similar sizes were selected for each pot to ensure consistency at the pot-level.

Following potting up, there was a two-week establishment period where pots were watered to saturation once-per-day and dead individuals were replaced.

5.3.4 Water availability levels

5.3.4.1 Starting conditions

The competition treatments were replicated across three levels of water availability: low, medium, and high. The high water availability level was designed to ensure that individuals were at no period water-limited, watering plants every day; the medium water availability level was designed to be partially water-limited by providing plants with a proportion of watering days in the week; and the low water availability level was designed to be significantly water-limited by providing plants with a conservative proportion of watering days.

To maintain and adjust the three watering levels, I set up three watering programs using a Hunter X-Core (EasyRain, Fyshwick, ACT). The four blocks of each water level were set to the same program. Each block had its own pump which delivered ~70 mL/min water to each of 34 pots via 34 dedicated 2 L/min drippers. Water was delivered to pots in timed-intervals per watering day. Watering intervals and days were adjusted based on seasonal changes, quantified using soil water content using a Campbell HYDROSENSE II (Campbell Scientific Ltd, Garbutt, QLD). Specifically, I calculated the field saturation point for the 2 L soil mixtures as ~30% weight by volume (w/v). Initially, to maintain this level, I set the high water level's program to deliver water to the pots at two 2-minute intervals, 7 days-per-week. Periodically, I measured the soil saturation to ensure pots were between 22-30% w/v. The medium water level was set at two 2-minute intervals, three-to-four times per week, ensuring pots averaged between 15-20% w/v. The low water level was set at two 2-minute intervals, one-to-two times per week, ensuring pots averaged between 5-10% w/v.

5.3.4.2 Watering regime adjustments

Initially, plants were going to be harvested 12 weeks following establishment. However, by this point plants across all water levels had not grown to expected sizes and much higher mortality deaths than anticipated. Nutrient addition was applied in the form of Hoagland's solution (Hoagland and Arnon 1950) from 25 November, every two weeks. The first application was 25% solution, the second 50%, the third 75%, then 100% was applied until harvesting. The

solution was added in 150 mL dilutions (to mimic a two-minute watering interval) and pots were not watered for that part of the day.

During the first four-weeks of nutrient addition, plant performance did not change, so I watered all pots to saturation every two days for two-weeks, commencing December 22. I then adjusted the three water programs to more constantly supply the units with more water until harvesting. High: three 5-minute intervals 7 days-per-week; medium: three 5-minute intervals 3-to-4 days-per-week; and low: three 5-minute intervals 1-to-2 days-per-week.

5.3.5 Biomass collection

Aboveground biomass was collected 34 weeks after establishment. Replicates were harvested in a random order, and each within one day. Aboveground biomass was considered all material above the roots. There was no reproductive tissue on any plant. Plants were considered alive if there was evidence of green biological material and placed into paper bags. Dead individuals were not collected because of their small biomasses. Plant material was then oven dried within paper bags at 70° for 72 h. Plants were weighed outside of bags to determine biomass.

5.3.6 Determining the effect of water availability on biomass and intracommunal and interspecific competition

I determined whether water availability had an effect on individual biomass and whether intracommunal and interspecific competition varied with water availability within and between the native community and three exotic grasses using a replacement series design (Jolliffe 2000). Replacement series designs takes into the account the confounding effect of density on species-species interactions by testing the difference in biomass across different densities and proportions of (in my case) native-exotic individuals (Figure 5.2, Table 5.1). This allowed me to calculate the expected change in an individual's biomass based on the identity of its neighbours: intraspecific native or exotic competition or interspecific exotic-native competition. I treated the three native species as one species. Exotic impact was defined as the difference in expected intraspecific and interspecific biomass for each of the three exotic species. I then tested whether overall biomass and the strength of intracommunal and interspecific competition varied along a water gradient (i.e. low, medium and high water levels).

The replacement series design is based on the law of constant yield (Weiner and Thomas 1986), which describes how the biomass of an individual changes with the density of neighbours (Freckleton and Watkinson 2000):

$$B_i = \frac{\lambda_i}{1 + \alpha_{ii}(N_i - 1)} \tag{1}$$

where B_i is the biomass of a target individual of species i, N_i is the number of individuals of species i in a pot (so $N_i - 1$ is the number of individuals that the target species is competing with), λ_i is the biomass of an individual when grown in a pot on its own (such that $N_i - 1 = 0$ and $B_i = \lambda_i$), and α_{ii} is the effect of each additional individual on the growth of the target individual (i.e. intraspecific competition).

This equation can be expanded to include situations where species are grown in competition with individuals of the same species and with another species j:

$$B_i = \frac{\lambda_i}{1 + \alpha_{ii}(N_i - 1) + \alpha_{ij}N_j} \tag{2a}$$

where α_{ij} is the effect that each additional individual of species j has on the growth of an individual of species i (i.e. interspecific competition) and N_j is the number of individuals of species j.

The effect of water availability can also be included as an effect on an individual's overall biomass:

$$B_i = \frac{\lambda_{ik}}{1 + \alpha_{ii}(N_i - 1) + \alpha_{ij}N_j} \tag{3a}$$

where λ_{ik} is how an individual's biomass λ_i varies based on water availability level k.

The effect of water availability on the strength of intracommunal and interspecific competition can also be determined using this framework, expanding the previous equation to:

$$B_i = \frac{\lambda_{ik}}{1 + \alpha_{iik}(N_i - 1) + \alpha_{ijk}N_j}$$

(4a)

where α_{iik} is the effect of water availability on intraspecific competition within species *i*, and α_{ijk} is the effect of water availability on interspecific competition between species *i* and species *j*.

The frequency of raw biomass values are often left-skewed, so that log-transforming biomass often normalises the data and stabilizes the variance. Log-transforming equations 2a, 3a and 4a allows these equations to be fitted using log biomass as the response variable:

$$\log(B_i) = \log(\lambda_i) - \log\left(1 + \alpha_{ii}(N_i - 1) + \alpha_{ij}N_j\right) + p$$

(2b)

$$\log(B_i) = \log(\lambda_{ik}) - \log\left(1 + \alpha_{ii}(N_i - 1) + \alpha_{ij}N_j\right) + p$$

(3b)

$$\log(B_i) = \log(\lambda_{ik}) - \log\left(1 + \alpha_{iik}(N_i - 1) + \alpha_{ijk}N_j\right) + p.$$

(4b)

In each of equations 2b, 3b, and 4b, I included *p* to account for the position of the pot in the glasshouse, where *p* was the bench ID of each pot. Mortality was relatively high and tended to occur early on in the experiment, meaning there were many dead individuals early on in the establishment period of the grasses (Table 5.2). To take account for the reduced density of individuals in pots for much of the growing period, I removed dead individuals from the analysis and adjusted the pot densities based on the number of surviving individuals. Equations 2b, 3b, and 4b are not in the form of a linear model due to the log(1 + a + b) form, so I used a Bayesian model framework to estimate the effect of water availability on biomass and intra and interspecific parameter values and competition-water availability interactions via the *jagsUI* package (v 1.5.1) in R (R Core Team 2020).

Equations 2b, 3b, 3b represent hypotheses (i), (ii) and (iii). Each equation builds on the hypothesis tested in the previous equation. Equation 2b tests whether the strength of native-

native (intracommunal) competition on individual biomass is greater or smaller than the strength of native-exotic (interspecific) (competition model). Equation 3b adds whether individual biomass also varies with water availability, expecting that exotic biomass may be lower than native biomass at low water availability but much greater at high water availability (competition + water model). Equation 4b tests whether water availability also varies the strength of intracommunal and interspecific competition, expecting that individual native biomass is more impacted by the presence of exotic individuals at higher levels of water availability (competition * water model).

I compared the fit of the three models using the deviance information criterion (DIC) value, which is similar to Akaike's information criterion (AIC): the model with the with the lowest variance and fewest parameters has the lowest DIC value and greatest relative support (Lunn et al. 2012). A difference in DIC values of > 10 indicates that there is a strong likelihood that the model with the lower value is the more suitable model, whereas a difference of < 5 indicates similar support for both models, and a differences between 5 and 10 indicate that there is likely a difference in model fit (Lunn et al. 2012). I applied a conservative threshold, requiring a difference of >10 between the model with the lowest DIC value and the next best-fitting model. If DIC values were within 10, I chose to interpret that the simplest model (i.e. equations 2b or 3b) had the greatest level of support.

5.4 Results

5.4.1 Native and exotic biomass and the effect of water availability

The model with the greatest level of support was the competition + water availability model (equation 3b) (Table 5.1). A difference in DIC values of 48.9 strongly suggested that water availability had an overall effect on native community and exotic species biomass, but water availability did not alter the strength of intra and interspecific competition. However, mean individual biomass of the native community and three exotic species did not decrease with a decrease in the level of water availability as expected (Figure 5.3). Instead, biomass estimates across all species groups were lower in the high water availability level compared to the medium and low availability levels (Figure 5.3). Additionally, mean individual biomass across the three water availability levels was low; the native community had the lowest biomass and *D. glomerata* had the highest (Figure 5.3).

Table 5.1 Model fits ranked by delta-DIC (deviance information criterion) values. Delta-DIC is the difference in DIC values from the best-fitting model and the other models. The three models were based on three hypotheses that each tested successive components of aims (i) – (iii): the effect of intracommunal and interspecific competition on mean individual biomass between a native community and three exotic species (competition); the effect of changing water availability on biomass (water); and the interaction between the strength of intracommunal and interspecific competition and water availability (competition * water).

Model (equation)	DIC value	Delta-DIC
Competition + water (3b)	8799.2	0
Competition * water (4b)	8849.0	49.9
Competition (2b)	8872.3	73.1

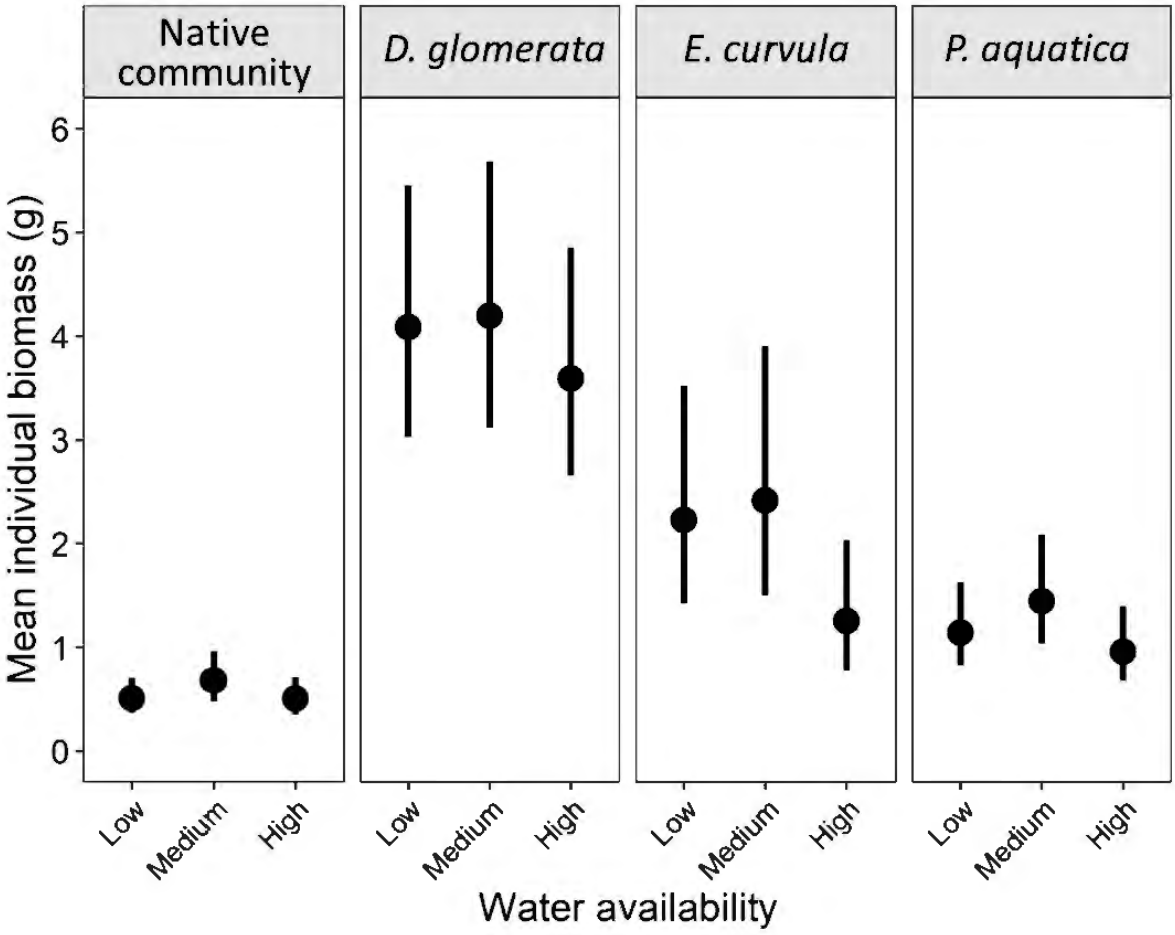

Figure 5.3 Individual biomass of the native community and each of the three exotic species by level of water availability, estimated using model equation 3b. Points are mean estimates from the model and error bars are 95% credible intervals. The Native community was made of *Bothriochloa macra, Chrolis truncata,* and *Rytidosperma auriculatum*.

There was small negative effect of density on the mean individual biomass of the species groups which did not vary by water availability (Figure 5.4).

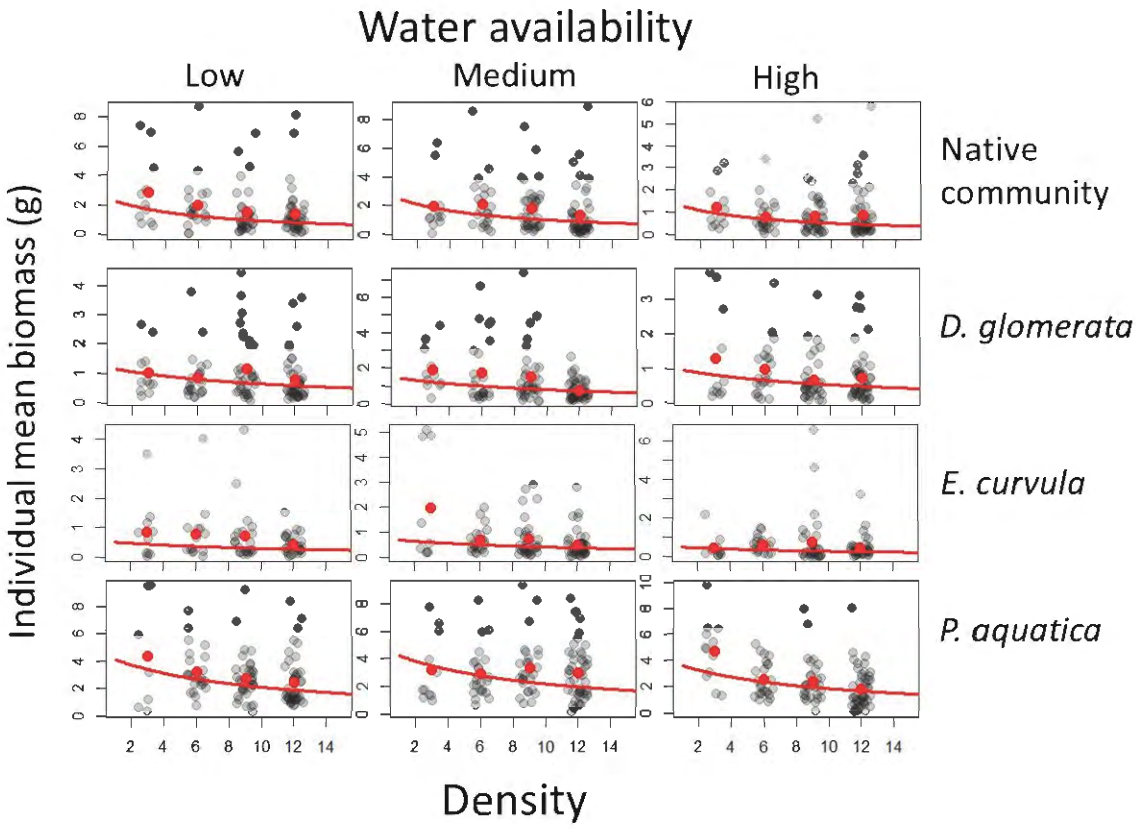

Figure 5.4 Expected individual biomass on observed biomass by water availability for the native community and three exotic species. Open circles, observed individual biomass; red dots, mean observed individual biomass; red line, expected mean individual biomass from modelled data. Data are for intracommunal competition treatments only. The native community consisted of *Bothriochloa macra, Chrolis truncata,* and *Rytidosperma auriculatum.*

Around 12% of the 3,600 individuals did not survive to the end of the experiment (Table 5.2). The three native species had a much higher mean mortality percentage compared to the three exotic species (21.8% compared to 5.9%, Table 5.2). Mortality percentage for five of the six species appeared to be positively associated with decreasing water availability, and the sixth species, *B. macra*, had consistently high mortality rates across all water availabilities (Table 5.2).

Table 5.2 Species mortality percentage following 34 weeks of growth.

Status	Species	Mortality by water availability (%)			Total frequency	Total individuals	Mortality percentage
		Low	Medium	High			
Native	*B. macra*	11.2	9.0	10.6	148	480	30.8%
	C. truncata	6.7	3.5	2.9	63	480	13.1%
	R. auriculatum	14.6	3.8	2.7	101	480	21.4%
Exotic	*D. glomerata*	3.3	1.9	1.4	48	720	6.6%
	E. curvula	3.1	1.1	0.6	34	720	4.8%
	P. aquatica	3.8	1.4	1.0	44	720	6.2%
Total		6.4	3.1	2.8	438	3600	12.3%

5.4.2 The effects of intracommunal and interspecific competition on native community biomass

Dactylis glomerata had the highest interspecific competition value on the native community, meaning its presence was strongly associated with a reduction in native community biomass (Figure 5.4, green box). There was no evidence that the native community had any competitive impact on *D. glomerata* biomass (Figure 5.4, blue box). There was little evidence of competition among the native community and the other two exotic species: the intracommunal effect of the native community on itself was small and similar to the interspecific competition effects of *P. aquatica* and *E. curvula* (Figure 5.4, green box), and vice versa (Figure 5.4, yellow and purple boxes).

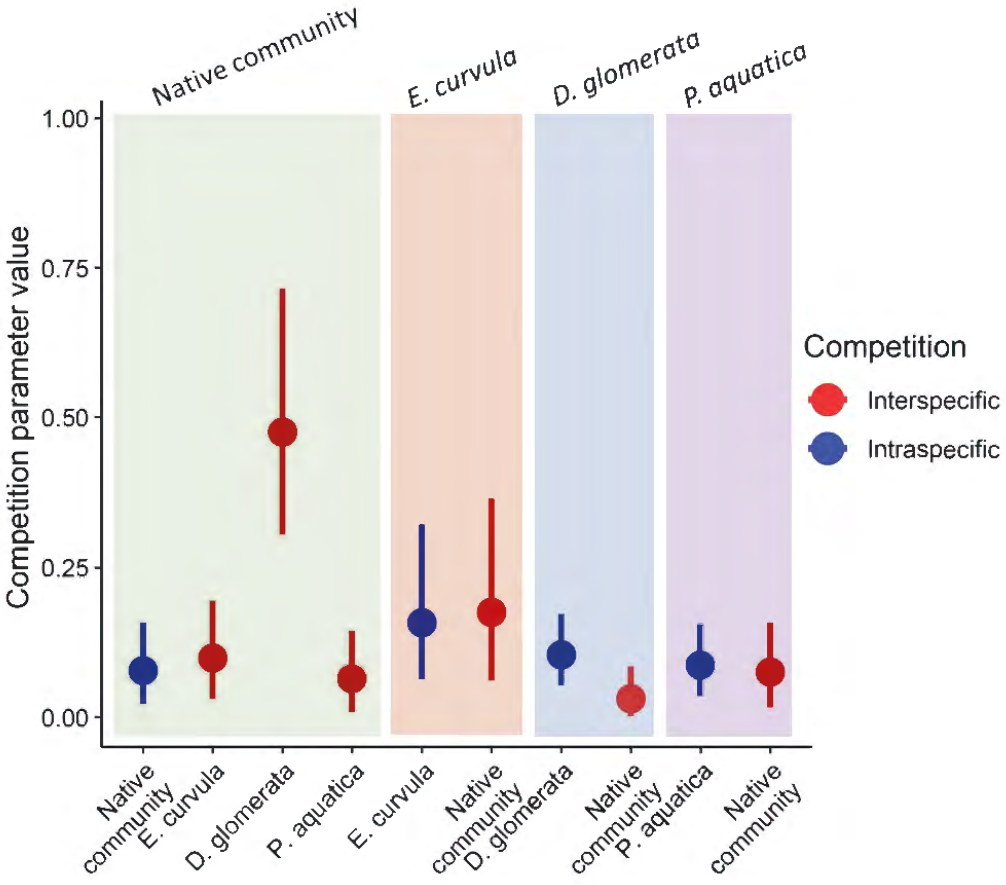

Figure 5.5 The strength of intra and interspecific competition for a native community and each of three exotic species, averaged across three levels of water availability (low, medium and high). Competitive interactions were as the effect of species *j* (bottom x-axis) on species *i* (top x-axis). Intraspecific or intracommunal competition parameter (blue circle) is the effect of the focal species/community on itself. Interspecific competition parameter (red circle) was measured as the effect of the native community on the exotic species, and of the exotic species on the native community. The error bars represent 95% credible intervals. The native community was made of *Bothriochloa macra, Chloris truncata* and *Rytidosperma auriculatum*.

5.5 Discussion

5.5.1 The effect of water availability on native and exotic performance

Increasing resource levels are thought to drive the degree of impact exotic species have on native communities (Davis and Pelsor 2001). Here, I found an effect of water availability on the biomass of the native community and three exotic grasses, suggesting that individual performance was affected by the level of water availability, but that water availability did not affect the strength of competition within or between the native community and the three exotic

species (Table 5.2). While there appeared to be an effect of water availability, it was in the opposing direction to what was expected: mean individual biomass of the native community and three exotic species was lowest in the high water availability treatment (Figure 5.3).

Grassland species biomass typically declines with decreasing water availability (Tilman et al. 1992; Knapp and Smith 2001; Sala et al. 2012). However, following seven months' growth, native community and exotic biomass was low across all three water levels (Figure 5.3, Table 5.2). The best performing species, *D. glomerata*, had a similar individual biomass compared to a field study which had particularly low annual rainfall (Zhouri et al. 2019). In the same study by Zhouri and colleagues, mean biomass *D. glomerata* was five and 20 times greater in two other years that had much greater rainfall levels. A glasshouse study by Fynn and Naiken (2009) found that *E. curvula* had around five times greater individual biomass compared to biomass values found here. Similarly, *C. truncata* mean biomass found here were comparable to biomass found in a study assessing the effect of water stress on individual performance (Weller et al. 2019).

Biomass did not vary much with increasing individual plant density and there was also high mortality across all three water treatments, highest in the low water treatment (Table 5.3; Table D.2). These results suggest that the experimental set up in this study may not have generated a high-to-low water gradient as intended, but instead tested native and exotic species performance across similar water-limited conditions for at least their first three-months of growth. The lower biomass in the high water treatment could have been due to overwatering following the first three-months of establishment.

The relatively high survival and biomass of the exotic grass species compared to the native community suggests that successful invaders have the ability to tolerate drought-like conditions at least as well if not better than resident native species. Similar conclusions were made by Han and colleagues (2012), who found *E. curvula* performed as well as two native grasses in water-limited conditions. These findings are in opposition to the perspective that native species are better adapted to stressful conditions compared to exotic species (Diez et al. 2012).

Grasses have a wide range of tolerances to differing water levels (Craine et al. 2013; da Silveira Pontes et al. 2015) but persistence through stressful conditions is key for grasses to establish in many parts of Southeast Australia (Garden et al. 2005; Waters et al. 2005). Exotic grasses may have the ability to cease growing during stressful periods to avoid damage from water stress

(Volaire et al. 2009). For example, C4 grasses such as *E. curvula* have adaptations to stop growing in cool and dry winter or hot and dry summer months as well as traits such as leaf rolling to reduce water loss (Fay et al. 2003; Bolger et al. 2005). Cultivars of C3 pasture grasses such as *P. aquatica* and *D. glomerata* have been selected for a summer dormancy period and deep roots associated with its persistence through hot and dry periods (Waters et al. 2005; Dear and Ewing 2008; Culvenor 2009).

5.5.2 The effects of intracommunal and interspecific competition on native community biomass and the implications for managing exotic species

There is mixed evidence of the relative importance of intraspecific and interspecific competition along resource gradients (Burke and Grime 1996; Goldberg and Novoplansky 1997). These ideas offer differing predictions about the outcome of competition between native species and exotic species at low resource levels. If interspecific competition remains steady along a resource gradient, we might expect native species to be impacted by exotic species at a range of resource levels (Tilman et al. 2006), but not if interspecific competition declines at low resource levels (Davis et al. 2000).

I also found mixed evidence of the effects of interspecific competition at the apparent low resource levels. For example, the competitive effect of *E. curvula* and *P. aquatica* on the native community was small (as was the effect of the native community on itself). This suggested low species-species interactions and, together with low biomass following seven months' growth, that in most cases abiotic effects were probably the greatest influence on plant performance.

When exotic species can attain higher biomass in resource-poor conditions, they may be able to do so at the expense of native species. The species with the greatest biomass, *D. glomerata*, also had a stronger suppressive effect on the native community, suggesting that the presence of *D. Glomerata* altered the resource conditions for the native community. Exotic impact on native grass species in water-stressed conditions has been observed in experimental studies and in field settings elsewhere in Australia (Mason et al. 2012; Manea et al. 2016). For example, the presence of *Cenchrus ciliaris* (Buffel grass) was strongly associated with a decline in native species abundance during a 28-year period following alleviation of grazing in semi-arid grasslands in Central Australia (Clarke et al. 2005). The impacts of Buffel grass were also greater than the effects of drought years; rapid Buffel growth was thought to drive competition with ground-dwelling species, while altered fire regimes were thought to impact woody species.

Predicting the effects on invaders remains challenging and those species that do the impacting remains challenging but central to managing exotic species. Often management is directed to areas that have intact native communities (e.g. high proportion of cover, species-level diversity) (Firn et al. 2008; Prober et al. 2009). Moreover, due to the high survival rate and growth of exotic species in these communities, exotic species may be poised to prosper following elevation of drought conditions, which may well increase their impacts (Boeck and Lemmens 2008; Bernard-verdier et al. 2018). Therefore, reducing the impacts of exotic species by targeting management efforts to areas or during periods of high-resource levels will leave some communities exposed to the effects of some invaders.

However, management efforts applied to a range of native communities may be useful for controlling the impacts of exotic species (Prober et al. 2005). Degraded sites, such as those which have low native cover or diversity, can benefit from changing disturbance regimes. Targeting sites which have the low native cover or diversity and highest exotic cover could provide the greatest benefit to increasing native communities, rather than restricting efforts to maintaining those areas with relatively intact native communities. For example, Prober and colleagues (2009) found that prescribed burning across a range of highly-invaded and degraded sites increased native cover and decreased exotic cover.

5.5.3 Experimental considerations

Despite the overall poor performance of the plants in this study, the experimental design captured the intracommunal and interspecific competitive interactions well. The methodological design was also able to partition the effects of density and identity of neighbouring individuals, which was useful in determining the strength of intracommunal and interspecific competition (Inouye 2001). In practical terms, this enables one to determine how plant *A* affects plant *B*, and plant *B* affects plant *A*. This is useful for comparing how competitive effects could change depending on resource level (Hambäck et al. 2014). I found that mean biomass estimates had acceptable levels of uncertainty to allow comparison of intracommunal and interspecific competition estimates. Therefore, for its complexity, the replacement series design is useful for testing multiple competitive interactions.

I chose native species that have differing water use requirements, meaning the contribution of each of the three native species to mean biomass could have differed between each water level, but overall mean biomass could have remained similar across the water treatments. However,

mean individual biomass of each of the native species were overall low and did not change much between each water treatment (Figure 5.3; Table D.2). Using intracommunal competition therefore may not have altered the results of this study; more than likely, native plants were grown in drought-like conditions during at least the first four months of establishment, contributing to native species' poor performance and high mortality.

5.5.4 Future directions

Reproducing this study across a larger water-availability gradient would be useful, aiming to capture native and exotic performance and interactions at high resource (water availability) levels. This could better test the third hypothesis of this study, that water availability could alter the strength of interspecific competitive interactions. Across a larger water availability gradient, it would be expected that *P. aquatica* and *E. curvula* could competitively dominate native species at higher resource levels, and that this effect could be comparable to the effect of water limitation (Boschma et al. 2009; Han et al. 2012). The results then could be extrapolated to a range of field conditions that grasses in the ACT occur in and used to predict competitive interactions in the field (e.g. Bates et al. 2021).

This study did not have the resources to test other measures of plant performance but these could be added in future studies. For instance, plant interactions in water-limited environments are thought to be most intense between below-ground systems (Goldberg and Novoplansky 1997). Exotic species often have more plastic traits which allow them to vary their phenologies to different environmental conditions, for example by increasing root-shoot ratio (Phillips et al. 2019). Measuring below-ground (i.e. root) biomass and the root:shoot ratio could also help determine how native and exotic species compete at varying resource levels (Mason et al. 2012). Nutrient levels also determine intracommunal and interspecific interactions between native and exotic grasses and can be added into the replacement series design used in this study (e.g. O'Reilly-Nugent et al. 2020).

Plants could be grown for a longer period of time. For example, Zhouri et al. (2019) found that mean *D. glomerata* biomass increased to 88.17 g in its second growing season, some 20 times its mean biomass in the first season, likely due to the effects of low rainfall. It would be useful, then, to understand the effect of competition within and between growing seasons and years. This could be particularly useful to explicitly test the effect of exotics persisting through

resource-poor periods, and then their capacity to ‘bounce back’ once resource levels are higher – and whether this increased their impacts on native species.

5.5.5 Conclusions

Here I showed that apparent low levels of water availability had large effects on the performance of a community of native species and three exotic grass species. Despite the water-limited conditions, exotic species performed as well if not better than native species, suggesting that exotic species can persist through stressful conditions. The overall survival of exotic species and the large impact of *D. glomerata* on the native community suggests that the presence of exotic species nor their impacts are excluded by stressful conditions. The findings of this study suggest that managing only high-resource areas or following periods of resource dumping (i.e. rainfall events) may not be adequate to control for the impacts of exotic species.

Chapter 6 – General Discussion

6.1 Summary of findings

This thesis had three broad aims. First, to determine the processes that drive plant species richness. Second to use this knowledge to develop a method to forecast patterns of native and exotic plant species richness. Third to examine the potential for resource availability to influence the impact of exotic species on a community of native species. My key questions were:

(i) Do patterns of native grass species richness provide a template for the invasion potential of exotic grasses in Australia?
(ii) Under what circumstances might native species richness be useful as a template for the invasion potential of exotic species?
(iii) Do species richness–environment gradient relationships in one region predict similar richness relationships in other regions?
(iv) Do the competitive impacts of exotic grass species on a native grass community vary as a function of water availability?

For my first question, I showed that within 100 × 100 km cells across Australia, for C3 and C4 grasses: (i) native and exotic species richness was positively correlated in areas where both native and exotic species co-occurred, meaning that cells with high native richness tended to also support high exotic richness; (ii) native and exotic species richness had similar associations with environmental variables, implying that (iii) native species richness patterns could be used as a template for potential exotic species richness (Chapter 2). From this, I inferred areas can potentially support greater numbers of exotic grass species were those areas with high native richness and proportionally lower exotic richness. Typically, native and exotic C3 grasses had similar richness patterns, suggesting the invasion potential of C3 grasses across Australia was generally low. In contrast, for C4 grasses large regions of northern Australia had large differences between native and exotic richness, implying that areas in this region have the potential to support much greater numbers of exotic C4 grasses.

I then investigated whether there was general support for the native richness template by testing whether the three criteria (i), (ii) and (iii) developed above on C3 and C4 grass species plus an additional 20 common native and exotic plant families across Australia (Chapter 3). I aimed to

find out how often native richness could provide a useful template for predicting exotic richness and if there were family-level characteristics that explained why the template might work for some families but not others. Among the 22 families (including the C3 and C4 grasses), I found mixed results in terms of support for (i) and (ii) and thus (iii). The template worked well for five families, but for most families, native and exotic richness was not strongly positively correlated in areas they co-occurred and/or native and exotic richness were not similarly associated with environmental gradients. For many families, I found that native species richness patterns were only weakly correlated with environmental gradients because of particularly high species richness in the south-western region of Australia, likely due to biogeographic influences, such as isolation and climate change. It is also likely that exotic species were dispersal-limited, which affected the locations where native and exotic richness co-occurred. In all families, areas with enough records per cell to estimate exotic species richness tended to be concentrated in areas with high levels of human impact. For some families, however, such areas were poorly suited for native species, which affected observing a strong correlation between native and exotic richness. Thus, the native richness template is unlikely to work in situations where native species richness patterns do not follow environmental gradients and/or exotic species are strongly dispersal-limited from otherwise suitable areas.

I then examined the potential roles of environmental gradients, biogeographic factors and human impacts on native and exotic plant assemblages (Chapter 4). I tested whether native C3 and C4 grass species richness in Australia could predict native and exotic grass species richness in New Zealand. I found that associations between Australian grass species richness and environmental variables predicted similar native and exotic species richness patterns in New Zealand. This strongly suggested that independently assembled grass communities have similar relationships to environmental gradients. However, after accounting for environmental conditions, New Zealand has lower native grass species richness compared to Australia. Lower species richness in smaller and more isolated landmasses is consistent with the predictions of the Theory of Island Biogeography (MacArthur and Wilson 1963; Warren et al. 2015). In New Zealand, exotic grass species richness was similar to or greater than that predicted by either New Zealand or Australian native grass richness, in line with other studies showing that islands support some of the greatest relative levels of exotic richness.

I found that the success of current grass invaders might be partly attributed to their ability to tolerate resource-poor conditions (Chapter 5). In a glasshouse experiment, the survival and performance of three common grassland invaders (*Eragrostis curvula, Phalaris aquatica*, and

Dactylis glomerata) in temperate grasslands in the ACT (Australia) was much greater than a community of native resident grasses. Additionally, it appeared that, despite the low levels of water availability, *D. glomerata* impacted the performance of native species. These findings suggest that, at apparently low resource levels, successful invaders can persist better than native species and that these conditions do not necessarily result in lower impacts on native communities.

6.2 Environmental influences on species richness

6.2.1 Native species

Globally, native terrestrial plant taxa species richness varies strongly along climatic and topographic gradients, suggesting environmental gradients are strong general influences on plant species assemblages (Francis and Currie 2003; Ben-Hur and Kadmon 2020; Huang et al. 2021). Environmental gradients are thought to affect species richness patterns because of the constraints that temperature, water availability, and temperature-water interactions have on plant physiology (Francis and Currie 2003). Thus, the relationship between species richness environmental gradients is stronger among more closely related taxa because more related species tend to have more similar physiological tolerances (Wiens 2004). I found support for the role of environmental (climatic and topographic) gradients on plant richness patterns at the family level, finding 10 of 22 common plant families in Australia had a moderate-to-high proportion of variation explained by environmental variables (Chapter 3). I also found that native C3 grass species in Australia had very similar richness-environment associations compared to New Zealand's native C3 grasses, and these environmental associations predicted similar Australian-origin and New Zealand-origin C3 richness across New Zealand (Chapter 4).

Stable, warm and wet conditions are thought to impose the fewest restrictions on plant physiologies and hence support the greatest numbers of plant species (Huang et al. 2021). As conditions stray from warm, wet or stable, plants experience greater water and heat (or cold) stress (Lukatkin 2003; Wright et al. 2005), thus species richness declines. In Australia, I found nine of the 22 families had high species richness in northern and north-eastern regions characterised by hot, wet and year-round stable climates. Thus, the majority (13 f 22) of common native plant families in Australia appear to have adapted into environmental conditions

which include those which are, at the kingdom level, relatively physiologically demanding. For example, Chenopodiaceae and Solanaceae had high species richness in the arid Western and Central regions of Australia (Appendix B).

I found that species richness of some large families (e.g. Fabaceae, Chenopodiaceae, Asteraceae, Brassicaceae) did not strongly vary across Australia. This is remarkable considering Australia's area (6.7 million square kilometres) and climatic diversity (deserts, mountains, tropics). This suggests that there is physiological plasticity within some families that may allow them to evolve and tolerate a large range of environmental conditions. For example, the grasses have evolved two photosynthetic pathways (C3 and C4 photosynthesis) which appear to have enabled them to colonise the vast majority of Australia, with particularly high C4 richness in hot and tropical northern regions, and high C3 richness in temperate southern regions (Chapters 2 and 3).

6.2.2 Exotic species

Johnstone (1986) put forward the idea that, at the individual plant level, invasion is no different to succession. At large spatial scales, then, are the products of many invader 'successions' any different from native successions? Are exotic species assemblages under the same large-scale influences as native assemblages? Evidence from other studies suggests that exotic species richness patterns are strongly influenced by environmental gradients (Stohlgren et al. 1999; Pyšek et al. 2010; de Albuquerque et al. 2011; Bellard et al. 2013; Mologni et al. 2021; Wohlwend et al. 2021). For example, Pouteau and colleagues (2021) determined that climatic and topographic factors were strongly linked with the distributions of 1,485 plants of European origin that are in other regions of the world. For 12 of the 22 families I examined in Australia, the associations that exotic species richness had with environmental variables suggested that exotic species had strong responses to environmental gradients (Chapter 3; Appendix B).

A plethora of studies have found that the areas that contain the most exotic species also tend to contain many native species (Table 1.1). This may be because native and exotic species have similar responses to variation in climatic conditions (Fridley and Sax, 2014; Gilbert and Lechowicz, 2005; Levine and D'Antonio, 1999; Peng et al., 2019), resource availability (Byers and Noonburg 2003), or habitat heterogeneity and disturbances (Davies et al. 2005; Brooks et al. 2013). For half of the 22 common native and exotic plant families in Australia, I found that where native and exotic species co-occur, native and exotic species richness was positively

correlated, with areas that support high native richness also tending to support high exotic richness (Chapter 3). I found the same trend among New Zealand's native and exotic C3 grasses (Chapter 4). This is strong evidence that the factors that strongly govern native richness patterns (environmental gradients in many cases) have similar and strong influences on exotic species richness. The native richness template was a useful way to determine the potential for exotic species to spread when there was evidence that there was a positive correlation between related native and exotic richness patterns and native and exotic richness had similar associations with environmental gradients (Chapters 2, 3 and 4).

6.3 Other influences on native and exotic richness

6.3.1 Continental species richness

Climate and topography are not the sole influences on species richness because, to varying extents, all species are limited in their ability to disperse to all locations (Soberón 2007). Over long time frames, communities form through the interwoven processes of dispersal, speciation and extinction (Gaston 1998). While these processes can be linked to environmental suitability (Rangel et al. 2018), these processes can also vary in different locations (e.g. landmasses) or within certain regions of a single landmass, which can alter species richness patterns independent of environmental conditions (Albert et al. 2017). For example, although I did not directly test for it, I found strong evidence that the biogeographic factors of land area and isolation influence species richness patterns for many plant families in Australia at large spatial scales (Chapter 3). Twelve of the twenty-two families had particularly high species richness in south-western Australia that was not explained by climatic or topographic gradients (Chapter 3). Moreover, high richness in south-western Australia occurred in families that otherwise had a large amount of variation in native richness explained by environmental gradients.

The reasons why there is particularly high species richness in south-western Australia are not fully understood. Outside of its northern connections, Australia is separated from other landmasses by vast stretches of ocean, but south-western Australia is also separated from other parts of Australia by deserts, which makes it particularly inaccessible to potential colonisers. Isolation from other parts of Australia is thought to have played a large role in the structure of the flora and fauna of south-western Australian. Rare long-distance dispersal events have led to new species arriving, and subsequent and multiple *in situ* speciation events have thought to

have driven the ~50% endemism of the species of the South-western region (Hopper 1979, 2004; Rix et al. 2014).

Yet why this region has particularly high species richness, when other isolated regions have lower species richness, has not been solved. One theory is that long-term changes in climate have provided varying habitat conditions for species, and many species have persisted into its contemporary climate (Rix et al. 2014). Another theory suggests as Australia became increasingly arid between 3 and 6 million years ago, some groups of species also promoted environmental change across much of Australia, such as fire frequency and intensity (e.g. C4 grasses) (Gill 1975; Snyman et al. 2013). But such groups of transformer species have been unable to colonise south-western Australia, meaning that older species have been able to remain and continue to diversify (Bryceson 2020, *pers. comms.*). Cape Fynbos in South Africa is another example of a region which has similarly high species richness, endemism, and contemporary climatic conditions as south-western Australia (Van Wilgen 2013). Yet the factors responsible are also not likely climate, with complex interactions thought to occur via isolation, dispersal and *in situ* speciation, relative to other parts of South Africa. Pinning down the processes that produce species assemblages within landscapes remains a challenge for macroecological models but approaching the problem from a variety of different angles should prove useful. For example, simulating speciation, extinction and dispersal rates alongside changes in climate over hundreds of thousands of years accurately predicts contemporary avian species richness in central and south America (Rangel et al. 2018).

Support for the native richness template was challenged when native species richness patterns were independent of climatic variation (Chapter 3). As a consequence of high native richness in south-western Australia, the drivers of native and exotic richness could not be inferred nor could the relationships to individual drivers (i.e. climatic variables) be compared. In areas where native and exotic species richness co-occurred, native and exotic richness could still be positively correlated, and hence areas with proportionately high native richness but low exotic richness could still provide an estimate of invasion potential. But without explaining enough variation in native richness patterns, native richness could not be accurately predicted across the continent, reducing the efficacy of the native richness template.

I also found exotic species richness of six families was particularly high in south-western Australia, consistent with respective native familial richness patterns. The reasons for this correlation were not explained by contemporary climatic conditions nor historical processes

(isolation or long-term climate change). Potentially, there are interactions between native and now exotic species facilitating co-existence over large spatial and temporal scales (Gouveia et al. 2014). For example, altered interactions in south-western Australia relative to other parts of Australia (such as different fire types) could explain why more exotic species can be supported in this region. Further investigation in the correlates of invasion in south-western Australia is warranted (Leishman et al. 2014; Monks et al. 2019).

6.3.2 Island species richness

Extreme cases of land isolation and size are islands, the most remote of which support unique but small species assemblages (Kier et al. 2009). The Theory of Island Biogeography (TIB) (MacArthur and Wilson 1963) is a predictive model outlining how biogeographic features (particularly the size and isolation of communities) affect patterns of species richness. The theory posits that isolation and land area can, independently, influence patterns of species richness and rival the influences of other large-scale factors (such as climate and topography). Unique because immigration rates are lower in smaller and less connected landmasses, so chance encounters can lead to one-off speciation and diversification directions (Mcglone et al. 2011; Johnson et al. 2017); and smaller assemblage sizes because fewer colonisation events lead to smaller specie assemblages and smaller landmasses have higher extinction risks (Keppel et al. 2009). These two predictions have been used to explain richness patterns in many different island and isolated continental species assemblages (Niet and Johnson 2009; Whittaker et al. 2009; Warren et al. 2015).

I used TIB to test differences in native richness between isolated landmasses, Australia and New Zealand (Chapter 4). Australia and New Zealand's environmental gradients predicted similar patterns of C3 and C4 grass species richness across New Zealand, but New Zealand richness was 15% lower than Australia after accounting for environmental conditions. This is in line with expectations from TIB, suggesting that models that can account for many factors (i.e. biogeographic and environmental) will be useful to advance our understanding of the large-scale patterns of species assemblages (Chase and Knight 2013). This also suggests native richness coupled with environmental gradients in one location can be used to predict species richness in another location, provided differences in isolation and land area are considered.

6.3.3 Human impacts and species occurrence data

Dispersal opportunity strongly influence exotic species richness patterns (Duncan et al. 2019). At least 16,926 exotic species have overcome dispersal barriers that have previously isolated plant communities with temperate regions and islands hosting the greatest numbers of exotic species (Seebens et al. 2017 onwards). Humans move species around into the areas we live and are active in, and introduction effort is a strong predictor of exotic species richness (Mack and Lonsdale 2001; Hulme 2009; Blackburn et al. 2020). For instance, species occurrence records in Australia are concentrated in areas that are easy to access, so recorded (native and exotic) richness is higher nearer to roads and cities (Dodd et al. 2016; Daru et al. 2017). Among Australia's common exotic families, I also found that cells with exotic richness estimates were concentrated within temperate regions and areas with high levels of human impacts (Chapter 3). For example, all families had enough records to estimate species richness in south-eastern Australia, a region with a high degree of introduction effort from human activities (Dodd et al. 2015). Exotic C4 grasses illustrate the effect of location and introduction effort on exotic species richness patterns. C4 Poaceae species are not suited to temperate climates (Edwards and Smith 2010) yet many areas within the temperate southeast had enough records to estimate exotic C4 Poaceae species richness, despite the low richness in this region (Chapters 2, 3). Conversely, in suitable northern regions of Australia, there were far fewer areas with enough records to estimate exotic C4 richness. Those northern areas that did have enough records to estimate exotic C4 richness typically had high richness values, suggesting northern C4 richness patterns were not due to environmental constraints.

Support for the native richness template was challenged by taxonomically and geographically widespread exotic dispersal limitations (Chapter 3). Eight families had exotic richness estimates that were concentrated in areas with high levels of human impacts, but those regions did not support high native richness. In these instances, it was challenging for co-occurring native and exotic richness estimates to demonstrate a strong positive correlation because few cells had proportionately high native richness. For example, Amaranthaceae richness had a strong positive association with annual mean temperature and a strong positive north-south richness gradient. Yet exotic Amaranthaceae richness was concentrated in south-eastern Australia, a region poorly suited for native Amaranthaceae species. Areas where native and exotic Amaranthaceae coincided did not generate a strongly positive native-exotic correlation, despite potential that they could, if Amaranthaceae had been introduced into northern regions.

Differences in sampling effort also contributed to the lower native-exotic correlation values (Chapters 2, 3 and 4). There were large differences among neighbouring cell estimates of native or exotic richness, even in families which had strong correlative support (i.e. $r > 0.3$) (Chapter 3). Strong differences in richness estimates (and native richness in particular) was related to the nature of digitised species occurrence data: people do not randomly sample taxa or areas (Meyer et al. 2016; Daru et al. 2017). Online herbaria records and citizen science projects are remarkably useful sources of biological data but require careful cleaning and preparatory steps to account for spatial biases (Lavoie 2013). Herbaria also lack data for many areas (Schmidt et al. 2005). Data deficiencies are perhaps the greatest drawback of the native richness template methodology. Moreover, this issue only gets worse at finer (and more useful) taxonomic scales (Appendix A) or with smaller taxonomic groups. Addressing spatial biases in species data is key to better understanding the drivers of native and exotic assemblages (Colwell and Coddington 1994; Colwell et al. 2012; Engemann et al. 2015).

6.4 The future of modelling the distributions of native and exotic species

When it was supported, the native richness template was useful for forecasting the potential for large areas to support large numbers of exotic species. This compares well with existing species distribution modelling tools. There are many species distribution models that have been very useful in forecasting the potential for small groups of species to invade through space and time (Elith and Leathwick 2009; Gallagher et al. 2010; Schmitt et al. 2017; Hao et al. 2019). Scaling such methods to hundreds or thousands of species is a logistical and computational challenge (Mateo et al. 2012). Estimating species richness is therefore a useful measure of getting a broad handle on the potential distributions of many exotic species across large spatial scales that invasions occur over (e.g. Bellard et al. 2013; Essl et al. 2019) and may be less encumbered by stochastic factors (e.g. enemy release, biotic interactions) that affect the distributions of individual species (e.g. Keane and Crawley 2002; Hawkes 2007).

The future of species distribution modelling is likely to move away from correlative modelling methods (e.g. Chapters 2 to 4) to mechanistic models (Kearney et al. 2010; Enriquez-Urzelai et al. 2019). Mechanistic models estimate the process by which species are limited by their surroundings, which seems a more sensible approach for both understanding the drivers of species richness and predicting species richness into different locations (Alexander et al. 2016).

Mechanistic models are getting better at working out how factors such as climate limit different species in different areas (rather than a corelative link), and computational power is increasing allowing one to scale models to hundreds or thousands of species across many (or all) locations (Liu et al. 2020*a*; Atwater and Barney 2021; Pouteau et al. 2021). For example, processes like dispersal, herbivory, frost tolerance and biotic interactions can be captured within mechanistic models (Austin 2007; Roy and Goldberg 2007). The relative importance of these influences can be tested on species occurrence and environmental data, and predictions made in different locations to determine the potential for species to distribute in new areas or landscapes. Of particular interest is forecasting exotic species' dispersal rates, which varies widely between species, but is useful for anticipating the timing of arrival of current problematic invaders into new areas (Pyšek and Hulme 2005; Duncan 2021).

The number of invaders is increasing, and the areas being invaded are also expanding (e.g. Antarctica) meaning coarse and correlative studies are still useful (Bellard et al. 2013; Galera et al. 2017; Seebens et al. 2017). Currently, the broad spatial and taxonomic scale that the native richness template provides is useful as a 'blanket' assessment of the potential for many species to invade large areas. And as mentioned by Algar (2009) and Chapter 2, coupling the large scale assessment with smaller scale (and potentially mechanistic) models can then predict the distributions of single or small groups of particularly troublesome invaders. Funding and management efforts can then be directed against particular invaders and/or areas that are deemed to have high conservation values (e.g. high native species richness or endemism) (Myers et al. 2000).

It seems likely that climatic and biogeographic processes work in tandem to influence species richness patterns. For example, Rangel et al. (2018) accurately predicted avian species richness at large (100 × 100 km) spatial scales across Central and South America by simulating species richness over an 800,000 year period as a function of dispersal, speciation and extinction processes alongside climatic and topographic changes. However, biogeographic influences (i.e. land area and isolation) are not included in many large scale correlative studies on plant species richness (e.g. Francis and Currie 2003; Kreft and Jetz 2007; Huang et al. 2021). This may be because the influence of biogeographic processes are more computationally challenging to run alongside large-scale environmental correlations (Connolly et al. 2017). Although, as Rangel and colleagues (2018) show, uniting the processes speciation, extinction and dispersal with climatic factors can be achieved with new modelling methods and/or computational power.

This approach is likely to be useful for further testing the relative strengths of different factors (and theories) on species richness around the globe.

6.5 Moving from forecasting exotic species richness to impacts

The ultimate aim of predicting exotic species distributions is to reduce their impacts in new areas by identifying potential invaders, the locations they can invade, and removing early colonisers (Looker 1991; Panetta et al. 1991; Downey et al. 2010*b*). Understanding the identity and potential distributions of exotic species alone is insufficient to determine exotic impacts on native communities. Some exotic species have no noticeable effects on the communities they invade, while others completely transform the structure and functioning of the ecosystems they invade (Kolar and Lodge 2001; Davis et al. 2005). For example, in Australia, *Eragrostis curvula* (African lovegrass) is competitively dominant C4 grass and can form monocultures across large areas (Firn 2009; Han et al. 2012), and *Cenchrus ciliaris* (buffel grass) alters the fire regime, which can lead to changes in the composition of native communities (Jackson 2005; Martin et al. 2015).

One mechanism by which exotic species impact native species is competition for shared resources (Davis et al. 2000). Exotic individuals have been shown to have traits (e.g. fast growth rate, large biomass) that allow them to acquire more resources than native individuals, and can reduce the size of native neighbours (Goodwin and Fahrig 1999; Hamilton et al. 2005). Thus, impacts from exotic species have been shown to be greater in conditions with nutrient enrichment and increased disturbance regimes, but lower impacts in resource-poor conditions (Lake and Leishman 2004).

However, exotic species can impact native species across a range of resource levels (Clarke et al. 2005; Han et al. 2012). I found mixed effects of the impact of exotic species on the performance of a native community at apparent low resource (water availability) levels (Chapter 5). I found that, unexpectedly, invasive exotic grassland species, *Dactylis glomerata*, *Eragrostis curvula* and *Phalaris aquatica* had higher survival and comparable biomass compared to a group of three native grass species. This was contrary to my expectations that invaders are good at growing under high resource levels but that occurs as a trade-off in performance at low resource levels (Reich 2014). Alternatively, successful exotic species may just have better combinations of traits that exist in trade-offs in other species (Bolger et al.

2005). Or high physiological plasticity is part of the success of invaders like *D. glomerata* (Firn et al. 2012; Schellberg and Pontes 2012).

Forecasting exotic impact to areas with high exotic species richness or resource levels may thus miss the large impacts that exotic species have in some area. Managers thus have a challenging task of mitigating impacts in most (if not all) areas of contemporary landscapes, particularly in south-eastern Australia, one of the most invaded regions by number of exotic species on earth (Pyšek et al. 2017) which also contains the critically endangered natural temperate grasslands (Grassland 1998). Management efforts such as prescribed burning that span a range of community states (i.e. areas with few native and/or exotic species to those that are highly invaded) seem promising (Thompson et al. 2001; Prober et al. 2016).

6.6 Conclusion

Assemblages of native and exotic species may be influenced by environmental gradients in similar ways. Species that are more related tend to have more similar physiologies and hence limits on their distributions. I showed that related groups of native and exotic taxa also tend to have similar species richness patterns across landscapes in areas they co-occur. Due to similar native and richness patterns and environmental responses, native species richness can be used as a template to forecast potential exotic species richness. Moreover, native and exotic richness patterns may be conserved between different locations altogether, suggesting species richness in one location can predict native and/or exotic richness in others. Due to the large numbers of exotic species worldwide, many more exotic species can invade areas compared to the numbers of resident native species. This is particularly relevant for islands, which support fewer native species for their environmental conditions but many more exotic species. But native and exotic richness patterns should hold, allowing a broad forecast of potential exotic richness in different locations.

Biogeographic factors also influence species richness patterns. Native species richness can be influenced by land area and isolation, sometimes positively (e.g. high richness in south-western Australia) and sometimes negatively (e.g. lower native C3 Poaceae richness in New Zealand relative to Australia). Curiously, exotic species can also follow patterns of native species richness. Quantifying the effects of biogeographic factors on native assemblages will help forecast native species richness into other locations with higher accuracy, which could then help

forecast the distributions of exotic species. This is particularly pressing for islands which are some of the most invaded areas on earth.

Many exotic species are strongly dispersal-limited, with richness estimates concentrated in areas with high levels of introduction effort, such as those areas around human settlements and transport routes. Introduction effort is important when accounting for current exotic richness patterns, but may not be indicative of the environmental constraints on potential exotic species richness patterns across a landscape.

Understanding potential exotic species richness may not be enough to predict the impacts of exotic species on the communities they invade. Even under resource-poor conditions, not all exotic species have the same effects on native species, but exotic species can also competitively impact native communities. Being able to predict which and when exotic species are likely to impact native species will be useful in mitigating exotic impacts on native communities.

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Appendix A – Supporting information for Chapter 2

Table A.1 Summary of Poaceae herbarium records in gridded cells of different sizes across Australia. I applied a cut off of fifteen records per cell to estimate species richness in this study (see Methods for details). The cell size shaded in grey (100 × 100 km) was chosen for this study.

Cell size (km × km)	Total number of cells	Number of cells with ≥ 15 records	Proportion of cells with ≥ 15 records	Cell records			Correlation between species richness and number of records
				Minimum	Maximum	Range	
10 × 10	102,228	12,350	0.12	15	3,726	3,711	0.77
20 × 20	26,028	6,786	0.26	15	8,342	8,327	0.73
50 × 50	4,355	2,678	0.61	15	22,013	21,998	0.68
100 × 100	1,157	985	0.85	15	33,687	33,672	0.67
150 × 150	540	514	0.95	15	67,533	67,518	0.64
250 × 250	209	202	0.97	16	106,685	106,669	0.63
500 × 500	65	62	0.95	16	177,578	177,562	0.67

Table A.2 Environmental and human impact variables identified as potentially explaining grass species richness. Shaded variables were retained as explanatory variables in the regression models (see text).

Category	Name	Abbreviation (manuscript name)	Units	Source resolution (km × km)	Source
Temperature	Annual mean temperature	AMT (annual mean temperature)	Degrees Celsius	1 × 1	Fick and Hijmans (2017)
	Isothermality	ISO	Percent	1 × 1	Fick and Hijmans (2017)
	Maximum temperature of the warmest month	TWARMM	Degrees Celsius	1 × 1	Fick and Hijmans (2017)
	Mean diurnal range	DR	Degrees Celsius	1 × 1	Fick and Hijmans (2017)
	Mean temperature of coldest Quarter	TCOLDQ	Degrees Celsius	1 × 1	Fick and Hijmans (2017)
	Mean temperature of driest quarter	TDRYQ	Degrees Celsius	1 × 1	Fick and Hijmans (2017)
	Mean temperature of Warmest Quarter	TWARMQ	Degrees Celsius	1 × 1	Fick and Hijmans (2017)
	Mean temperature of wettest quarter	TWETQ	Degrees Celsius	1 × 1	Fick and Hijmans (2017)
	Minimum temperature of the coldest month	TCOLDM	Degrees Celsius	1 × 1	Fick and Hijmans (2017)
	Temperature annual range	TAR	Degrees Celsius	1 × 1	Fick and Hijmans (2017)
	Temperature seasonality	TS (temperature seasonality)	Percent	1 × 1	Fick and Hijmans (2017)
Precipitation	Annual precipitation	AP	mm	1 × 1	Fick and Hijmans (2017)
	Precipitation of the coldest quarter	PCOLDQ (winter rainfall)	mm	1 × 1	Fick and Hijmans (2017)
	Precipitation of driest month	PDRYM	mm	1 × 1	Fick and Hijmans (2017)
	Precipitation of driest quarter	PDRYQ	mm	1 × 1	Fick and Hijmans (2017)
	Precipitation seasonality	PS	Percent	1 × 1	Fick and Hijmans (2017)
	Precipitation of wettest month	PWARMM	mm	1 × 1	Fick and Hijmans (2017)
	Precipitation of the warmest quarter	PWARMQ (summer rainfall)	mm	1 × 1	Fick and Hijmans (2017)
	Precipitation of wettest quarter	PWETQ	mm	1 × 1	Fick and Hijmans (2017)
Temperature-precipitation interaction	Aridity index	AI (aridity)	None	1 × 1	Zomer et al. (2008)
	Potential evapotranspiration	PET	Mm/yr^{-1}	1 × 1	Zomer et al. (2008)
Landscape	Elevation	ELEV	M	1 × 1	Fischer et al. (2008)

Category	Name	Abbreviation (manuscript name)	Units	Source resolution (km × km)	Source
	Plant-available water capacity	PAWC	mL	25 × 25	McKenzie et al. (2005)
	Plant-extractable water capacity	PEWC (soil water availability)	mL	25 × 25	Dunne et al. (1996)
	Potential storage of water derived from root zone	RZ	mm	25 × 25	Webb et al. (2000)
	Potential storage of water in the soil profile	SP	mm	25 × 25	Webb et al. (2000)
	Potential storage of water derived from soil texture	ST	mm	25 × 25	Webb et al. (2000)
	Topographic heterogeneity	TH (topographic heterogeneity)	SD	1 × 1	Fischer et al. (2008)
Human impact	Human influence index	HII (human impact)	None	1 × 1	Sanderson et al. (2002)

Table A.3 Correlation matrix of *Pearson's* r values for the twenty-seven explanatory variables in Table S2.2. Abbreviations are given in Table A.2.

	AMT	AP	ARID	CLAY	ELEV	HII	ISO	MDR	PAWC	PCOLDQ	PDRYM	PDRYQ	PEWC	PS
AMT	1	0.04	-0.28	-0.13	-0.17	-0.58	0.55	0.53	-0.18	-0.73	-0.78	-0.76	-0.61	0.84
AP	0.04	1	0.91	0.01	-0.13	0.35	0.58	-0.63	0.12	0.36	0.38	0.42	0.33	0.36
ARID	-0.28	0.91	1	0.03	-0.07	0.48	0.32	-0.76	0.19	0.64	0.66	0.69	0.45	0.07
CLAY	-0.13	0.01	0.03	1	-0.23	0.13	-0.13	-0.04	0.2	-0.03	0.22	0.21	0.25	-0.21
ELEV	-0.17	-0.13	-0.07	-0.23	1	-0.18	-0.33	0.19	0.11	0.04	0.15	0.14	-0.07	-0.11
HII	-0.58	0.35	0.48	0.13	-0.18	1	-0.12	-0.67	0.12	0.66	0.59	0.59	0.67	-0.31
ISO	0.55	0.58	0.32	-0.13	-0.33	-0.12	1	-0.02	-0.09	-0.26	-0.33	-0.31	-0.08	0.75
MDR	0.53	-0.63	-0.76	-0.04	0.19	-0.67	-0.02	1	-0.08	-0.68	-0.63	-0.64	-0.6	0.24
PAWC	-0.18	0.12	0.19	0.2	0.11	0.12	-0.09	-0.08	1	0.14	0.31	0.31	0.19	-0.13
PCOLDQ	-0.73	0.36	0.64	-0.03	0.04	0.66	-0.26	-0.68	0.14	1	0.77	0.78	0.58	-0.41
PDRYM	-0.78	0.38	0.66	0.22	0.15	0.59	-0.33	-0.63	0.31	0.77	1	0.99	0.58	-0.59
PDRYQ	-0.76	0.42	0.69	0.21	0.14	0.59	-0.31	-0.64	0.31	0.78	0.99	1	0.57	-0.56
PEWC	-0.61	0.33	0.45	0.25	-0.07	0.67	-0.08	-0.6	0.19	0.58	0.58	0.57	1	-0.34
PS	0.84	0.36	0.07	-0.21	-0.11	-0.31	0.75	0.24	-0.13	-0.41	-0.59	-0.56	-0.34	1
PWARMQ	0.39	0.85	0.63	0.07	-0.09	0.09	0.63	-0.32	0.06	-0.07	0.08	0.11	0.08	0.58
PWETM	0.41	0.9	0.67	-0.06	-0.2	0.1	0.79	-0.37	-0.01	0.01	-0.03	0.01	0.1	0.68
PWETQ	0.37	0.92	0.69	-0.06	-0.21	0.13	0.78	-0.41	0	0.04	0	0.04	0.12	0.65
RZ	-0.03	0.2	0.17	0.52	-0.07	0.18	0.16	-0.05	0.24	0.08	0.14	0.14	0.28	0.13
SP	-0.03	0.03	0.01	0.39	-0.08	-0.01	0.05	0.02	0.22	-0.05	0.04	0.03	0.17	-0.02
ST	-0.02	-0.03	-0.05	0.31	-0.08	-0.06	0.03	0.08	0.19	-0.09	0	-0.02	0.11	-0.04
TAR	0.12	-0.84	-0.8	0.04	0.34	-0.49	-0.61	0.79	-0.03	-0.42	-0.33	-0.35	-0.45	-0.27
TCOLDM	0.83	0.51	0.2	-0.14	-0.35	-0.24	0.83	0.03	-0.15	-0.42	-0.52	-0.48	-0.3	0.9
TCOLDQ	0.93	0.33	0	-0.15	-0.3	-0.39	0.78	0.26	-0.17	-0.57	-0.66	-0.63	-0.42	0.92
TDRYQ	0.53	0.13	-0.06	-0.29	-0.33	-0.06	0.52	0.08	-0.3	-0.2	-0.55	-0.53	-0.1	0.61
TH	-0.4	0.46	0.56	0.02	0.43	0.33	-0.03	-0.45	0.09	0.46	0.58	0.58	0.34	-0.11
TS	-0.12	-0.81	-0.69	0.09	0.37	-0.32	-0.82	0.56	0.01	-0.2	-0.11	-0.13	-0.3	-0.48

	AMT	AP	ARID	CLAY	ELEV	HII	ISO	MDR	PAWC	PCOLDQ	PDRYM	PDRYQ	PEWC	PS
TWARMM	0.89	-0.35	-0.61	-0.09	0.01	-0.71	0.17	0.81	-0.16	-0.81	-0.8	-0.79	-0.72	0.57
TWARMQ	0.92	-0.28	-0.55	-0.09	-0.04	-0.68	0.2	0.72	-0.18	-0.79	-0.81	-0.8	-0.7	0.61
TWETQ	0.85	-0.09	-0.34	0.02	0.03	-0.64	0.24	0.59	-0.07	-0.74	-0.6	-0.58	-0.69	0.58

Table A.3 Continued.

	PWARMQ	PWETM	PWETQ	RZ	SP	ST	TAR	TCOLDM	TCOLDQ	TDRYQ	TH	TS	TWARMM	TWARMQ	TWETQ
AMT	0.39	0.41	0.37	-0.03	-0.03	-0.02	0.12	0.83	0.93	0.53	-0.4	-0.12	0.89	0.92	0.85
AP	0.85	0.9	0.92	0.2	0.03	-0.03	-0.84	0.51	0.33	0.13	0.46	-0.81	-0.35	-0.28	-0.09
ARID	0.63	0.67	0.69	0.17	0.01	-0.05	-0.8	0.2	0	-0.06	0.56	-0.69	-0.61	-0.55	-0.34
CLAY	0.07	-0.06	-0.06	0.52	0.39	0.31	0.04	-0.14	-0.15	-0.29	0.02	0.09	-0.09	-0.09	0.02
ELEV	-0.09	-0.2	-0.21	-0.07	-0.08	-0.08	0.34	-0.35	-0.3	-0.33	0.43	0.37	0.01	-0.04	0.03
HII	0.09	0.1	0.13	0.18	-0.01	-0.06	-0.49	-0.24	-0.39	-0.06	0.33	-0.32	-0.71	-0.68	-0.64
ISO	0.63	0.79	0.78	0.16	0.05	0.03	-0.61	0.83	0.78	0.52	-0.03	-0.82	0.17	0.2	0.24
MDR	-0.32	-0.37	-0.41	-0.05	0.02	0.08	0.79	0.03	0.26	0.08	-0.45	0.56	0.81	0.72	0.59
PAWC	0.06	-0.01	0	0.24	0.22	0.19	-0.03	-0.15	-0.17	-0.3	0.09	0.01	-0.16	-0.18	-0.07
PCOLDQ	-0.07	0.01	0.04	0.08	-0.05	-0.09	-0.42	-0.42	-0.57	-0.2	0.46	-0.2	-0.81	-0.79	-0.74
PDRYM	0.08	-0.03	0	0.14	0.04	0	-0.33	-0.52	-0.66	-0.55	0.58	-0.11	-0.8	-0.81	-0.6
PDRYQ	0.11	0.01	0.04	0.14	0.03	-0.02	-0.35	-0.48	-0.63	-0.53	0.58	-0.13	-0.79	-0.8	-0.58
PEWC	0.08	0.1	0.12	0.28	0.17	0.11	-0.45	-0.3	-0.42	-0.1	0.34	-0.3	-0.72	-0.7	-0.69
PS	0.58	0.68	0.65	0.13	-0.02	-0.04	-0.27	0.9	0.92	0.61	-0.11	-0.48	0.57	0.61	0.58
PWARMQ	1	0.91	0.9	0.22	0.1	0.05	-0.63	0.7	0.59	0.17	0.31	-0.69	0.03	0.1	0.3
PWETM	0.91	1	1	0.18	0.04	-0.01	-0.75	0.78	0.66	0.37	0.25	-0.82	-0.01	0.07	0.19
PWETQ	0.9	1	1	0.18	0.04	-0.01	-0.77	0.77	0.64	0.36	0.25	-0.84	-0.05	0.03	0.15
RZ	0.22	0.18	0.18	1	0.57	0.49	-0.15	0.06	0.03	-0.11	0.12	-0.17	-0.1	-0.1	0.01
SP	0.1	0.04	0.04	0.57	1	0.98	0	-0.02	-0.02	-0.12	-0.03	-0.01	-0.02	-0.03	0.01
ST	0.05	-0.01	-0.01	0.49	0.98	1	0.05	-0.05	-0.03	-0.11	-0.07	0.03	0.01	-0.01	0.02
TAR	-0.63	-0.75	-0.77	-0.15	0	0.05	1	-0.46	-0.24	-0.24	-0.36	0.95	0.56	0.48	0.35

	PWARMQ	PWETM	PWETQ	RZ	SP	ST	TAR	TCOLDM	TCOLDQ	TDRYQ	TH	TS	TWARMM	TWARMQ	TWETQ
TCOLDM	0.7	0.78	0.77	0.06	-0.02	-0.05	-0.46	1	0.97	0.6	-0.16	-0.64	0.48	0.55	0.56
TCOLDQ	0.59	0.66	0.64	0.03	-0.02	-0.03	-0.24	0.97	1	0.63	-0.27	-0.47	0.66	0.72	0.68
TDRYQ	0.17	0.37	0.36	-0.11	-0.12	-0.11	-0.24	0.6	0.63	1	-0.27	-0.38	0.33	0.38	0.08
TH	0.31	0.25	0.25	0.12	-0.03	-0.07	-0.36	-0.16	-0.27	-0.27	1	-0.26	-0.5	-0.5	-0.31
TS	-0.69	-0.82	-0.84	-0.17	-0.01	0.03	0.95	-0.64	-0.47	-0.38	-0.26	1	0.34	0.27	0.16
TWARMM	0.03	-0.01	-0.05	-0.1	-0.02	0.01	0.56	0.48	0.66	0.33	-0.5	0.34	1	0.99	0.87
TWARMQ	0.1	0.07	0.03	-0.1	-0.03	-0.01	0.48	0.55	0.72	0.38	-0.5	0.27	0.99	1	0.87
TWETQ	0.3	0.19	0.15	0.01	0.01	0.02	0.35	0.56	0.68	0.08	-0.31	0.16	0.87	0.87	1

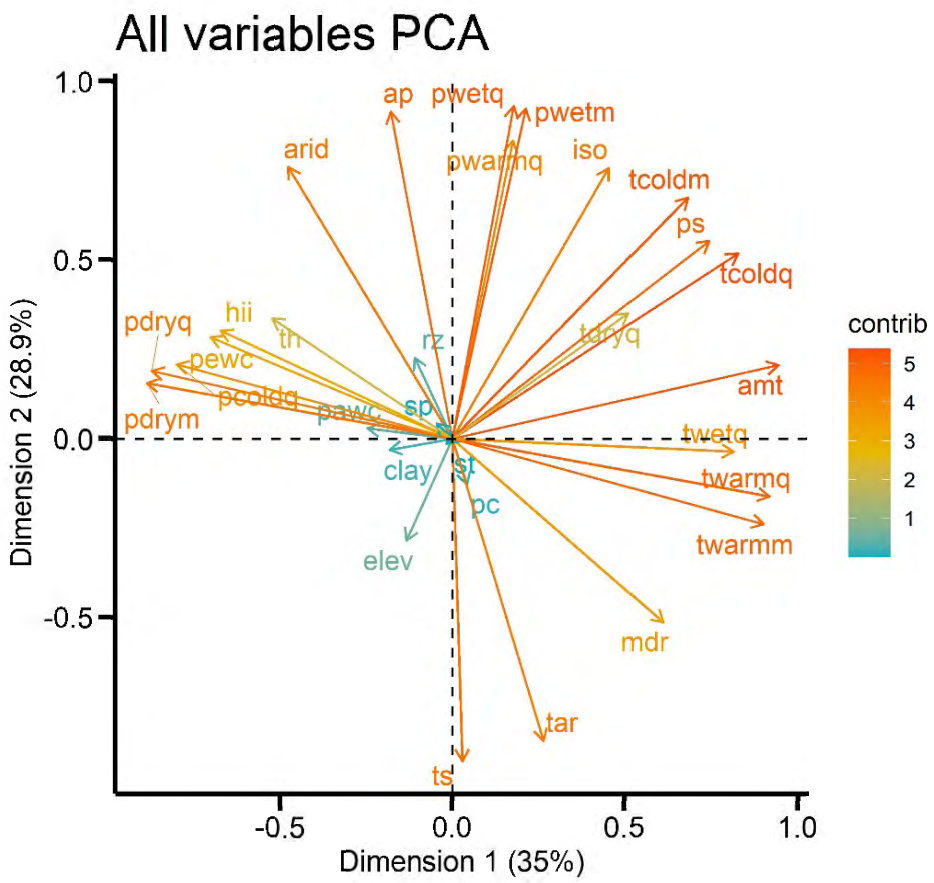


Figure A.1 Principal coordinate analysis (PCA) of the twenty-seven explanatory variables in Table A2.2. Dimension 1 (x axis) explained 35% of the variation among the variables and Dimension 2 (y axis) explained 28.9%. Variable colours indicate the contribution (contrib) of each variable to the variation explained in the first two dimensions.

Table A.4 Correlation matrix of *Pearson's* r values among the seven environmental and one human impact variable retained as explanatory variables in the regression models. Correlations greater than the |0.7| collinearity threshold are highlighted in grey.

	PCOLDQ	PWARMQ	AMT	TS	ARID	PEWC	TH	HII
PCOLDQ	1							
PWARMQ	-0.07	1						
AMT	-0.73	0.39	1					
TS	-0.20	-0.69	-0.12	1				
ARID	0.64	0.63	-0.28	-0.69	1			
PEWC	0.58	0.08	-0.61	-0.3	0.45	1		
TH	0.46	0.31	-0.40	-0.26	0.56	0.34	1	
HII	0.66	0.09	-0.58	-0.32	0.48	0.67	0.33	1

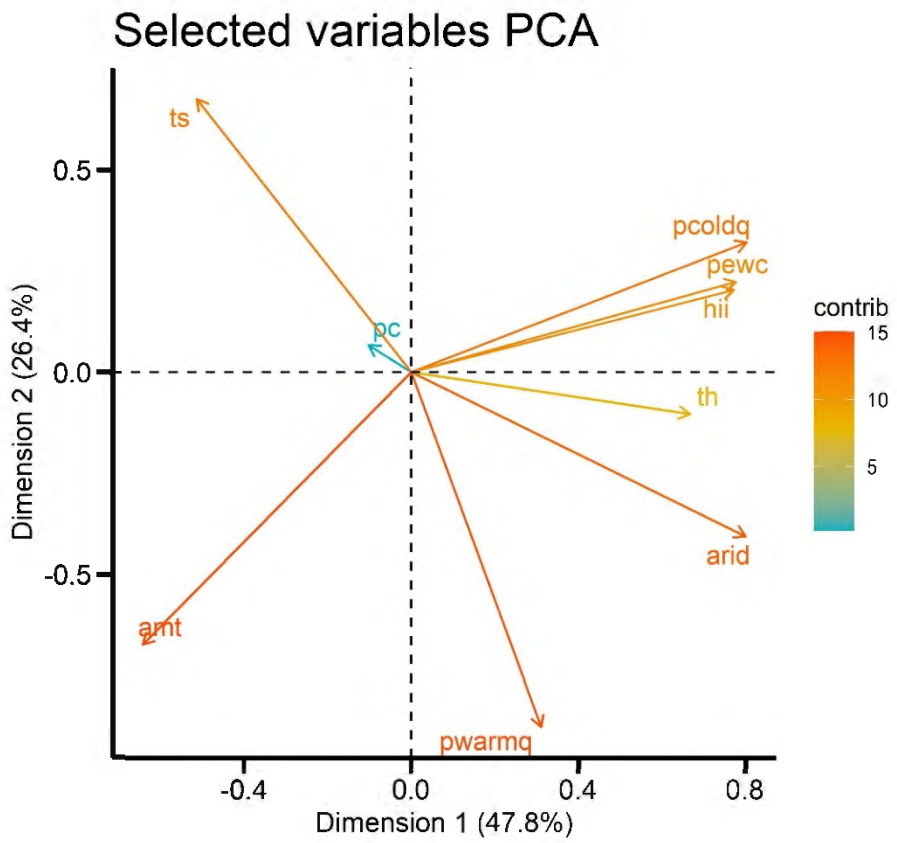


Figure A.2 Principal coordinate analysis (PCA) of the eight variables in Table A2.4. Dimension 1 (x axis) explained 35% of the variation among the variables and Dimension 2 (y axis) explained 28.9%. Variable colours indicate the contribution (contrib) of each variable to the variation explained in the first two dimensions.

Table A.5 Moran's I test for autocorrelation for native and exotic C3, C4 and total Poaceae species richness. P values <0.05 indicate significant spatial autocorrelation among predictor variables for each taxa.

Taxa	Expected	Observed	SD	P value
Native C3	-0.0909	-0.0021	0.0013	0.0000
Native C4	-0.1278	-0.0013	0.0008	0.0000
Native total	-0.1054	-0.0013	0.0007	0.0000
Exotic C3	-0.0431	-0.0038	0.0027	0.0000
Exotic C4	-0.0776	-0.0031	0.0019	0.0000
Exotic total	-0.0693	-0.0023	0.0014	0.0000

Table A.6 Model fits ranked by delta-AICc (the difference in AICc values between a model and the best-fitting model) among two model classes, generalized least-squares (gls) and a linear regression (lm). GLS model classes included four types of spatial autocorrelation structures. The model for each taxon was selected with the lowest AICc score, highlighted in grey*.

Taxa	Model class	GLS spatial autocorrelation structure†	df	Log-likelihood	AICc	Delta-AICc	Weight
Native C3	gls	Gaussian	13	468.33	-909.88	0.00	0.64
	gls	Ratio	13	467.42	-908.05	1.83	0.26
	gls	Exponential	13	466.48	-906.18	3.70	0.10
	gls	Spherical	13	461.44	-896.09	13.79	0.00
	lm		11	387.09	-751.61	158.26	0.00
Native C4	gls	Exponential	13	815.63	-1604.76	0.00	0.95
	gls	Spherical	13	812.17	-1597.85	6.91	0.03
	gls	Ratio	13	811.52	-1596.54	8.22	0.02
	gls	Gaussian	13	799.39	-1572.28	32.48	0.00
	lm		11	614.74	-1207.13	397.64	0.00
Native total	gls	Exponential	13	982.00	-1937.53	0.00	0.64
	gls	Spherical	13	981.33	-1936.20	1.33	0.33
	gls	Ratio	13	978.96	-1931.47	6.06	0.03
	gls	Gaussian	13	971.91	-1917.35	20.18	0.00
	lm		11	750.21	-1478.09	459.44	0.00
Exotic C3	gls	Exponential	13	211.81	-396.19	0.00	0.49
	gls	Gaussian	13	210.88	-394.32	1.87	0.19
	gls	Ratio	13	210.74	-394.05	2.14	0.17
	gls	Spherical	13	210.68	-393.93	2.26	0.16
	lm		11	173.73	-324.43	71.76	0.00
Exotic C4	gls	Exponential	13	161.01	-294.83	0.00	0.47
	gls	Ratio	13	160.50	-293.83	1.01	0.28
	gls	Spherical	13	159.95	-292.71	2.12	0.16
	gls	Gaussian	13	159.32	-291.46	3.37	0.09
	lm		11	67.89	-112.92	181.91	0.00
Exotic total	gls	Exponential	13	314.71	-602.54	0.00	0.41
	gls	Ratio	13	314.38	-601.89	0.66	0.29
	gls	Spherical	13	314.25	-601.64	0.90	0.26
	gls	Gaussian	13	312.32	-597.77	4.78	0.04
	lm		11	200.67	-378.71	223.83	0.00

*All models included additional parameters: Taxon ~ human impact + topographic heterogeneity + winter rainfall + summer rainfall + temperature seasonality + aridity + annual mean temperature + proportion cover.

†Linear models did not contain spatial autocorrelation terms.

Table A.7 Adjusted R^2 values from regressions of observed versus predicted values for native and exotic C3, C4 and total Poaceae species richness.

Taxa	Observed richness data	Predicted richness data	Adjusted R^2
Native C3	Native	Native	0.58
Native C4	Native	Native	0.60
Native Total	Native	Native	0.24
Exotic C3	Exotic	Exotic	0.05
Exotic C4	Exotic	Exotic	-0.19
Exotic Total	Exotic	Exotic	-0.22
Exotic C3	Exotic	Native	0.39
Exotic C4	Exotic	Native	0.22
Exotic Total	Exotic	Native	0.35

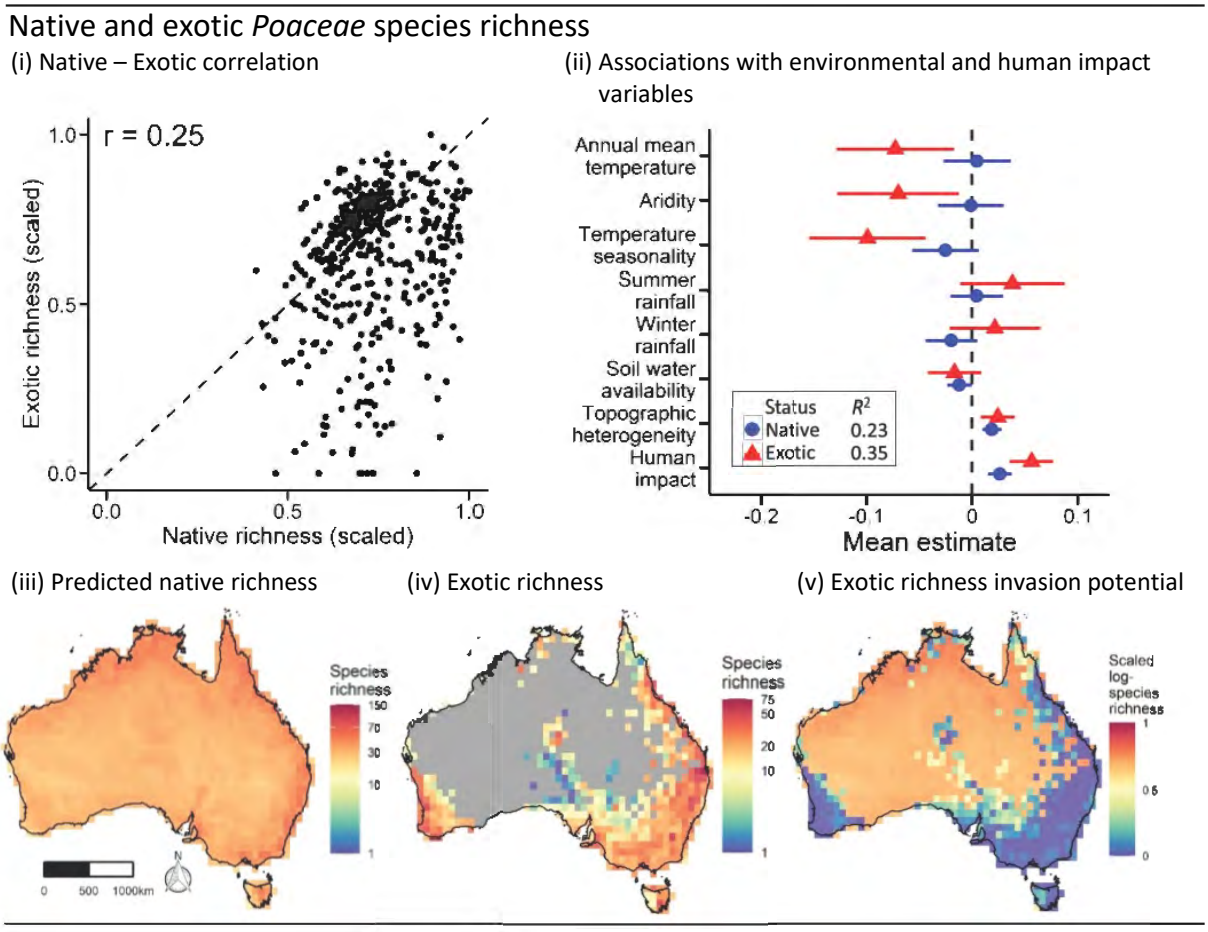
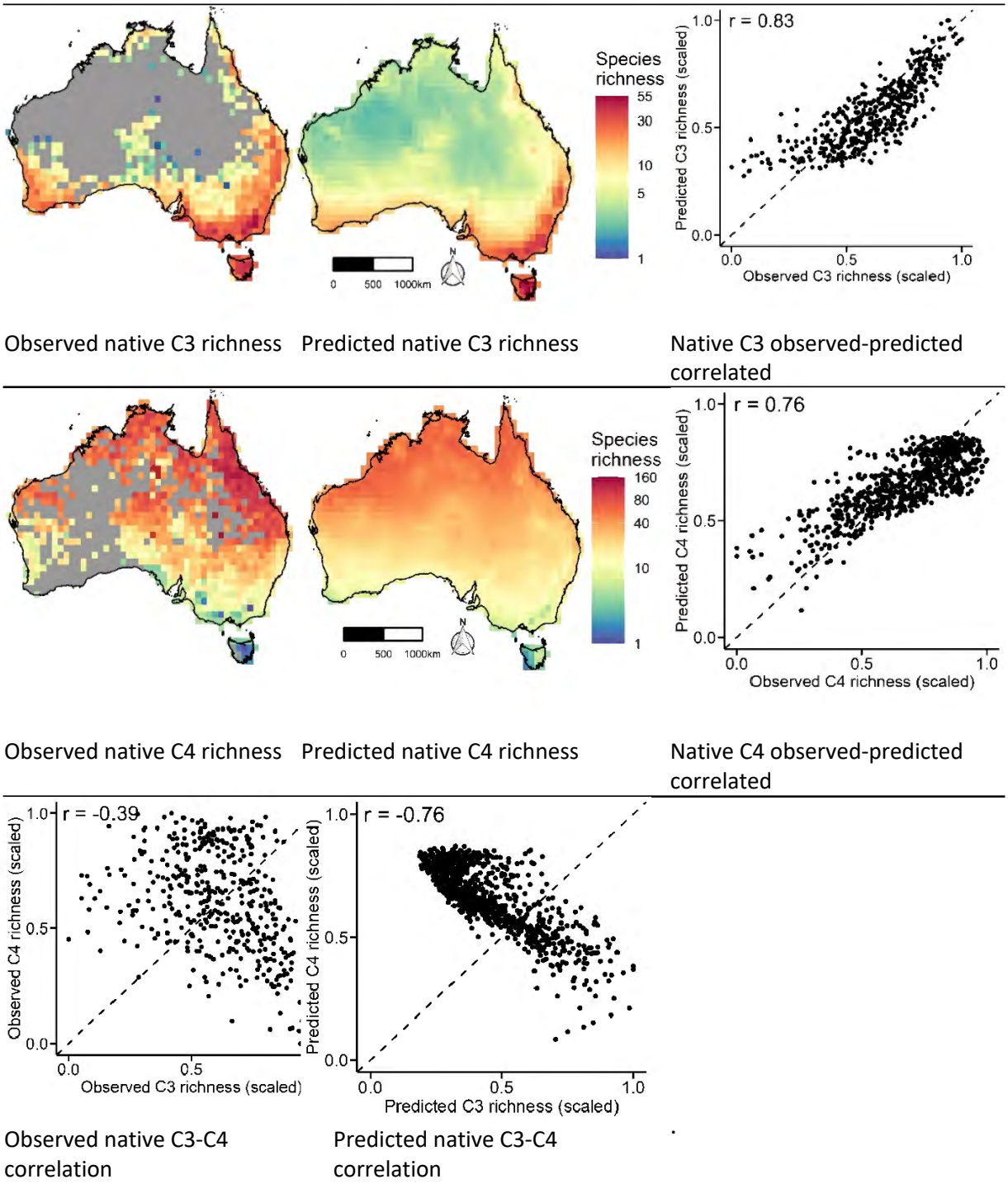


Figure A.3 Native Poaceae species richness as a template for invasion potential of exotic Poaceae species richness across Australia. (i) Predicted native richness (x-axis) and observed exotic richness (y-axis) scaled to between zero and one. Each point is species richness estimated in a 100 × 100 km grid cell with both a predicted native and observed exotic richness estimate. (ii) Parameter estimates of native (blue) and exotic (red) log-transformed and scaled species richness compared to six environmental variables and a single human impact variable using multiple linear regression. Error bars represent 95% confidence intervals of the mean, which

are significant ($P < 0.05$) if they exclude zero (vertical dashed line). The explanatory variables were scaled prior to modelling to compare estimate values. The mean estimates of two covariates (proportion of land cover and a spatial autocorrelation term) were excluded from plots. (iii) Native species richness predicted across all areas of the Australia using mean estimates from (ii). Note that species richness was modelled in log-transformed units but is displayed with raw species richness to indicate the large difference in the number of species represented by cells with hot colours (red-orange) and cool colours (blue-yellow). (iv) Exotic species richness observed across Australia. Grey zones did not meet criteria to estimate species richness and were not analysed. (v) Exotic invasion potential across all areas of Australia, calculated for each area as the difference between scaled and log-transformed predicted native richness and scaled and log-transformed observed exotic richness. Negative invasion potential values were truncated to zero. Maps were projected in the Australian Albers equal area projection.



Observed native C3 richness | Predicted native C3 richness | Native C3 observed-predicted correlated

Observed native C4 richness | Predicted native C4 richness | Native C4 observed-predicted correlated

Observed native C3-C4 correlation | Predicted native C3-C4 correlation

Figure A.4 Native C3 and C4 predicted and observed distributions and correlations.

Table A.8 Correlation matrix among observed and predicted native and exotic C3 and C4 richness.

		Native C3		Native C4		Exotic C3		Exotic C4	
		Observed	**Predicted**	**Observed**	**Predicted**	**Observed**	**Predicted**	**Observed**	**Predicted**
Native C3	**Observed**	1	0.83	-0.39	-0.62	0.69	0.74	0.06	0.51
	Predicted	0.83	1	-0.41	-0.75	0.55	0.82	0.12	0.31
Native C4	**Observed**	-0.39	-0.41	1	0.76	-0.19	-0.65	0.35	0.21
	Predicted	-0.62	-0.75	0.76	1	-0.4	-0.94	0.20	0.24
Exotic C3	**Observed**	0.69	0.55	-0.19	-0.4	1	0.62	0.19	0.56
	Predicted	0.74	0.82	-0.65	-0.94	0.62	1	-0.06	-0.07
Exotic C4	**Observed**	0.06	0.12	0.35	0.20	0.19	-0.06	1	0.45
	Predicted	0.51	0.31	0.21	0.24	0.56	-0.07	0.45	1

Appendix B – Supporting information for Chapter 3

Table B.1 Autocorrelation measured using Moran's I among native and exotic family species richness. P values <0.05 indicate significant spatial autocorrelation among a family's native or exotic species richness estimates.

Family	Status	Observed	Expected	SD	P value
Amaranthaceae	Native	-0.14	0.00	0.00	0.0000
	Exotic	-0.01	-0.01	0.01	0.7273
Apiaceae	Native	-0.09	0.00	0.00	0.0000
	Exotic	-0.07	-0.01	0.01	0.0000
Apocynaceae	Native	-0.20	0.00	0.00	0.0000
	Exotic	-0.14	-0.01	0.01	0.0000
Asparagaceae	Native	-0.10	0.00	0.00	0.0000
	Exotic	-0.12	-0.01	0.01	0.0000
Asteraceae	Native	-0.07	0.00	0.00	0.0000
	Exotic	-0.07	0.00	0.00	0.0000
Boraginaceae	Native	-0.18	0.00	0.00	0.0000
	Exotic	-0.04	-0.01	0.00	0.0000
Brassicaceae	Native	-0.02	0.00	0.00	0.0000
	Exotic	-0.08	0.00	0.00	0.0000
Chenopodiaceae	Native	-0.08	0.00	0.00	0.0000
	Exotic	-0.02	-0.01	0.01	0.0685
Convolvulaceae	Native	-0.25	0.00	0.00	0.0000
	Exotic	-0.09	-0.02	0.01	0.0000
Cyperaceae	Native	-0.07	0.00	0.00	0.0000
	Exotic	-0.20	-0.01	0.01	0.0000
Ericaceae	Native	-0.06	0.00	0.00	0.0000
	Exotic	-0.09	-0.05	0.03	0.1770
Euphorbiaceae	Native	-0.13	0.00	0.00	0.0000
	Exotic	-0.16	-0.01	0.01	0.0000
Fabaceae	Native	-0.08	0.00	0.00	0.0000
	Exotic	-0.05	0.00	0.00	0.0000
FNA*	Native	-0.08	0.00	0.00	0.0000
Juncaceae	Exotic	-0.10	0.00	0.00	0.0000
	Native	-0.03	-0.01	0.01	0.0006
Lamiaceae	Exotic	-0.07	0.00	0.00	0.0000
	Native	-0.10	-0.01	0.00	0.0000
Malvaceae	Exotic	-0.13	0.00	0.00	0.0000
	Native	-0.04	-0.01	0.00	0.0000
Plantaginaceae	Exotic	-0.07	0.00	0.00	0.0000
	Native	-0.05	-0.01	0.00	0.0000
Poaceae C3	Exotic	-0.08	0.00	0.00	0.0000
	Native	-0.04	0.00	0.00	0.0000
Poaceae C4	Exotic	-0.14	0.00	0.00	0.0000

Family	Status	Observed	Expected	SD	P value
	Native	-0.09	0.00	0.00	0.0000
Rubiaceae	Exotic	-0.15	0.00	0.00	0.0000
	Native	-0.05	-0.01	0.01	0.0000
Scrophulariaceae	Exotic	-0.17	0.00	0.00	0.0000
	Native	-0.03	-0.01	0.01	0.0393
Solanaceae	Exotic	-0.05	0.00	0.00	0.0000
	Native	-0.12	0.00	0.00	0.0000

*FNA = Fabaceae species richness without species in the genus *Acacia*.

Table B.2 Native and exotic family richness model fits accounting for autocorrelation. Model fits were ranked by delta-AICc (the difference in AICc values between a model and the best-fitting model) among two model classes, generalized least-squares (gls) and a linear regression (lm). GLS model classes included four types of spatial autocorrelation terms. All models included additional parameters: taxon ~ annual mean temperature + temperature seasonality + aridity + summer rainfall + winter rainfall + topographic heterogeneity + human impact + proportion cover.

Family	Status	Model class	Spatial auto-correlation term*	df	Log-likelihood	AICc	Delta-AICc	Weight
Amaranthaceae	Native	gls	Exponential	12	464.0	-903.6	0.00	0.53
		gls	Ratio	12	463.4	-902.2	1.34	0.27
		gls	Spherical	12	462.9	-901.2	2.38	0.16
		gls	Gaussian	12	461.3	-898.1	5.47	0.03
		lm		10	378.8	-737.2	166.38	0.00
	Exotic	gls	Spherical	12	15.7	-2.0	0.00	0.27
		gls	Gaussian	12	15.7	-1.8	0.14	0.25
		gls	Exponential	12	15.3	-1.2	0.78	0.18
		gls	Ratio	12	15.1	-0.8	1.17	0.15
		lm		10	12.2	-0.6	1.37	0.14
Apiaceae	Native	gls	Spherical	12	156.5	-287.8	0.00	0.56
		gls	Exponential	12	156.1	-287.0	0.79	0.37
		gls	Ratio	12	154.3	-283.6	4.28	0.07
		gls	Gaussian	12	151.5	-277.8	10.04	0.00
		lm		10	34.3	-47.8	240.04	0.00
	Exotic	gls	Gaussian	12	18.0	-8.4	0.00	0.41
		gls	Exponential	12	17.8	-7.8	0.54	0.31
		gls	Ratio	12	17.5	-7.4	0.98	0.25
		gls	Spherical	12	15.0	-2.3	6.09	0.02
		lm		10	11.0	0.5	8.86	0.00
Apocynaceae	Native	gls	Spherical	12	283.9	-542.7	0.00	0.70
		gls	Exponential	12	283.0	-540.8	1.88	0.27
		gls	Gaussian	12	280.7	-536.2	6.56	0.03
		gls	Ratio	12	277.3	-529.5	13.20	0.00
		lm		10	172.6	-324.5	218.23	0.00
	Exotic	gls	Spherical	12	21.2	-14.6	0.00	0.28
		gls	Gaussian	12	21.2	-14.6	0.04	0.27
		gls	Ratio	12	21.1	-14.4	0.25	0.25
		gls	Exponential	12	20.9	-13.9	0.70	0.20
		lm		10	10.5	1.7	16.32	0.00
Asparagaceae	Native	gls	Exponential	12	304.9	-584.7	0.00	0.62
		gls	Spherical	12	304.3	-583.6	1.10	0.36
		gls	Ratio	12	301.1	-577.2	7.52	0.01
		gls	Gaussian	12	298.9	-572.7	11.98	0.00
		lm		10	179.3	-337.9	246.81	0.00
	Exotic	gls	Spherical	12	22.9	-18.1	0.00	0.36

Family	Status	Model class	Spatial auto-correlation term*	df	Log-likelihood	AICc	Delta-AICc	Weight
		gls	Exponential	12	22.4	-17.1	0.95	0.22
		gls	Gaussian	12	22.4	-17.1	1.01	0.22
		gls	Ratio	12	22.3	-16.9	1.17	0.20
		lm		10	4.5	13.6	31.61	0.00
Asteraceae	Native	gls	Exponential	12	942.6	-1860.7	0.00	0.85
		gls	Ratio	12	940.7	-1857.1	3.61	0.14
		gls	Gaussian	12	937.3	-1850.3	10.41	0.00
		gls	Spherical	12	937.0	-1849.6	11.09	0.00
		lm		10	834.4	-1648.5	212.15	0.00
	Exotic	gls	Gaussian	12	362.9	-701.0	0.00	0.71
		gls	Spherical	12	361.2	-697.6	3.36	0.13
		gls	Ratio	12	361.1	-697.4	3.64	0.12
		gls	Exponential	12	360.0	-695.1	5.89	0.04
		lm		10	274.6	-528.5	172.47	0.00
Boraginaceae	Native	gls	Exponential	12	179.3	-333.7	0.00	0.53
		gls	Ratio	12	178.7	-332.5	1.13	0.30
		gls	Spherical	12	177.5	-330.1	3.51	0.09
		gls	Gaussian	12	177.4	-329.9	3.76	0.08
		lm		10	140.9	-261.2	72.42	0.00
	Exotic	gls	Exponential	12	30.7	-35.1	0.00	0.40
		gls	Ratio	12	30.4	-34.5	0.61	0.30
		gls	Gaussian	12	30.3	-34.4	0.71	0.28
		gls	Spherical	12	27.5	-28.7	6.37	0.02
		lm		10	17.0	-12.5	22.59	0.00
Brassicaceae	Native	gls	Exponential	12	184.1	-343.3	0.00	0.32
		gls	Ratio	12	184.1	-343.2	0.04	0.31
		gls	Gaussian	12	183.6	-342.3	1.01	0.19
		gls	Spherical	12	183.6	-342.1	1.14	0.18
		lm		10	172.5	-324.4	18.89	0.00
	Exotic	gls	Gaussian	12	184.9	-344.7	0.00	0.39
		gls	Exponential	12	184.7	-344.2	0.52	0.30
		gls	Ratio	12	184.5	-343.8	0.91	0.25
		gls	Spherical	12	183.2	-341.2	3.45	0.07
		lm		10	152.5	-284.1	60.54	0.00
Chenopodiaceae	Native	gls	Spherical	12	660.2	-1295.9	0.00	0.70
		gls	Exponential	12	659.3	-1294.1	1.76	0.29
		gls	Ratio	12	656.1	-1287.7	8.20	0.01
		gls	Gaussian	12	651.4	-1278.3	17.56	0.00
		lm		10	502.0	-983.7	312.20	0.00
	Exotic	lm		10	23.2	-23.6	0.00	0.57
		gls	Spherical	12	24.5	-20.8	2.83	0.14
		gls	Gaussian	12	24.4	-20.6	2.94	0.13
		gls	Exponential	12	24.1	-20.0	3.57	0.10

Family	Status	Model class	Spatial auto-correlation term*	df	Log-likelihood	AICc	Delta-AICc	Weight
		gls	Ratio	12	23.8	-19.4	4.21	0.07
Convolvulaceae	Native	gls	Exponential	12	288.8	-552.9	0.00	0.42
		gls	Ratio	12	288.6	-552.5	0.40	0.34
		gls	Gaussian	12	287.7	-550.7	2.23	0.14
		gls	Spherical	12	287.4	-550.1	2.80	0.10
		lm		10	227.4	-434.3	118.55	0.00
	Exotic	gls	Spherical	12	22.0	-13.0	0.00	0.39
		gls	Exponential	12	21.5	-12.0	1.04	0.23
		gls	Gaussian	12	21.4	-11.9	1.13	0.22
		gls	Ratio	12	21.1	-11.2	1.85	0.15
		lm		10	15.5	-6.3	6.77	0.01
Cyperaceae	Native	gls	Exponential	12	576.7	-1128.9	0.00	0.73
		gls	Ratio	12	575.5	-1126.5	2.33	0.23
		gls	Spherical	12	573.7	-1122.9	5.98	0.04
		gls	Gaussian	12	568.9	-1113.3	15.53	0.00
		lm		10	444.6	-868.8	260.10	0.00
	Exotic	gls	Exponential	12	40.0	-52.4	0.00	0.31
		gls	Gaussian	12	39.8	-52.0	0.39	0.25
		gls	Spherical	12	39.6	-51.8	0.66	0.22
		gls	Ratio	12	39.6	-51.7	0.72	0.22
		lm		10	10.4	1.6	54.04	0.00
Ericaceae	Native	gls	Exponential	12	216.4	-407.6	0.00	0.62
		gls	Spherical	12	215.4	-405.6	2.04	0.22
		gls	Ratio	12	215.0	-404.8	2.84	0.15
		gls	Gaussian	12	210.2	-395.1	12.50	0.00
		lm		10	77.8	-134.8	272.85	0.00
	Exotic	lm		10	1.6	38.8	0.00	1.00
		gls	Ratio	12	3.3	56.3	17.55	0.00
		gls	Exponential	12	2.6	57.9	19.14	0.00
		gls	Gaussian	12	1.6	59.8	21.00	0.00
		gls	Spherical	12	1.6	59.8	21.00	0.00
Euphorbiaceae	Native	gls	Spherical	12	324.7	-624.7	0.00	0.67
		gls	Exponential	12	323.8	-622.9	1.79	0.27
		gls	Ratio	12	322.0	-619.3	5.44	0.04
		gls	Gaussian	12	320.3	-615.9	8.84	0.01
		lm		10	231.2	-442.0	182.73	0.00
	Exotic	gls	Spherical	12	30.0	-32.3	0.00	0.27
		gls	Exponential	12	30.0	-32.2	0.09	0.26
		gls	Gaussian	12	29.9	-32.0	0.30	0.24
		gls	Ratio	12	29.8	-31.9	0.40	0.23
		lm		10	20.2	-17.7	14.53	0.00
Fabaceae	Native	gls	Exponential	12	1199.9	-2375.5	0.00	0.90

Family	Status	Model class	Spatial auto-correlation term*	df	Log-likelihood	AICc	Delta-AICc	Weight
		gls	Spherical	12	1197.2	-2370.2	5.32	0.06
		gls	Ratio	12	1196.8	-2369.3	6.14	0.04
		gls	Gaussian	12	1188.3	-2352.3	23.19	0.00
		lm		10	847.5	-1674.8	700.71	0.00
	Exotic	gls	Spherical	12	281.0	-537.1	0.00	0.45
		gls	Exponential	12	280.3	-535.7	1.41	0.22
		gls	Ratio	12	280.2	-535.3	1.77	0.18
		gls	Gaussian	12	280.0	-534.9	2.16	0.15
		lm		10	213.5	-406.4	130.69	0.00
Juncaceae	Native	gls	Spherical	12	173.0	-320.5	0.00	0.51
		gls	Exponential	12	172.8	-320.0	0.47	0.41
		gls	Ratio	12	171.2	-316.7	3.78	0.08
		gls	Gaussian	12	167.8	-310.1	10.41	0.00
		lm		10	148.8	-276.4	44.07	0.00
	Exotic	lm		10	35.0	-47.2	0.00	0.78
		gls	Exponential	12	35.0	-41.9	5.26	0.06
		gls	Ratio	12	35.0	-41.9	5.27	0.06
		gls	Spherical	12	35.0	-41.9	5.27	0.06
		gls	Gaussian	12	35.0	-41.9	5.27	0.06
Lamiaceae	Native	gls	Exponential	12	377.0	-729.3	0.00	0.63
		gls	Spherical	12	376.0	-727.5	1.84	0.25
		gls	Ratio	12	375.3	-725.9	3.42	0.11
		gls	Gaussian	12	371.4	-718.2	11.08	0.00
		lm		10	168.1	-315.7	413.63	0.00
	Exotic	gls	Exponential	12	81.0	-136.2	0.00	0.47
		gls	Spherical	12	80.7	-135.6	0.56	0.36
		gls	Ratio	12	79.8	-133.8	2.38	0.14
		gls	Gaussian	12	78.2	-130.7	5.50	0.03
		lm		10	44.5	-67.7	68.47	0.00
Malvaceae	Native	gls	Exponential	12	642.1	-1259.9	0.00	0.70
		gls	Ratio	12	641.1	-1257.8	2.02	0.26
		gls	Spherical	12	639.3	-1254.2	5.70	0.04
		gls	Gaussian	12	634.6	-1244.9	14.98	0.00
		lm		10	454.4	-888.4	371.41	0.00
	Exotic	gls	Exponential	12	59.9	-93.3	0.00	0.34
		gls	Ratio	12	59.6	-92.8	0.53	0.26
		gls	Spherical	12	59.6	-92.8	0.55	0.26
		gls	Gaussian	12	59.0	-91.5	1.83	0.14
		lm		10	48.2	-74.7	18.67	0.00
Plantaginaceae	Native	gls	Exponential	12	120.0	-214.8	0.00	0.44
		gls	Ratio	12	119.9	-214.5	0.30	0.38
		gls	Spherical	12	119.0	-212.9	1.95	0.16

Family	Status	Model class	Spatial auto-correlation term*	df	Log-likelihood	AICc	Delta-AICc	Weight
		gls	Gaussian	12	117.1	-209.0	5.82	0.02
		lm		10	93.8	-166.7	48.10	0.00
	Exotic	gls	Spherical	12	19.0	-11.6	0.00	0.36
		gls	Exponential	12	18.7	-10.9	0.72	0.25
		gls	Ratio	12	18.4	-10.4	1.20	0.20
		gls	Gaussian	12	18.4	-10.3	1.25	0.19
		lm		10	-2.6	26.8	38.41	0.00
Poaceae C3	Native	gls	Spherical	12	471.1	-917.6	0.00	0.63
		gls	Gaussian	12	470.2	-915.7	1.93	0.24
		gls	Ratio	12	469.0	-913.4	4.26	0.07
		gls	Exponential	12	468.8	-913.0	4.62	0.06
		lm		10	394.2	-768.0	149.66	0.00
	Exotic	gls	Exponential	12	220.7	-416.3	0.00	0.56
		gls	Ratio	12	219.6	-414.1	2.20	0.19
		gls	Spherical	12	219.3	-413.4	2.84	0.14
		gls	Gaussian	12	219.1	-413.0	3.23	0.11
		lm		10	182.5	-344.1	72.16	0.00
Poaceae C4	Native	gls	Exponential	12	876.7	-1729.0	0.00	0.99
		gls	Ratio	12	872.4	-1720.4	8.55	0.01
		gls	Spherical	12	863.1	-1701.9	27.10	0.00
		gls	Gaussian	12	853.0	-1681.5	47.47	0.00
		lm		10	645.2	-1270.2	458.80	0.00
	Exotic	gls	Exponential	12	182.2	-339.3	0.00	0.60
		gls	Ratio	12	181.3	-337.7	1.65	0.27
		gls	Spherical	12	180.4	-335.9	3.48	0.11
		gls	Gaussian	12	179.0	-333.0	6.37	0.02
		lm		10	70.0	-119.4	219.99	0.00
Rubiaceae	Native	gls	Exponential	12	378.4	-732.0	0.00	0.63
		gls	Spherical	12	377.3	-729.8	2.21	0.21
		gls	Ratio	12	377.0	-729.2	2.74	0.16
		gls	Gaussian	12	373.6	-722.5	9.49	0.01
		lm		10	291.9	-563.3	168.70	0.00
	Exotic	gls	Spherical	12	46.1	-65.4	0.00	0.31
		gls	Gaussian	12	46.0	-65.2	0.19	0.28
		gls	Exponential	12	45.7	-64.6	0.77	0.21
		gls	Ratio	12	45.6	-64.5	0.96	0.19
		lm		10	37.9	-53.8	11.58	0.00
Scrophulariaceae	Native	gls	Ratio	12	492.3	-960.1	0.00	0.43
		gls	Spherical	12	491.9	-959.2	0.84	0.29
		gls	Exponential	12	491.4	-958.3	1.84	0.17
		gls	Gaussian	12	490.9	-957.3	2.81	0.11
		lm		10	274.9	-529.4	430.65	0.00

Family	Status	Model class	Spatial auto-correlation term*	df	Log-likelihood	AICc	Delta-AICc	Weight
	Exotic	lm		10	19.2	-14.8	0.00	0.80
		gls	Exponential	12	19.4	-9.5	5.31	0.06
		gls	Ratio	12	19.3	-9.4	5.46	0.05
		gls	Spherical	12	19.2	-9.2	5.65	0.05
		gls	Gaussian	12	19.2	-9.2	5.65	0.05
Solanaceae	Native	gls	Exponential	12	321.4	-618.3	0.00	0.67
		gls	Spherical	12	320.1	-615.6	2.64	0.18
		gls	Ratio	12	319.8	-615.1	3.14	0.14
		gls	Gaussian	12	316.5	-608.5	9.83	0.00
		lm		10	174.0	-327.7	290.57	0.00
	Exotic	gls	Exponential	12	87.8	-150.1	0.00	0.36
		gls	Spherical	12	87.7	-149.9	0.23	0.32
		gls	Ratio	12	87.2	-148.9	1.16	0.20
		gls	Gaussian	12	86.6	-147.7	2.36	0.11
		lm		10	64.0	-107.0	43.04	0.00

*Linear models did not contain spatial autocorrelation terms.

Table B.3 Native and exotic family richness model fits for two model types, linear terms and models including quadratic terms. Model fits were ranked by delta-AICc (the difference in AICc values between each model and the best-fitting model) for two model types, models with solely linear associations to environmental and human impact variables (linear), and models with linear and significant quadratic associations to environmental and human impact variables (quadratic). To be selected, quadratic models were required to have a delta-AICc value greater than 10 compared to the linear model to justify the added model complexity. Quadratic models that were selected are highlighted in grey.

Family	Model type	Log likelihood	df	AICc	Delta	Weight
Amaranthaceae	Quadratic	514.15	19	-989.07	0.00	1.00
	Linear	464.05	12	-903.59	85.48	0.00
Apiaceae	Linear	156.48	12	-287.84	0.00	1.00
	Quadratic	158.32	19	-275.80	12.03	0.00
Apocynaceae	Linear	283.93	12	-542.73	0.00	0.97
	Quadratic	288.45	19	-536.02	6.71	0.03
Asparagaceae	Linear	304.85	12	-584.73	0.00	1.00
	Quadratic	305.92	19	-571.34	13.39	0.00
Asteraceae	Linear	942.55	12	-1860.67	0.00	0.89
	Quadratic	947.76	19	-1856.46	4.21	0.11
Boraginaceae	Linear	179.29	12	-333.66	0.00	0.98
	Quadratic	182.87	19	-325.47	8.19	0.02
Brassicaceae	Linear	184.13	12	-343.28	0.00	1.00
	Quadratic	182.72	19	-324.97	18.31	0.00
Chenopodiaceae	Linear	660.19	12	-1295.89	0.00	0.84
	Quadratic	665.89	19	-1292.55	3.34	0.16
Convolvulaceae	Linear	288.84	12	-552.90	0.00	0.66
	Quadratic	295.77	19	-551.61	1.29	0.34
Cyperaceae	Quadratic	586.54	19	-1133.73	0.00	0.92
	Linear	576.70	12	-1128.87	4.86	0.08
Ericaceae	Linear	216.45	12	-407.64	0.00	0.65
	Quadratic	223.78	19	-406.36	1.28	0.35
Euphorbiaceae	Linear	324.70	12	-624.72	0.00	0.99
	Quadratic	327.15	19	-614.63	10.09	0.01
Fabaceae	Quadratic	1231.24	19	-2423.64	0.00	1.00
	Linear	1199.91	12	-2375.47	48.16	0.00
FNA*	Quadratic	930.26	14	-1831.99	0.00	1.00
	linear	918.23	12	-1812.07	19.93	0.00
Juncaceae	Quadratic	183.56	19	-325.09	0.00	0.91
	Linear	173.05	12	-320.51	4.58	0.09
Lamiaceae	Quadratic	389.47	19	-739.41	0.00	0.99
	Linear	376.96	12	-729.31	10.10	0.01
Malvaceae	Quadratic	655.34	19	-1271.64	0.00	1.00
	Linear	642.14	12	-1259.86	11.79	0.00
Plantaginaceae	Linear	120.01	12	-214.81	0.00	0.82
	Quadratic	126.40	19	-211.76	3.05	0.18
Poaceae C3	Quadratic	486.09	19	-932.56	0.00	1.00
	Linear	471.13	12	-917.61	14.94	0.00
Poaceae C4	Quadratic	902.25	19	-1765.46	0.00	1.00
	Linear	876.70	12	-1728.97	36.49	0.00
Rubiaceae	Linear	378.39	12	-731.97	0.00	0.99

Family	Model type	Log likelihood	df	AICc	Delta	Weight
	Quadratic	381.32	19	-722.64	9.33	0.01
Scrophulariaceae	Linear	492.30	12	-960.09	0.00	1.00
	Quadratic	490.17	19	-941.06	19.03	0.00
Solanaceae	Quadratic	334.22	19	-629.11	0.00	1.00
	Linear	321.41	12	-618.28	10.83	0.00

*FNA = Fabaceae species richness without species in the genus *Acacia*.

Table B.4 Native family species richness Model fits by R^2 values. Adjusted R^2 values were calculated for two model types, linear associations to environmental variables (linear) and linear and quadratic associations to environmental variables (quadratic). The model selected for each family was based on a combination of model type and delta-AICc scores. (For details see Appendix Table S3.)

Family	Selected model	Adjusted R^2	
		Linear	Quadratic
Amaranthaceae	Quadratic	0.573	0.552
Apiaceae	Linear	0.254	0.255
Apocynaceae	Linear	0.624	0.877
Asparagaceae	Linear	0.108	0.220
Asteraceae	Linear	0.517	0.570
Boraginaceae	Linear	0.476	0.463
Brassicaceae	Linear	0.145	0.166
Chenopodiaceae	Linear	0.022	0.644
Convolvulaceae	Linear	0.702	0.714
Cyperaceae	Linear	0.491	0.581
Ericaceae	Linear	0.081	0.277
Euphorbiaceae	Linear	0.311	0.540
Fabaceae	Quadratic	0.197	0.273
FNA*	Quadratic	0.211	0.353
Juncaceae	Linear	0.347	0.701
Lamiaceae	Quadratic	0.227	0.232
Malvaceae	Quadratic	0.520	0.604
Plantaginaceae	Linear	0.340	0.435
Poaceae C3	Quadratic	0.614	0.658
Poaceae C4	Quadratic	0.594	0.776
Rubiaceae	Linear	0.589	0.740
Scrophulariaceae	Linear	0.301	0.336
Solanaceae	Quadratic	0.192	0.323

*FNA = Fabaceae species richness without species in the genus *Acacia*.

Table B.5 Native and exotic family correlation and adjusted R^2 values. Groups A to D correspond to the tendency for the native template to work, defined as native-exotic family correlation richness values above 0.3 and native richness R^2 values above 0.40. Group A = complete support, B = partial support, and C and D = no support.

Group	Family	Prefix	Correlation	Native R^2	Exotic R^2
A	Cyperaceae	Cyp	0.707	0.491	0.163
	Poaceae C3	C3	0.667	0.658	0.482
	Apocynaceae	Apo	0.604	0.624	-0.013
	Rubiaceae	Rub	0.501	0.589	0.311
	Poaceae C4	C4	0.402	0.776	0.314
	Convolvulaceae	Con	0.377	0.702	0.357
B	Euphorbiaceae	Eup	0.628	0.311	0.139
	Fabaceae	Fab	0.551	0.273	0.599
	Solanaceae	Sol	0.490	0.323	0.435
	Lamiaceae	Lam	0.473	0.232	0.414
	Apiaceae	Api	0.403	0.254	0.248
	Juncaceae	Jun	0.336	0.347	0.352
C	Malvaceae	Mal	0.212	0.604	0.297
	Amaranthaceae	Ama	0.135	0.552	-0.068
	Boraginaceae	Bor	0.043	0.476	0.122
	Asteraceae	Ast	-0.078	0.517	0.136
D	Plantaginaceae	Pla	0.226	0.340	-0.017
	Asparagaceae	Asp	0.205	0.108	-0.372
	Ericaceae	Eri	0.111	0.081	-0.232
	Scrophulariaceae	Scr	0.062	0.301	0.276
	Brassicaceae	Bra	-0.060	0.145	0.398
	Chenopodiaceae	Che	-0.104	0.022	0.138

Table B.6 The number of native and exotic family records and species for Fabaceae with and without *Acacia* species. Data taken from the Australasian Virtual Herbarium via the Atlas of Living Australia (https://biocache.ALA.org.au/; CHAH 2018). FNA = Fabaceae species richness without species in the endemic Australian genus *Acacia*.

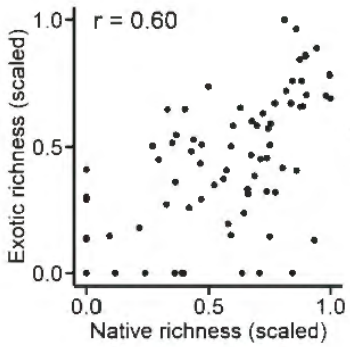
Family	Species			Records		
	Native	Exotic	Total	Native	Exotic	Total
Fabaceae	2,466	290	2,756	791,447	96,930	888,377
FNA	1,455	290	1,745	418,191	96,930	515,121

Table B.7 Predictors of the correlation between native and exotic species richness for 22 common native and exotic plant families in Australia. Native R^2 = adjusted R^2 value as a measure of the variation in native family species richness explained by associations with environmental and human activity variables. Worldwide species and C4 species = the total number of species in the family and C4 species in the family, data taken from Christenhusz **and** Byng (2016), Sage (2016), and Hernández-Ledesma et al. (2015). Exotic first occurrence = mean year of first record for each species within family. Cell occupation = the proportion of the total number of cells with ≥ 15 records between native and exotic species.

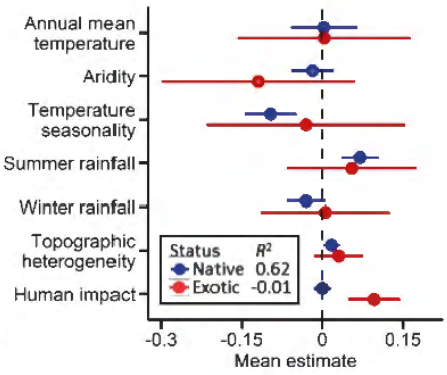
Parameter	Estimate	Std. error	t-value	p-value
Intercept	-0.014	±0.789	-0.017	0.986
Native R^2	0.603	±0.404	1.492	0.158
Worldwide species (log)	0.000	±0.000	-0.957	0.355
Worldwide C4 species (log)	0.000	±0.000	-0.479	0.639
Exotic records (log)	0.114	±0.111	1.027	0.322
Exotic first occurrence	-0.010	±0.007	-1.556	0.142
Cell occupation	0.118	±0.636	0.186	0.855

(a) *Apocynaceae*

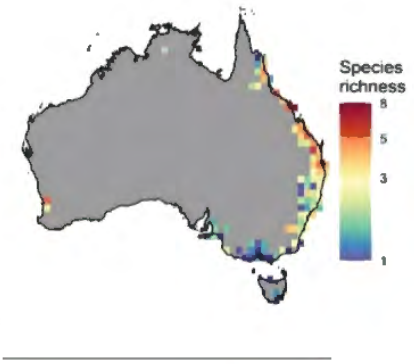
(i) Native – exotic correlation



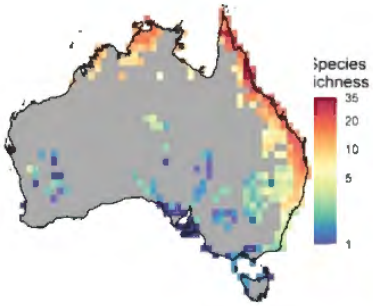
(ii) Associations with environmental and human impact variables



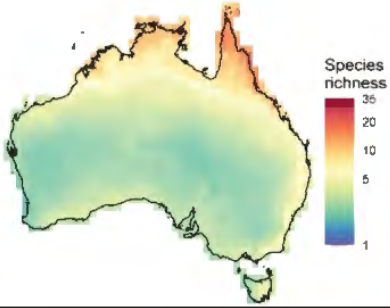
(iii) Observed exotic richness



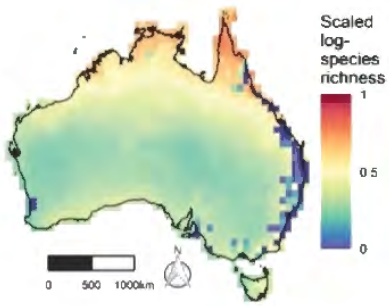
(iv) Observed native richness



(v) Predicted native richness

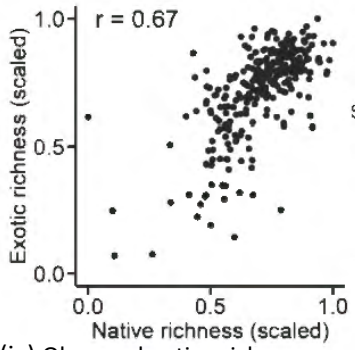


(vi) Exotic richness invasion potential

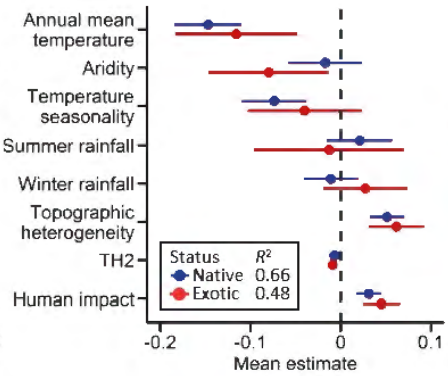


(b) *Poaceae* C3

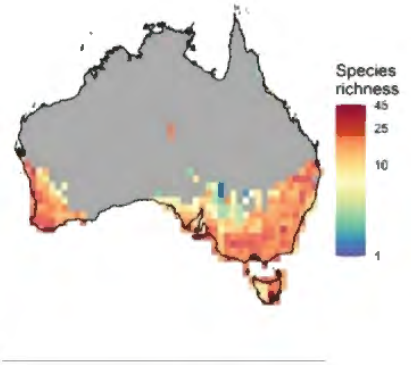
(i) Native – exotic correlation



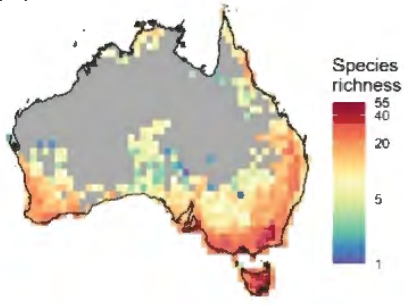
(ii) Associations with environmental and human impact variables



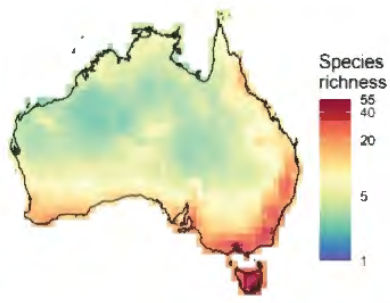
(iii) Observed exotic richness



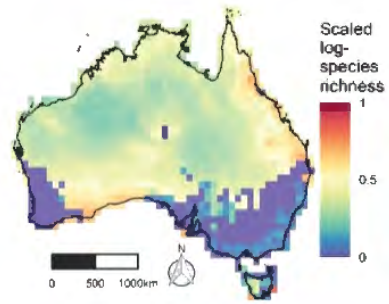
(iv) Observed native richness



(v) Predicted native richness

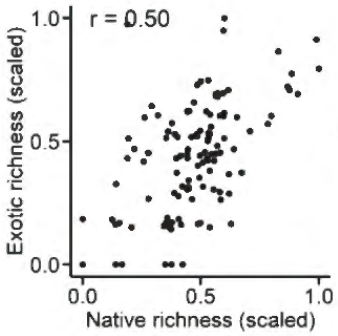


(vi) Exotic richness invasion potential

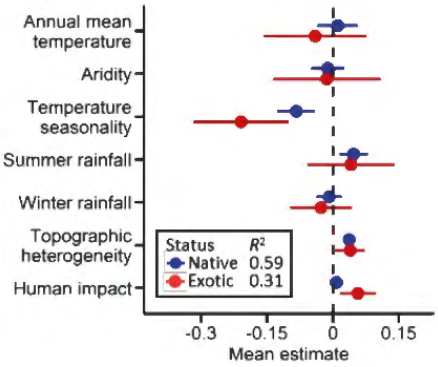


(c) *Rubiaceae*

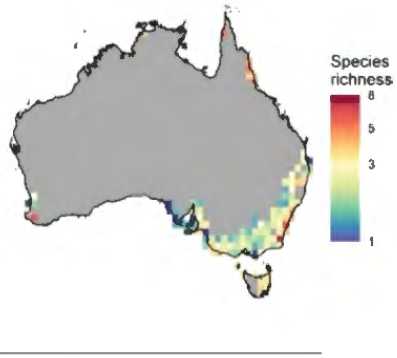
(i) Native – exotic correlation



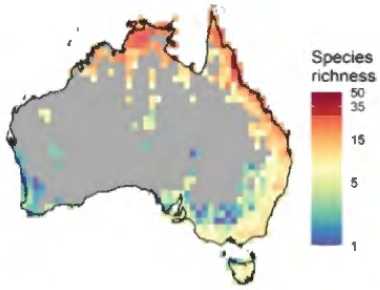
(ii) Associations with environmental and human impact variables



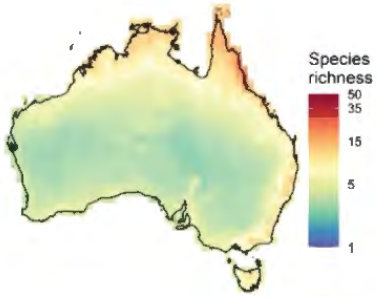
(iii) Observed exotic richness



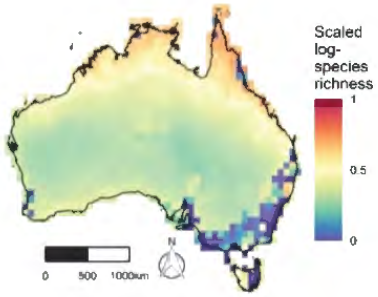
(iv) Observed native richness



(v) Predicted native richness

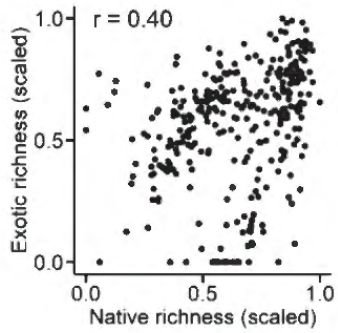


(vi) Exotic richness invasion potential

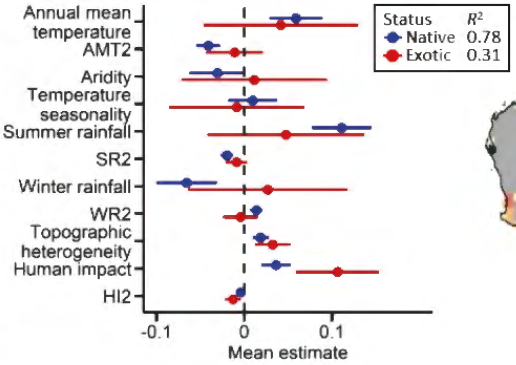


(d) *Poaceae* C4

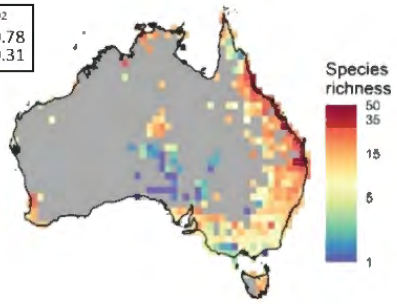
(i) Native – exotic correlation



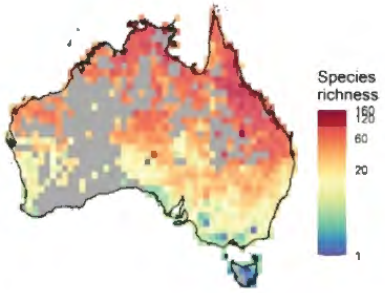
(ii) Associations with environmental and human impact variables



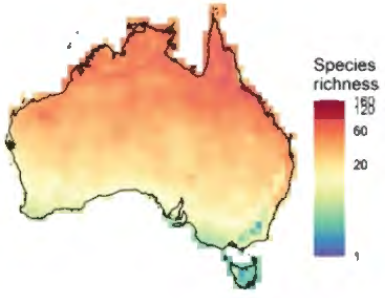
(iii) Observed exotic richness



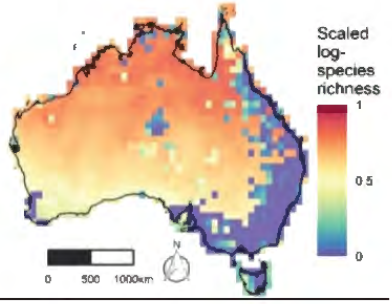
(iv) Observed native richness



(v) Predicted native richness



(vi) Exotic richness invasion potential



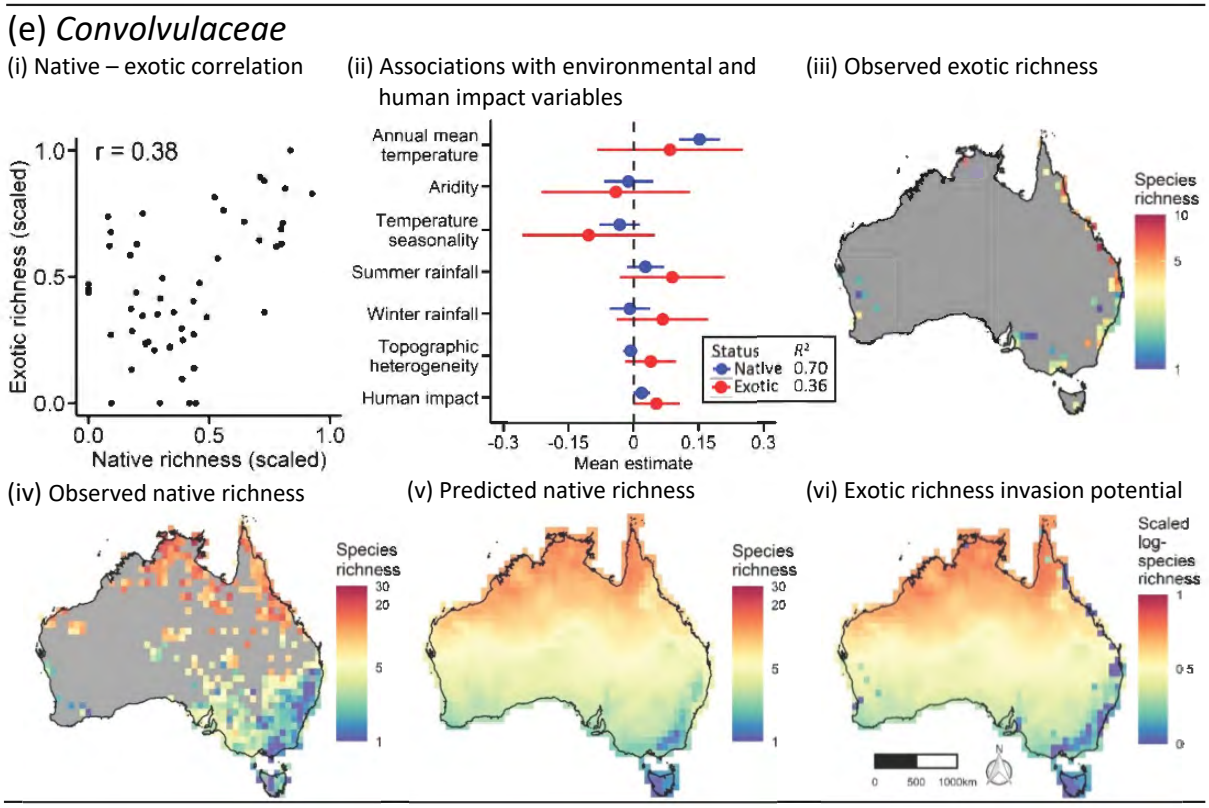
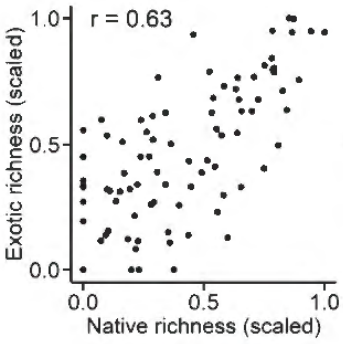


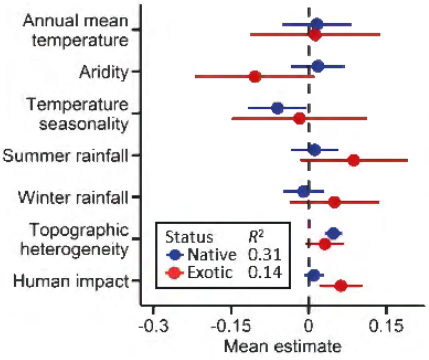
Figure B.1 Native family species richness as templates for potential exotic family species richness at large spatial scales across Australia. Box (a) Euphorbiaceae, (b) *Apocynaceae*, (c) Poaceae C3, (d) Rubiaceae, (e) Poaceae C4, and (f) Convolvulaceae. (i) Observed native richness (x-axis) and observed exotic richness (y-axis) scaled to between zero and one. Each point represents a 100 × 100 km cell across Australia with both a both a native and exotic richness estimate. (ii) Mean estimates of native (blue) and exotic (red) log-transformed species richness compared to six environmental variables and a single human impact variable using multiple linear regression. Error bars represent 95% confidence intervals of the mean, which are significant ($P < 0.05$) if they exclude zero (vertical dashed line). The explanatory variables were scaled prior to modelling to compare mean estimate values. The mean estimates of two variables (proportion of land cover and a spatial autocorrelation term) were excluded from plots. AMT = (annual mean temperature)^2, SR2 = (summer rainfall)^2, TH2 = (topographic heterogeneity)^2, and WR2 = (winter rainfall)^2. (iii) Observed native and (iv) observed exotic species richness across Australia. Note that species richness was modelled in log-transformed units but is displayed with raw species richness to indicate the large difference in the number of species represented by cells with hot colours (red-orange) and cool colours (blue-yellow). Grey zones did not meet criteria to estimate species richness and were not analysed. (v) Exotic invasion potential across Australia, calculated for each area for as the difference between log-transformed predicted native richness and log-transformed observed exotic richness both scaled to values between 0 and 1. Negative invasion potential values were truncated to zero.

(a) *Euphorbiaceae*

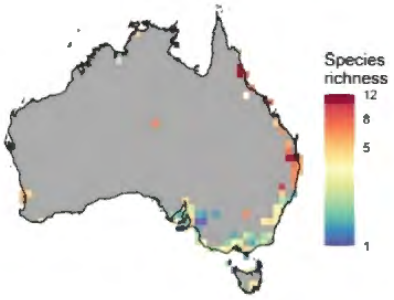
(i) Native – exotic correlation



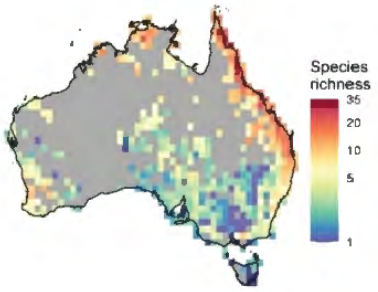
(ii) Associations with environmental and human impact variables



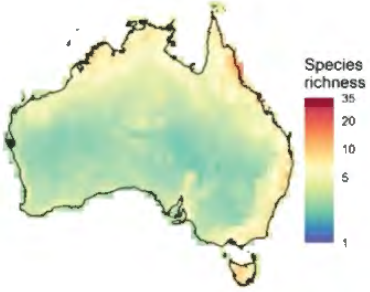
(iii) Observed exotic richness



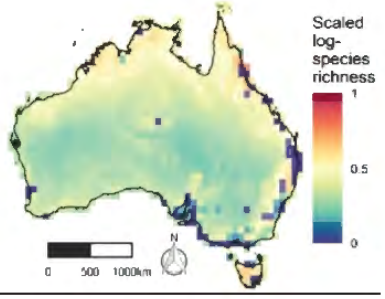
(iv) Observed native richness



(v) Predicted native richness

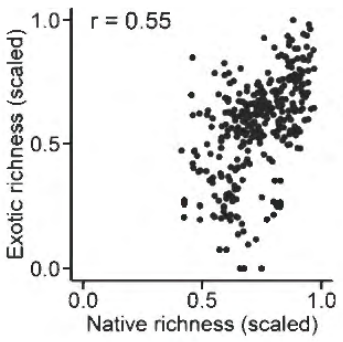


(vi) Exotic richness invasion potential

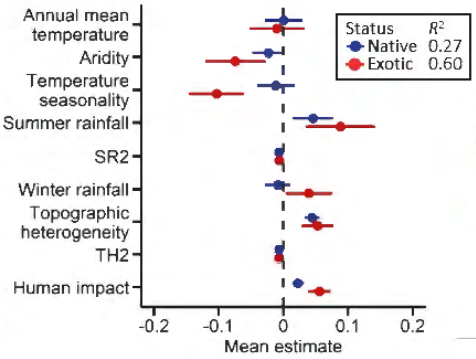


(b) *Fabaceae*

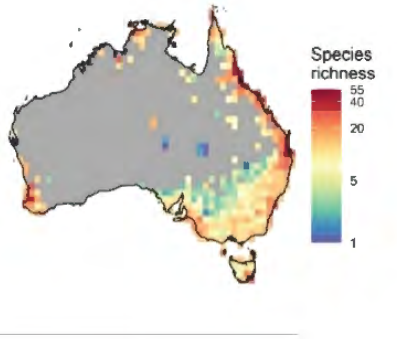
(i) Native – exotic correlation



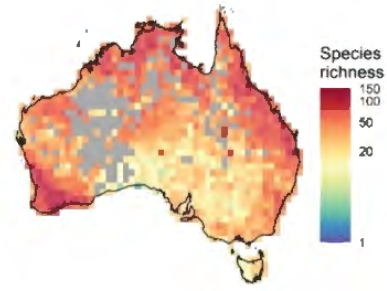
(ii) Associations with environmental and human impact variables



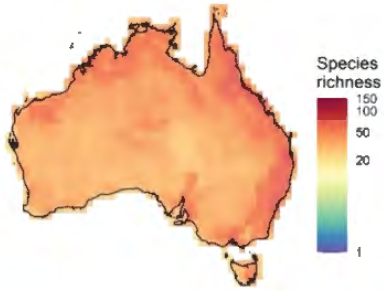
(iii) Observed exotic richness



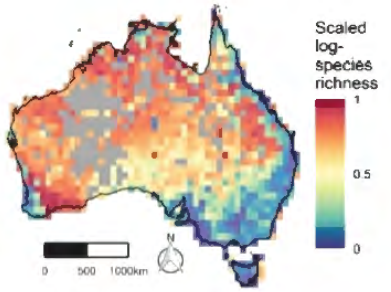
(iv) Observed native richness



(v) Predicted native richness

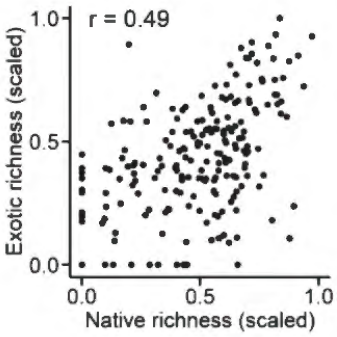


(vi) Exotic richness invasion potential

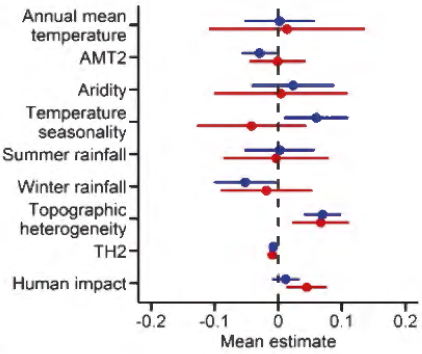


(c) *Solanaceae*

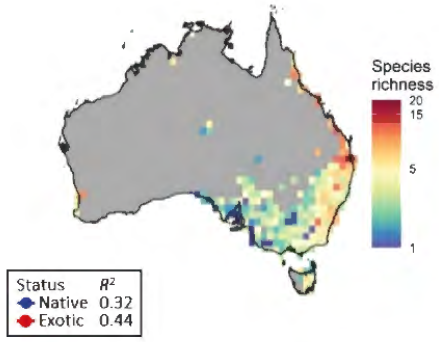
(i) Native – exotic correlation



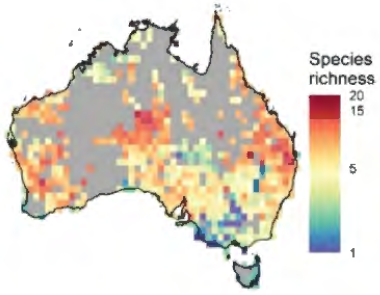
(ii) Associations with environmental and human impact variables



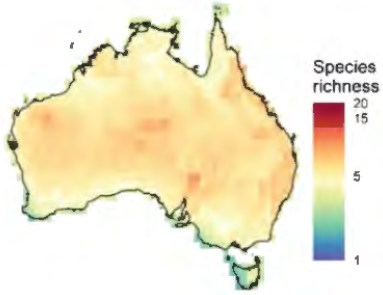
(iii) Observed exotic richness



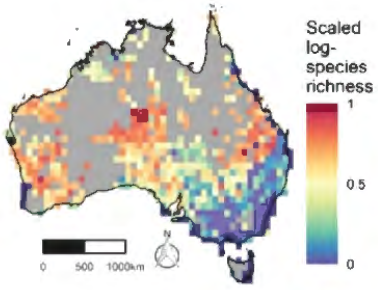
(iv) Observed native richness



(v) Predicted native richness

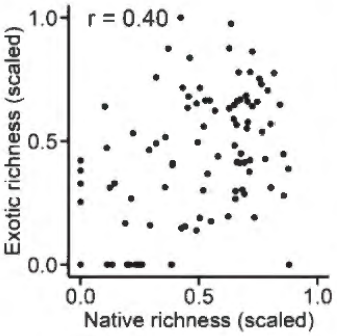


(vi) Exotic richness invasion potential

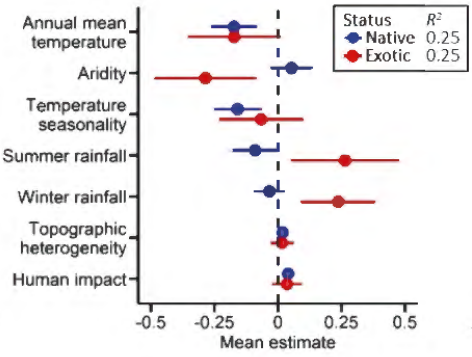


(d) *Apiaceae*

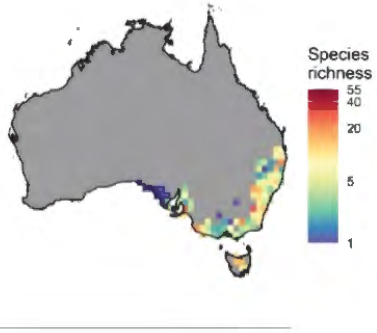
(i) Native – exotic correlation



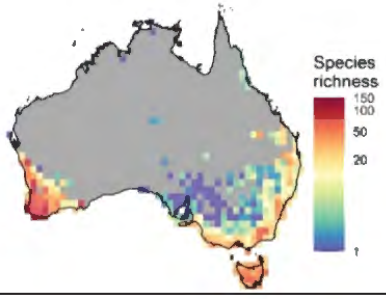
(ii) Associations with environmental and human impact variables



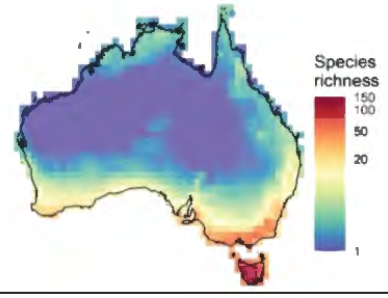
(iii) Observed exotic richness



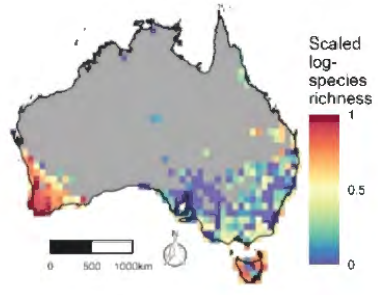
(iv) Observed native richness



(v) Predicted native richness



(vi) Exotic richness invasion potential



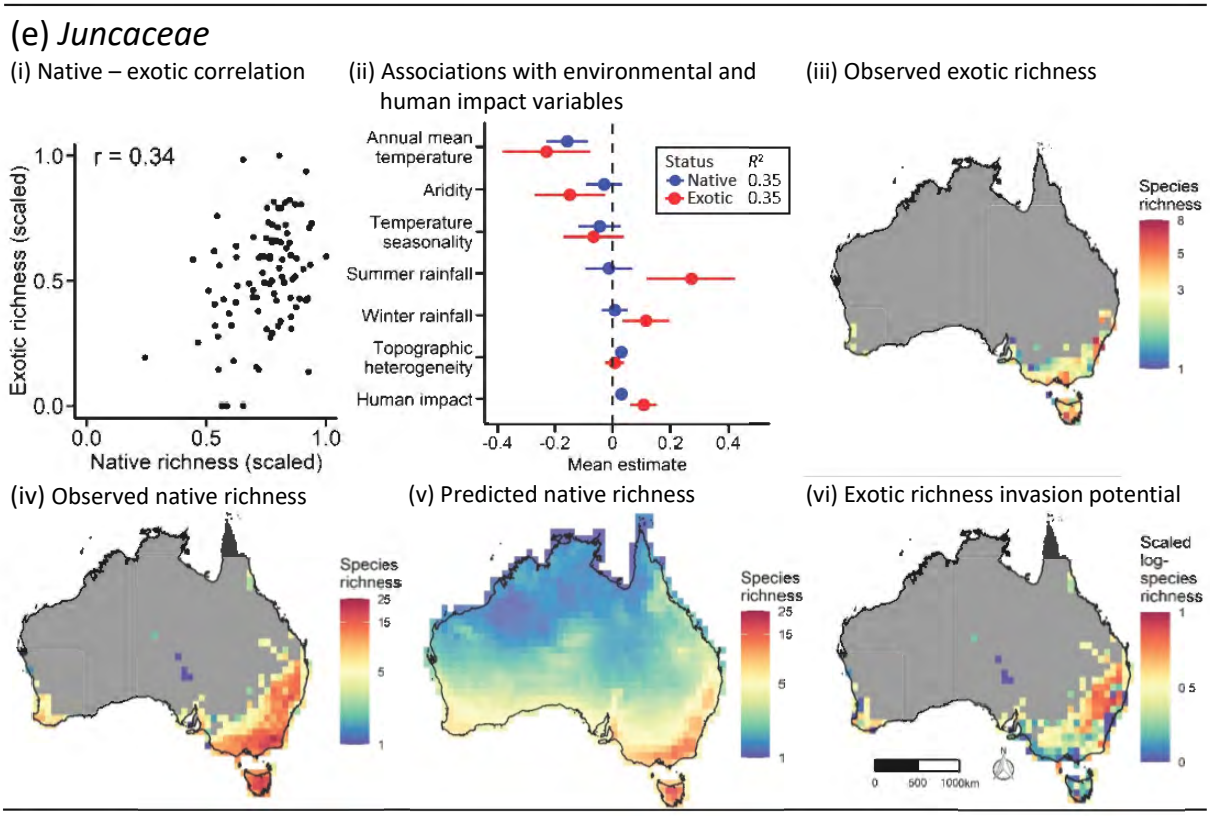
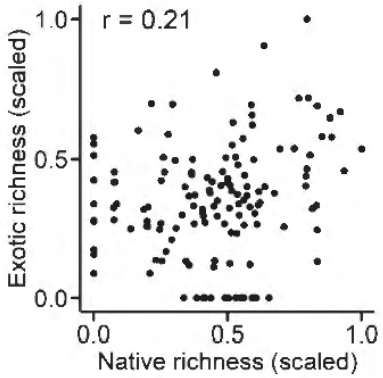


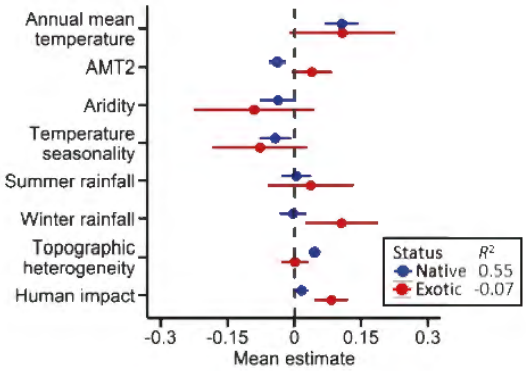
Figure B.2 Native family species richness as incomplete templates for potential exotic family species richness at large spatial scales across Australia. Box (a) Fabaceae species richness, (b) Solanaceae species richness, (c) Apiaceae species richness, and (d) Juncaceae species richness. (i) Observed native richness (x-axis) and observed exotic richness (y-axis) scaled to between zero and one. Each point represents a 100 × 100 km cell across Australia with both a both a native and exotic richness estimate. (ii) Mean estimates of native (blue) and exotic (red) log-transformed species richness compared to six environmental variables and a single human impact variable using multiple linear regression. Error bars represent 95% confidence intervals of the mean, which are significant (P <0.05) if they exclude zero (vertical dashed line). The explanatory variables were scaled prior to modelling to compare mean estimate values. The mean estimates of two variables (proportion of land cover and a spatial autocorrelation term) were excluded from plots. AMT2 = (annual mean temperature)^2, SR2 = (summer rainfall)^2, and TH2 = (topographic heterogeneity)^2. (iii) Observed native and (iv) observed exotic species richness across Australia. Note that species richness was modelled in log-transformed units but is displayed with raw species richness to indicate the large difference in the number of species represented by cells with hot colours (red-orange) and cool colours (blue-yellow). Grey zones did not meet criteria to estimate species richness and were not analysed. (v) Native species richness predicted across all areas of Australia using mean estimates from (ii). (vi) Exotic invasion potential across Australia, calculated for each area for as the difference between log-transformed observed native richness and log-transformed observed exotic richness both scaled to values between 0 and 1. Invasion potential was not calculated for areas missing observed native species richness values. Negative invasion potential values were truncated to zero.

(a) *Amaranthaceae*

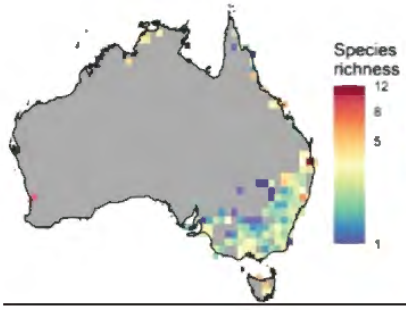
(i) Native – exotic correlation



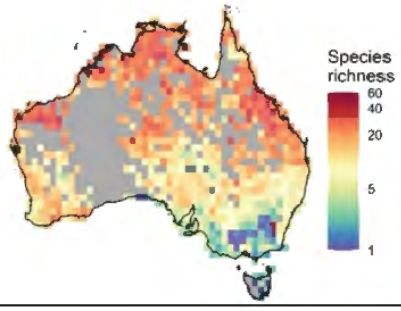
(ii) Associations with environmental and human impact variables



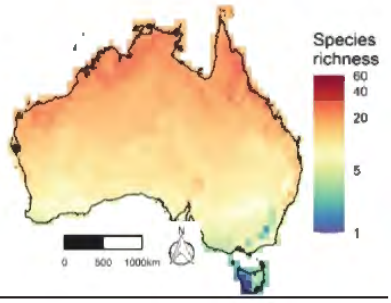
(iii) Observed exotic richness



(iv) Observed native richness

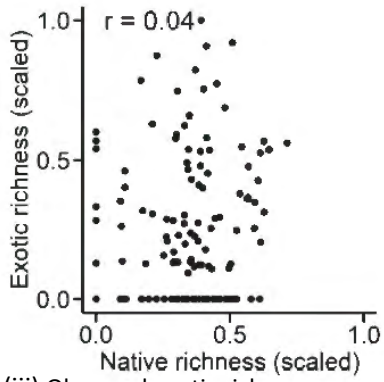


(v) Predicted native richness

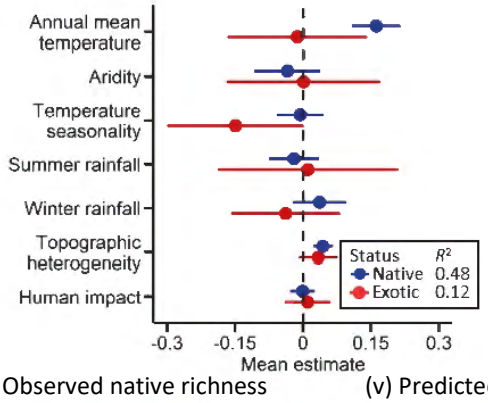


(b) *Boraginaceae*

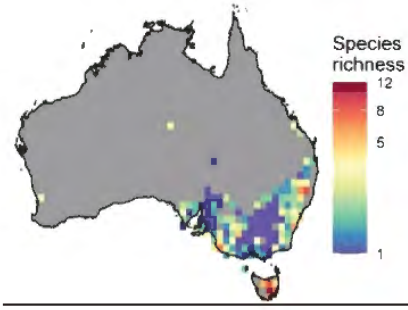
(i) Native – exotic correlation



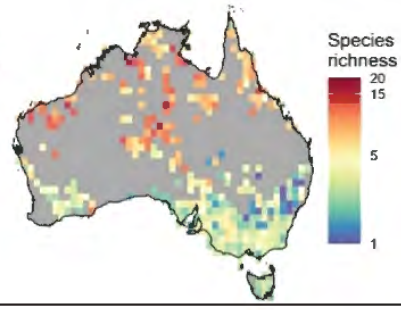
(ii) Associations with environmental and human impact variables



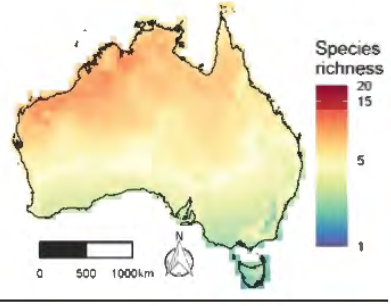
(iii) Observed exotic richness



(iv) Observed native richness



(v) Predicted native richness



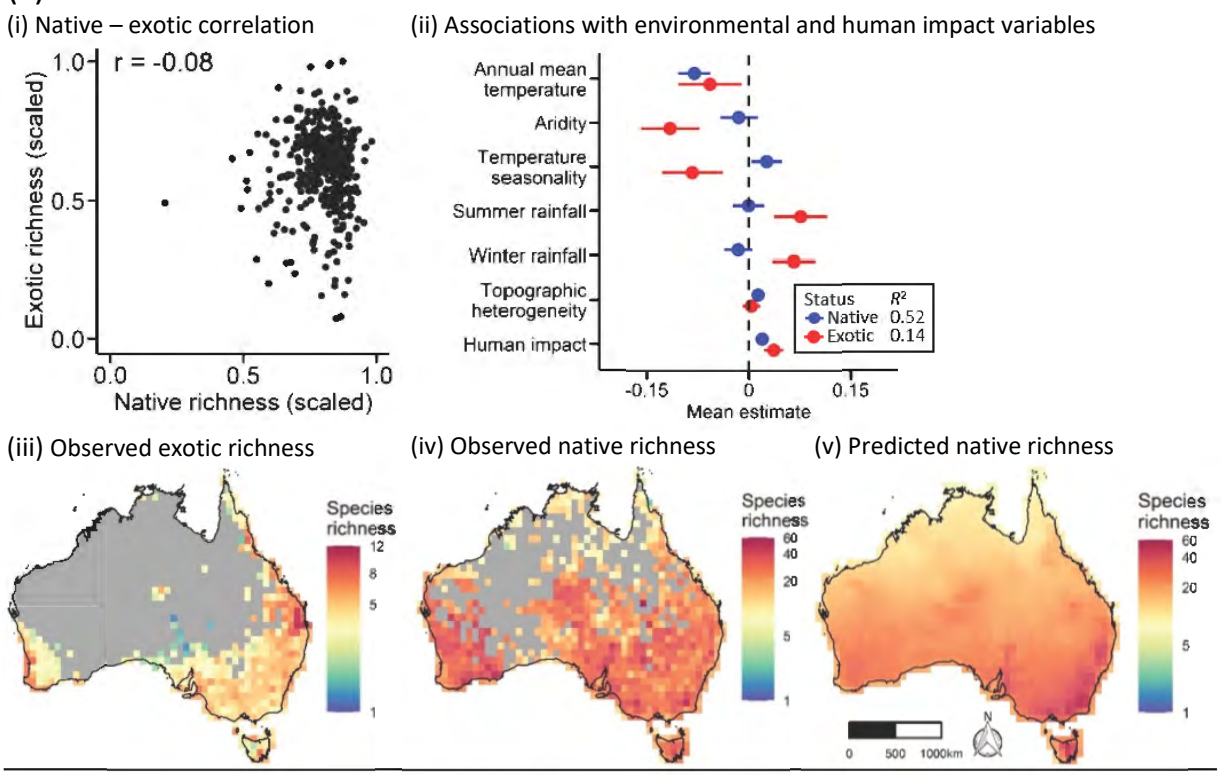
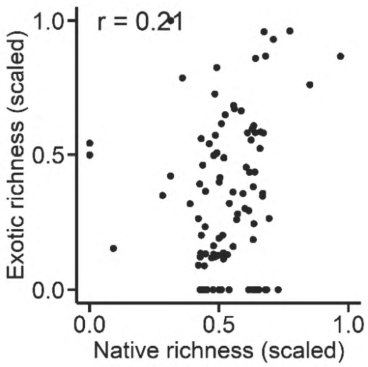


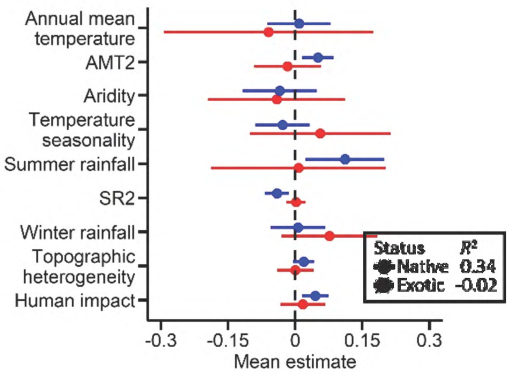
Figure B.3 Native family species richness as poor templates for potential exotic family species richness at large spatial scales across Australia. Box (a) Amaranthaceae species richness, (b) Boraginaceae species richness, and (c) Asteraceae species richness. (i) Observed native richness (x-axis) and observed exotic richness (y-axis) scaled to between zero and one. Each point represents a 100 × 100 km gridded cell across Australia with both a both a native and exotic richness estimate. (ii) Mean estimates of native (blue) and exotic (red) log-transformed species richness compared to six environmental variables and a single human impact variable using multiple linear regression. Error bars represent 95% confidence intervals of the mean, which are significant ($P < 0.05$) if they exclude zero (vertical dashed line). The explanatory variables were scaled prior to modelling to compare estimate values. The mean estimates of two variables (proportion of land cover and a spatial autocorrelation term) were excluded from plots. AMT2 = (annual mean temperature)^2 and SR = (summer rainfall)^2. (iii) Observed exotic and (iv) observed native species richness across Australia. Note that species richness was modelled in log-transformed units but is displayed with raw species richness to indicate the large difference in the number of species represented by cells with hot colours (red-orange) and cool colours (blue-yellow). Grey zones did not meet criteria to estimate species richness and were not analysed**.** (v) Native species richness predicted across all areas of Australia using mean estimates from (ii).

(a) *Plantaginaceae*

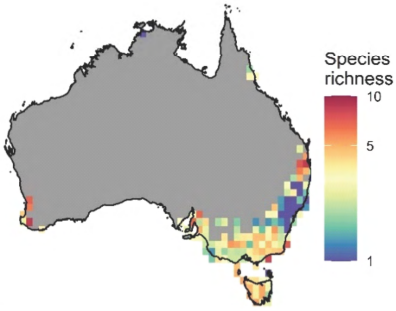
(i) Native – exotic correlation



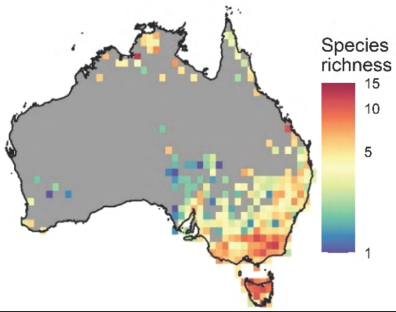
(ii) Associations with environmental and human impact variables



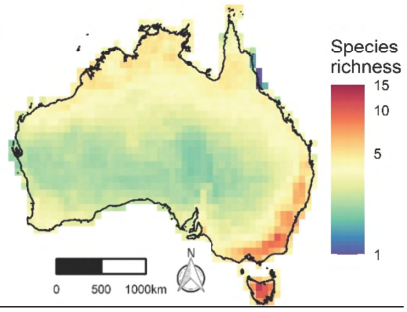
(iii) Observed exotic richness



(iv) Observed native richness

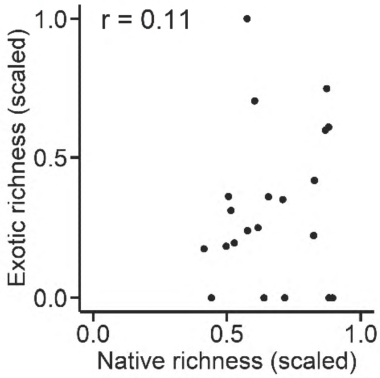


(v) Predicted native richness

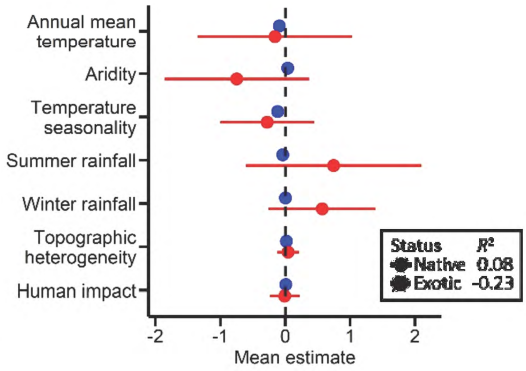


(b) *Ericaceae*

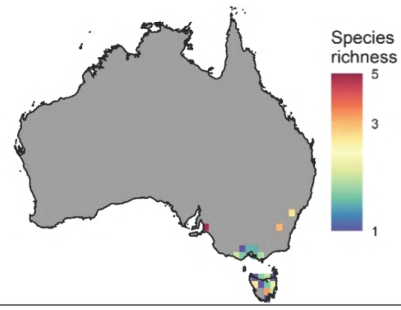
(i) Native – exotic correlation



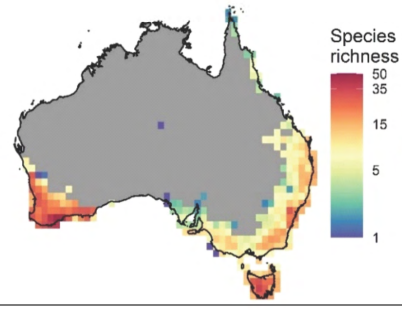
(ii) Associations with environmental and human impact variables



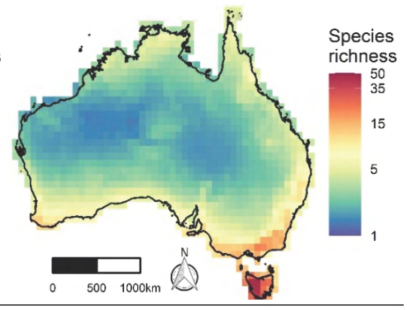
(iii) Observed exotic richness



(iv) Observed native richness

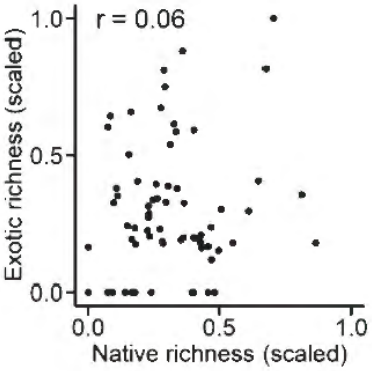


(v) Predicted native richness

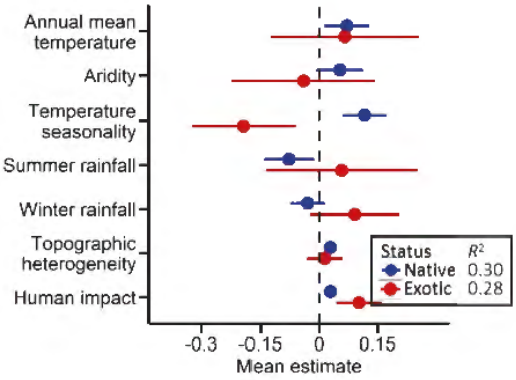


(c) *Scrophulariaceae*

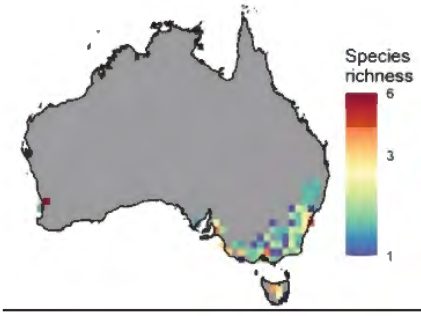
(i) Native – exotic correlation



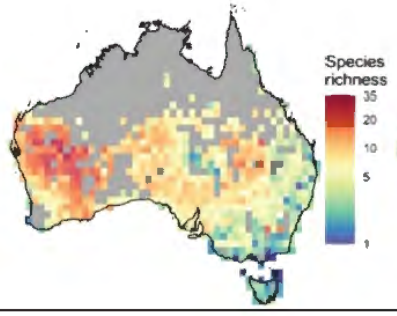
(ii) Associations with environmental and human impact variables



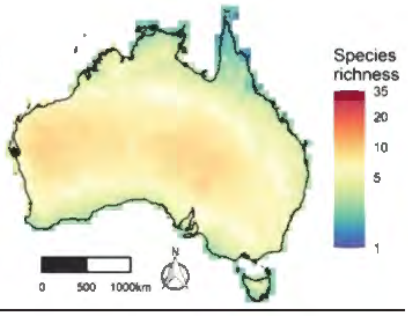
(iii) Observed exotic richness



(iv) Observed native richness

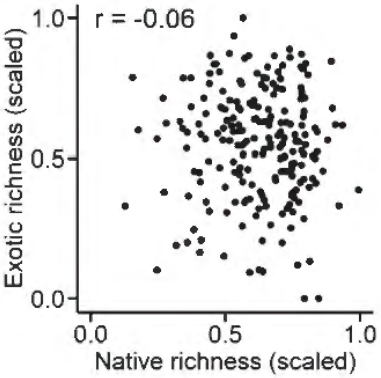


(v) Predicted native richness

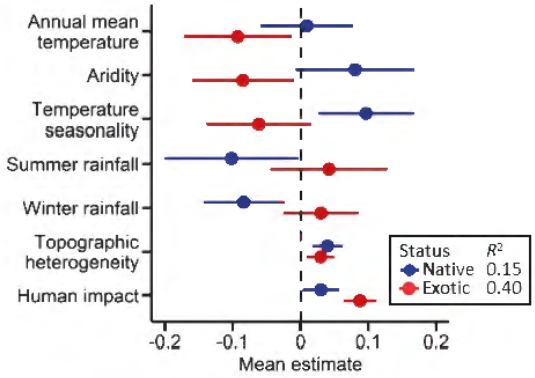


(d) *Brassicaceae*

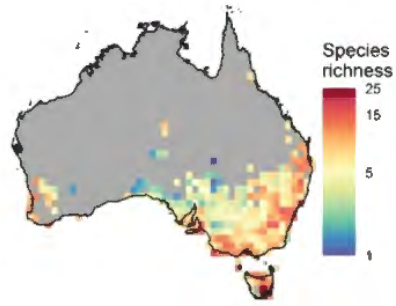
(i) Native – exotic correlation



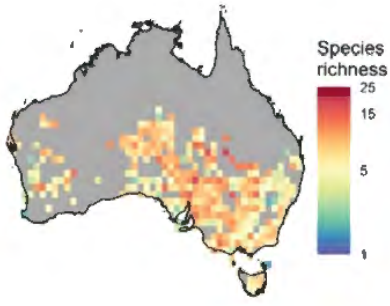
(ii) Associations with environmental and human impact variables



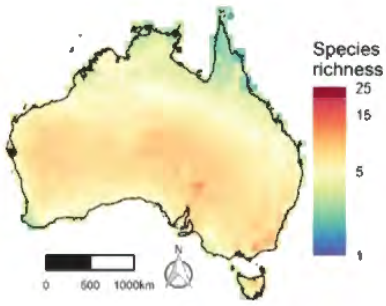
(iii) Observed exotic richness



(iv) Observed native richness



(v) Predicted native richness



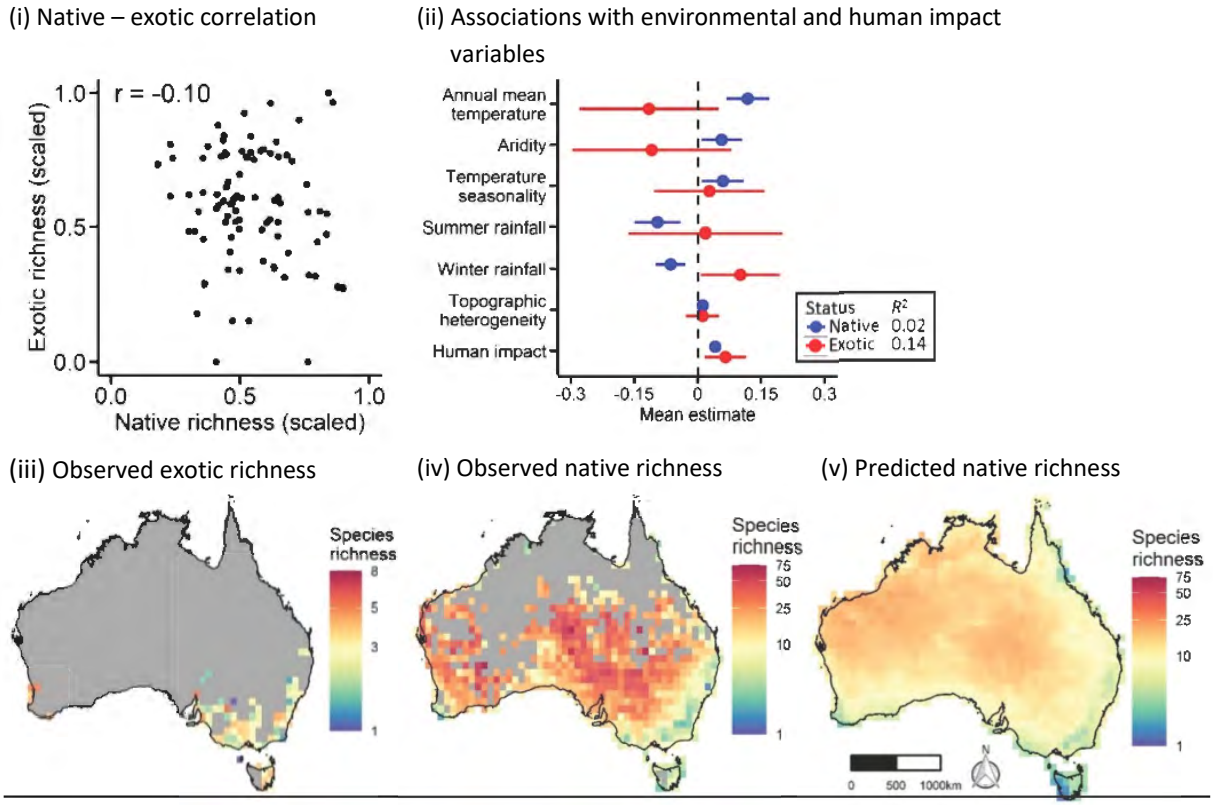


Figure B.4 Native family species richness as poor templates for potential exotic family species richness at large spatial scales across Australia. Box (a) Plantaginaceae species richness, (b) Ericaceae species richness, (c) Scrophulariaceae species richness, (d) Brassicaceae species richness, and (e) Chenopodiaceae species richness. (i) Observed native richness (x-axis) and observed exotic richness (y-axis) scaled to between zero and one. Each point represents a 100 × 100 km gridded cell across Australia with both a both a native and exotic richness estimate. (ii) Mean estimates of native (blue) and exotic (red) log-transformed species richness compared to six environmental variables and a single human impact variable using multiple linear regression. Error bars represent 95% confidence intervals of the mean, which are significant ($P < 0.05$) if they exclude zero (vertical dashed line). The explanatory variables were scaled prior to modelling to compare estimate values. The mean estimates of two variables (proportion of land cover and a spatial autocorrelation term) were excluded from plots**.** (iii) Observed exotic and (iv) observed native species richness across Australia. Note that species richness was modelled in log-transformed units but is displayed with raw species richness to indicate the large difference in the number of species represented by cells with hot colours (red-orange) and cool colours (blue-yellow). Grey zones did not meet criteria to estimate species richness and were not analysed. (v) Native species richness predicted across all areas of Australia using mean estimates from (ii).

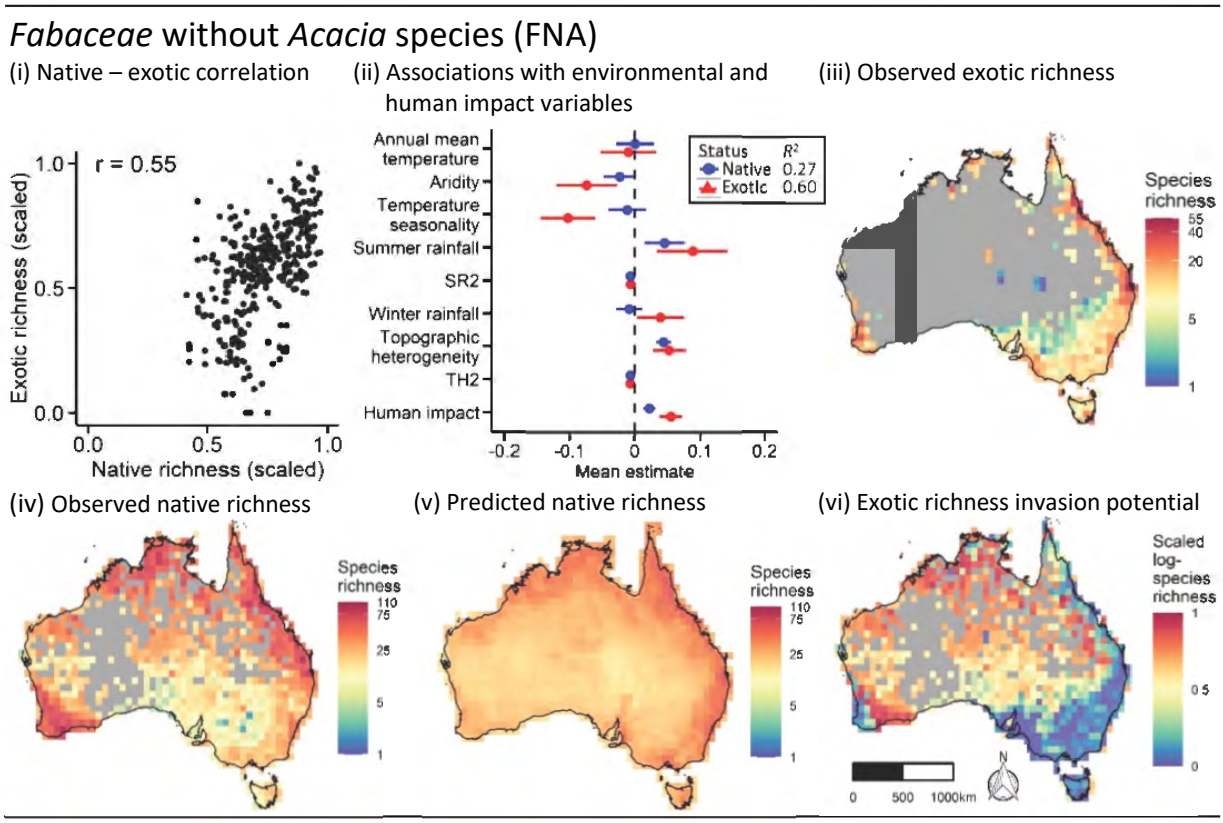


Figure B.5 Native Fabaceae species richness without the genus *Acacia* (FNA) as an incomplete template for potential exotic Fabaceae species richness at large spatial scales across Australia. (i) Observed native richness (x-axis) and observed exotic richness (y-axis) scaled to between zero and one. Each point represents a 100 × 100 km cell across Australia with both a both a native and exotic richness estimate. (ii) Mean estimates of native (blue) and exotic (red) log-transformed species richness compared to six environmental variables and a single human impact variable using multiple linear regression. Error bars represent 95% confidence intervals of the mean, which are significant (P <0.05) if they exclude zero (vertical dashed line). The explanatory variables were scaled prior to modelling to compare mean estimate values. The mean estimates of two variables (proportion of land cover and a spatial autocorrelation term) were excluded from plots. SR2 = (summer rainfall)^2. (iii) Observed native and (iv) observed exotic species richness across Australia. Note that species richness was modelled in log-transformed units but is displayed with raw species richness to indicate the large difference in the number of species represented by cells with hot colours (red-orange) and cool colours (blue-yellow). Grey zones did not meet criteria to estimate species richness and were not analysed. (v) Native species richness predicted across all areas of Australia using mean estimates from (ii). (vi) Exotic invasion potential across Australia, calculated for each area for as the difference between log-transformed observed native richness and log-transformed observed exotic richness both scaled to values between 0 and 1. Invasion potential was not calculated for areas missing observed native species richness values. Negative invasion potential values were truncated to zero

Appendix C – Supporting information for Chapter 4

Table C.1 Moran's I test for autocorrelation for combinations of native and exotic Australian and New Zealand C3 and C4 Poaceae species richness. P values <0.05 indicate significant spatial autocorrelation for each taxa.

Country	Taxa	Expected	Observed	SD	P value
Australia	Native C3	-0.08	0	0	0
	Native C4	-0.13	0	0	0
New Zealand	Native C3	-0.17	-0.02	0.01	0
	Exotic C3	-0.1	-0.03	0.02	0
	Exotic C4	-0.08	-0.05	0.03	0.15

Table C.2 Model fits ranked by delta-AICc (the difference in AICc values between a model and the best-fitting model) among two model classes, generalized least-squares (gls) and a linear regression (lm). GLS model classes included four types of spatial autocorrelation terms. The model for each taxon was selected with the lowest AICc score, highlighted in grey*.

Country	Origin and pathway	Model class	GLS spatial autocorrelation term†	df	Log-likelihood	AICc	Delta-AICc	Weight
Australia	Native C3	gls	Spherical	12	-204.53	433.71	0.00	0.57
		gls	Gaussian	12	-205.43	435.51	1.80	0.23
		gls	Ratio	12	-206.25	437.15	3.44	0.10
		gls	Exponential	12	-206.28	437.22	3.51	0.10
		lm		10	-280.27	580.99	147.28	0.00
	Native C4	gls	Exponential	12	-371.65	767.71	0.00	0.97
		gls	Ratio	12	-375.67	775.75	8.04	0.02
		gls	Spherical	12	-376.35	777.10	9.40	0.01
		gls	Gaussian	12	-392.79	809.99	42.28	0.00
		lm		10	-597.17	1214.63	446.92	0.00
New Zealand	Native C3	lm		10	-3.20	31.39	0.00	0.46
		gls	Gaussian	12	-0.54	32.51	1.11	0.27
		gls	Spherical	12	-0.80	33.02	1.62	0.21
		gls	Exponential	12	-2.52	36.47	5.07	0.04
		gls	Ratio	12	-2.87	37.16	5.77	0.03
	Exotic C3	lm		10	-20.52	68.63	0.00	0.93
		gls	Gaussian	12	-20.52	76.60	7.97	0.02
		gls	Exponential	12	-20.52	76.60	7.97	0.02
		gls	Spherical	12	-20.52	76.60	7.97	0.02
		gls	Ratio	12	-20.52	76.60	7.97	0.02

*All models included additional parameters: taxon ~ annual mean temperature + temperature seasonality + aridity + summer rainfall + winter rainfall + topographic heterogeneity + human impact + proportion cover.
†Linear models did not contain spatial autocorrelation terms.

Table C.3 Adjusted R^2 values from regressions of observed versus predicted values for combinations of native and Exotic Australian and New Zealand C3 and C4 Poaceae species richness.

Photosynthetic pathway	Origin and location		Adjusted R^2
	Observed richness	Predicted richness	
C3	Native Australian	Exotic New Zealand	-1.40
	Native Australian	Native New Zealand	-0.02
	Native New Zealand	Exotic New Zealand	-1.22
C4	Native Australian	Exotic New Zealand	-13.8

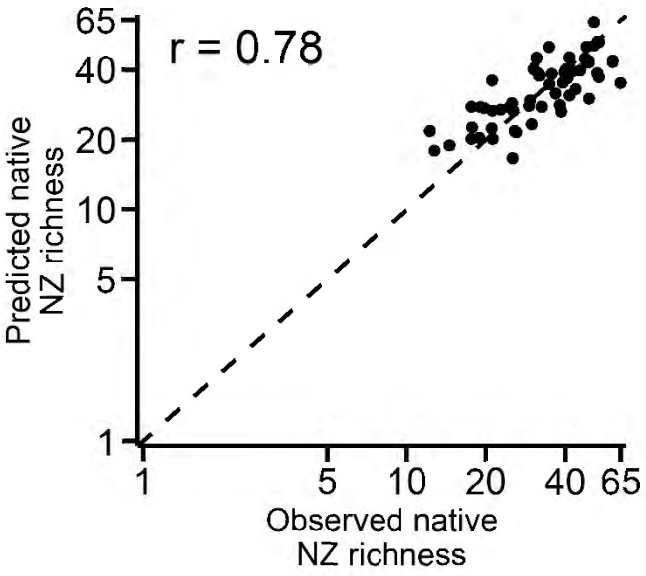


Figure C.1 Observed and predicted New Zealand native C3 Poaceae species richness. Each point represents a 100 × 100 km gridded cell across New Zealand with both an observed and predicted species richness estimate. Note species richness was calculated on the log scale but axes units are in raw species richness values.

Appendix D – Supporting information for Chapter 5

Table D.1 The thirty-four competition treatments varying total density and the relative frequency of native and exotic individuals. Four total densities were tested (3, 6, 9, or 12 individuals) full replicated across native-only, exotic-only and native-exotic mixtures. The native community was made up of three species, *Bothriochloa maca*, *Chloris truncata* and *Rytidosperma auriculatum*. All three native species were included in all treatments containing the native community, with each species contributing 1/3 of the total number of native community individuals. The exotic species were *Dactylis glomerata*, *Eragrostis curvula* and *Phalaris aquatica*.

Exotic species	Number of individuals		
	Native community	Exotic	Total
	3	0	3
	6	0	6
	9	0	9
	12	0	12
D. glomerata	0	3	3
D. glomerata	0	6	6
D. glomerata	0	9	9
D. glomerata	0	12	12
D. glomerata	3	3	6
D. glomerata	3	6	9
D. glomerata	3	9	12
D. glomerata	6	3	9
D. glomerata	6	6	12
D. glomerata	9	3	12
E. curvula	0	3	3
E. curvula	0	6	6
E. curvula	0	9	9
E. curvula	0	12	12
E. curvula	3	3	6
E. curvula	3	6	9
E. curvula	3	9	12
E. curvula	6	3	9
E. curvula	6	6	12
E. curvula	9	3	12
P. aquatica	0	3	3
P. aquatica	0	6	6
P. aquatica	0	9	9
P. aquatica	0	12	12
P. aquatica	0	3	3
P. aquatica	0	6	6
P. aquatica	3	3	6
P. aquatica	3	6	9
P. aquatica	3	9	12
P. aquatica	6	3	9
P. aquatica	6	6	12
P. aquatica	9	3	9

Table D.2 Mean individual biomass of each of the three native species across all competition and water availility levels.

Native species	Mean individual biomass by water availability (±SEM) (g)		
	Low	**Medium**	**High**
Bothriochloa macra	0.429 (0.023)	0.551 (0.062)	0.521 (0.063)
Chloris truncata	0.392 (0.059)	0.519 (0.090)	0.232 (0.030)
Rytidosperma auriculatum	0.684 (0.062)	0.880 (0.087)	0.650 (0.064)