

ENVIRONMENTAL CONTROLS ON THE FUNCTIONAL ECOLOGY OF RIPARIAN PLANT COMMUNITIES



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For Noel.

Certificate

This thesis constitutes an original contribution and has not been submitted, in any form, for a higher degree at any other university or institution.

The work of others has been used to prepare some aspects of this thesis and their contribution is clearly acknowledged in each chapter.

For Chapter 4, Cassandra James provided vegetation survey data, and Rachael Gallagher provided the majority of the trait data. I initiated and led the project, curated the trait dataset, performed the analysis and wrote the manuscript.

All other projects described here were designed, carried out, analysed and prepared for publication by me.

I certify that all information sources and literature used are cited in this thesis.

The research presented here did not require the approval of the Macquarie University Ethics Review Committee.

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Abstract

Riparian ecosystems are biophysically complex, highly biodiverse and provide a broad array of essential ecosystem services to both humans and surrounding landscapes. Extensive catchment modification and alteration of natural river flows have resulted in widespread degradation of riparian ecosystems worldwide, with human population expansion and climatic change likely to exacerbate this situation over the next century. Basic information about the ecology of riparian plant communities in Australia is needed to inform riparian conservation and rehabilitation efforts.

In this thesis, I used a functional trait approach to investigate how hydrology and other environmental variables template the ecology of riparian plant communities in temperate and subtropical eastern Australia. Functional traits such as wood density or seed mass provide fundamental information about the ecological strategies of plants, and facilitate comparison of communities in terms of how component species respond to and influence their environment.

Chapters 2 and 3 present the findings of a field campaign across south-eastern Australia, and describe the role of fluvial disturbance and flow variability in determining functional trait composition and diversity in riparian plant communities. Chapter 4 investigates the role of environmental heterogeneity as a control on taxonomic and functional trait diversity in riparian plant communities of south-eastern Queensland, with an emphasis on the impacts of flow modification and land-use intensification. Chapter 5 describes a

manipulative glasshouse experiment on the interactive effects of inundation and elevated atmospheric CO₂ on gas exchange, growth, and functional traits of three riparian tree species native to south-eastern Australia.

In south-eastern Australia (Chapters 2 and 3), community wood density and functional trait diversity increased strongly with metrics describing flood magnitude and flow heterogeneity. In south-eastern Queensland (Chapter 4), species richness decreased and abundance of exotic species increased as hydrological conditions became more heterogeneous. Flow homogenisation by dams increased species richness, contrary to expectation. Functional trait diversity was associated with only a limited set of hydrological metrics, and was not influenced by flow modification or catchment land use. I found differing effects of atmospheric CO₂ concentration and waterlogging status on growth, gas exchange and functional traits between species (Chapter 5).

This work highlights the importance of natural hydrological heterogeneity and anthropogenic alteration of flows availability as determinants of diversity in riparian vegetation communities.

1 Introduction

Riparian ecosystems are biophysically complex and highly diverse taxonomically, structurally and functionally (Naiman et al., 1993; Nilsson and Svedmark, 2002; Poff, 2002). They provide a disproportionately high quantity of ecosystem goods and services relative to the fraction of the landscape that they occupy (Capon et al., 2013) and play a critical role in maintaining regional biodiversity (Naiman et al., 1993). Riparian landscapes have been heavily modified by humans; in many parts of the world this modification has taken place rapidly and has resulted in significant habitat degradation and biodiversity loss (Arthington et al., 2010). In particular, catchment-scale clearing of vegetation, impoundment and flow regulation have altered the hydrology of river systems globally (Nilsson and Berggren, 2000). As demand for water increases with growing human populations, river systems are likely to become increasingly modified. Changing climatic conditions over the next century are also expected to cause shifts in hydrological patterns. Predictions are regionally specific but typically include changes to total discharge, flow seasonality and flow variability (Stocker et al., 2013). In regions with projected increases in climatic variability, changes to the prevalence, intensity and timing of extreme flooding or drought events can be expected (Hennessy et al., 2008). This combination of flow regulation and alterations to baseline discharges may well produce dramatically altered future flow regimes, with significant consequences for the diversity and functional composition of riparian vegetation communities (Poff and Zimmerman, 2010). Due to their central role in maintaining diversity and ecosystem functioning at the landscape scale (Naiman et al., 1993), riparian ecosystems are the target of substantial management effort (Goodwid et al., 1997). Vegetation assemblages receive particular attention in riparian management as they set the coarse physical structure of biotic communities and play an important role in generating and maintaining the characteristic geomorphology of river systems (Corenblit et al., 2007; Richardson et al., 2007). Conservation planning in fluvial landscapes therefore requires context-specific understanding of environmental

controls on plant community assembly.

1.1 The importance of flow regime to riparian plant communities

Flow regime is thought to be a dominant abiotic control on the composition and structure of riparian plant communities (Poff et al., 1997). Stream flows affect plant communities directly by causing flooding disturbance and driving variation in nutrient and moisture availability (Naiman and Decamps, 1997), as well as by interaction with sediment and geomorphic processes (Corenblit et al., 2007). The inherently heterogeneous nature of fluvial interaction with vegetated landforms results in structurally complex, patchy landscapes containing strong energy and resource gradients (Naiman et al., 2005). Spatial and temporal heterogeneity in the magnitude, frequency, duration, timing, rates of change and predictability of flow discharge (Kennard et al., 2010; Poff et al., 1997) translates to heterogeneous influence of stream flows on riparian patches (Naiman et al., 2008; Poff et al., 1997). Niche-oriented models of riparian ecology hold that it is this environmental heterogeneity which supports the high degree of biodiversity observed in riparian ecosystems (Bornette et al., 2008; Palmer and Poff, 1997).

Given the profound influence of fluvial hydrology on riparian vegetation communities, determining specific flow-ecology relationships has long been a goal in riparian research (Auble and Friedman, 1994; Lytle and Poff, 2004). To date, this research has been largely driven by work on impacts of dams on vegetation (Goodwid et al., 1997; Nilsson and Svedmark, 2002). The resulting insight into the comparative hydroecology of *Populus* and *Salix spp.* and invasive *Tamarix spp.* in North American river systems (Mahoney and Rood, 1998; Shafroth et al., 2002) has led to significant advances in design of environmental flows to support indige-

nous vegetation assemblages (Shafroth et al., 2010). This approach is effective in western North America, where well-understood systems are dominated by a limited set of species. However, approaches centred on deterministic species-specific flow response models are less practical in more diverse or less understood systems.

1.2 The intersection between hydroecology and functional ecology

Maintenance of biodiversity and ecosystem functioning may be a more appropriate conservation target than supporting the persistence of specific assemblages (Aerts and Honnay, 2011; Cadotte et al., 2011; Montoya et al., 2012) given the predictions of future climate and other environmental change. Where sites harbour dissimilar species assemblages, comparison becomes challenging. Taxonomic descriptors of communities such as species richness or species diversity are widely used to compare communities across landscapes, but are unable to provide information about how elements of a community influence ecosystem functioning, provision of ecosystem services, or contribute to system resilience (Díaz et al., 1998; Díaz and Lavorel, 2007; Tilman et al., 1997). Describing communities in terms of functional traits - any morphological, physiological or phenological feature measurable at the individual level (Violle et al., 2007) - dissolves species distinctions and emphasises ecological strategies: what species do within their community and how they do it (Díaz et al., 1998). This allows dissimilar communities to be compared in terms of how their component species both respond to and have an effect on their environment (Lavorel and Garnier, 2002; Suding et al., 2008). A functional trait oriented approach applied to flow-vegetation interactions facilitates the search for regional generalities in hydrological controls on ecosystem processes and patterns of diversity.

Species are different, but not equally so, and the nature and extent of species differences characterises ecological communities. Data about appropriately selected quantitative functional traits (such as specific leaf area, wood density, seed mass etc.) can form the basis for mechanistic assessments of diversity which describe the range and distribution of ecological strategies in a community and their associated environmental effects (Schleuter and Daufresne, 2010). These indices of functional trait diversity are increasingly being employed in ecosystem assessment and management as a complement to traditional taxonomic metrics of diversity (Lavorel et al., 2013; Tilman et al., 1997).

Hydroecologically derived plant functional groups have been described for some time (Casanova, 2011; Stromberg et al., 2010), but advances in quantitative plant ecology based on functional traits are only beginning to be applied to riparian systems. Notable early contributions to the quantitative riparian functional hydroecology literature include discussion of variation in functional traits according to species origin (i.e. native or exotic), geomorphology and fluvial disturbance (Kyle and Leishman, 2009a,b), and evidence for reduced functional trait diversity in riparian wetlands in response to flow impoundment (Catford et al., 2011). Merritt and Poff (2010) outlined a framework for defining riparian vegetation flow response guilds according to functional traits, and functional traits have been discussed as a means by which to predict riparian community responses to climate change (Catford et al., 2012; Kominoski et al., 2013). Momentum is now building for insights from plant functional ecology to be applied to riparian conservation planning and management.

1.3 Anthropogenic impacts on riparian plant communities

Rapid development of catchments has changed fundamental processes which create and maintain biodiversity in riparian ecosystems (Nilsson and Svedmark, 2002),

and as such, riparian management often takes place within this context of catchment modification. Environmental homogenisation of riparian landscapes by flow modification, land-use change and invasion by exotic plants has profound implications for riparian biodiversity (Brierley et al., 1999; Poff and Zimmerman, 2010; Richardson et al., 2007).

Given the dominance of flow regime in shaping and driving riparian ecosystems, flow modification is likely to have the greatest impact, although anthropogenic stressors are typically not independent from each other. Dams, weirs and diversions affect river systems in populated regions worldwide (Nilsson and Svedmark, 2002), resulting in diminished discharge, reduced flow variability, dampening of flood peaks and changes to seasonality of flows (Graf, 2006; Singer, 2007). Depending on the magnitude of change, biogeomorphic simplification and weedy invasion may occur downstream of dams (Catford et al., 2011; Graf, 2006; Naiman et al., 2008). The impact of these changes on riparian plant communities is likely to be compounded by the deleterious effects of land transformation, primarily habitat fragmentation and loss of catchment-scale alpha and beta diversity (Gerstner et al., 2014; Vitousek et al., 1997). Exotic invasion is closely associated with human activity (Vitousek et al., 1996) and itself represents a significant threat to riparian plant communities (Richardson et al., 2007).

Rising atmospheric carbon dioxide represents a further unexplored variable with the potential to alter future riparian plant communities. Atmospheric CO₂ has risen substantially over the past century and a doubling of pre-industrial levels by 2100 is projected (IPCC et al., 2014). A substantial body of research describes dramatic effects of elevated CO₂ (eCO₂) on plant growth, physiology and community ecology (Curtis, 1996; Poorter and Navas, 2003; Reich et al., 2014). Typical responses to eCO₂ include stimulation of photosynthetic carbon assimilation (Curtis, 1996), reduced stomatal conductance (Ainsworth and Rogers, 2007), greater water use efficiency (Holtum and Winter, 2010; van der Sleen et al., 2014), greater

biomass accumulation (Wang et al., 2012), altered biomass allocation (Nie et al., 2013), and changes to functional traits indicative of positions along economic spectra (i.e. slow vs fast growth strategy) (Bader et al., 2010; Poorter and Navas, 2003). The effects of eCO₂ vary between species and are often contingent on other environmental variables such as availability of water and macronutrients (Körner, 2006; Manea and Leishman, 2014; Reich et al., 2014).

Plants growing adjacent to stream channels enjoy the best access to water in the landscape, but the privilege is not free. Along with exposure to flooding disturbance, most riparian plants must at some point endure waterlogging or inundation (Colmer and Voesenek, 2009; Tabacchi et al., 1998). Inundation represents a significant stress to riparian plants, and root zone anoxia is well established as the mechanism driving plant physiological and functional responses to waterlogging, impairing root metabolism and uptake of water and nutrients (Drew, 1997; Piedade et al., 2010; Voesenek and Bailey-Serres, 2015), altering root traits (Steffens et al., 2013) and disrupting mutualisms with soil biota (Dawson et al., 1989; Shimono et al., 2012).

Elevated atmospheric levels of CO₂ and inundation appear likely to have opposing effects on plant growth, but the possibility that eCO₂ may mitigate growth reduction under waterlogging warrants investigation of the interactive effects of these two important environmental variables. The limited literature describing the interactive effects of eCO₂ and waterlogging or inundation on plant growth presents an inconsistent picture, with effects varying widely between species (Arenque et al., 2014; Megonigal et al., 2005; Shimono et al., 2012). Generation of harmful reactive oxygen species has been shown to accompany reaeration after waterlogging (Drew, 1997), and as such recovery from flooding represents a different stress to tolerance of the event itself. To date, no research has described the effects of eCO₂ on recovery from waterlogging.

1.4 Research questions

In this thesis, I set out to identify the fundamental relationships between riparian plant communities and the various environmental controls and stresses which define them. To this end, I used concepts and tools from modern functional ecology to determine the mechanisms by which communities organise themselves along gradients of these environmental conditions.

In Chapter 2, I asked how wood density, a key plant functional trait integrating the trade-off between rapid growth and tolerance of physical disturbance and drought, varies along gradients of fluvial disturbance intensity and variability in water availability across 15 sites in natural landscapes of south-eastern Australia. Chapter 3 extended this research question, using the same set of sites to investigate relationships between functional diversity and environmental heterogeneity. In Chapter 4, data from sites spanning gradients of flow modification and land-use intensity in south-east Queensland, Australia, were analysed to determine the relative importance of natural and anthropogenic controls on taxonomic and functional diversity. This chapter is again guided by hypotheses about relationships between environmental variability and diversity. In Chapter 5, I described a manipulative glasshouse experiment designed to assess how elevated atmospheric concentrations of CO₂ might affect future responses of riparian trees to waterlogging. Finally, in Chapter 6 (Discussion), I summarise my key findings, assess the contribution of my thesis to the broader literature, and suggest avenues for future research.

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2 Hydrological conditions explain variation in wood density in riparian plants of south-eastern Australia

Abstract

Wood density is a key plant functional trait which integrates the trade-offs characteristic to riparian plant ecological strategies. Although high density wood is costly to construct, it confers mechanical stiffness to stems, increasing a plants capacity to withstand flooding, and also enables increased tolerance to water stress. For riparian plants, fluctuations in soil moisture driven by surface hydrology should therefore be an important driver of variation in wood density.

We asked the following questions in the study: (1) does wood density increase with increasing frequency and magnitude of flood disturbance? (2) does wood density increase with increasing unpredictability of water availability in the riparian zone? (3) does dispersion of wood density peak at intermediate levels of hydrological disturbance?

We surveyed wood density of dominant species at 15 riparian sites along flow-gauged rivers across south-eastern Australia. Due to the broad range of hydrological variability associated with Australian river systems, this set of sites functions as a useful model for assessing the response of riparian plants to changing hydrological conditions.

We found wood density varied strongly along a single axis of hydrological variability. This axis integrates flood intensity and frequency with metrics of hydrological unpredictability, and can be conceptualised as a gradient of environmental harshness, with higher wood density associated with harsher conditions.

Our study highlights the importance of hydrological conditions, particularly disturbance and environmental unpredictability, as determinants of ecological strategy in riparian plants. Large, rare flood events in particular appear to favour higher wood density strategies. This is likely to have significant ecological consequences for riparian plant communities in a south-east Australian context, as well as in other regions where increasing climatic variability and frequency of extreme events

are hallmarks of climate change predictions.

2.1 Introduction

Functional trait oriented approaches to understanding community assembly (McGill et al., 2006) have become increasingly common over the last decade, particularly in the plant ecological literature (Kattge et al., 2011). These approaches attempt to understand community assembly processes by linking morphological or physiological attributes of species to organismal success under given environmental conditions. Suites of traits can be conceptualized as axes of variation in terms of ecological strategy and the distribution of this variation across environmental gradients can provide an insight into where these strategies are successful (Westoby et al., 2002).

Hydrology is widely considered to be the dominant abiotic force structuring riparian ecosystems (Poff et al., 1997). Hydrological variability in turn drives variation in moisture and substrate availability and flooding disturbance, with cyclical resets to early successional conditions being characteristic of the riparian environment (Merritt and Poff, 2010). These are the conditions which determine the dominant selection pressures and environmental filters, which in turn dictate success of a particular plant ecological strategy in a riparian system (Naiman and Decamps, 1997). Several authors have recently suggested functional trait biology as a means of understanding the response of riparian plant communities to hydrological gradients (Catford et al., 2012; Merritt and Poff, 2010). While ecohydrological classification is becoming established as a tool to explain plant community attributes such as species richness, stand structure and composition (Arthington et al., 2012; Poff et al., 2010), functional approaches to investigating the ecohydrology of riparian plant communities remain largely unexplored.

Woody plants determine the coarse physical structure of many riparian plant communities and are integral to the interplay of biological and physical elements that drive fluvial biogeomorphic processes (Corenblit et al., 2009). Consequently,

an understanding of the mechanisms of riparian woody plant community assembly will provide important insights into the structure and function of fluvial landscapes. Wood density, defined as the ratio of kiln-dried mass to green volume of a wood sample (Cornelissen et al., 2003), is widely recognised as an important functional trait in plant ecology (Swenson and Enquist, 2007; Westoby and Wright, 2006), and has been proposed as one of just several key axes of variation within which all major plant ecological strategies can be described (Westoby et al., 2002). Wood density is in fact an emergent property of a combination of woody tissue traits, including vessel geometry and arrangement, and the density and proportion of surrounding lignified tissue (Chave et al., 2009). Combined variation in these traits corresponds to the wide range of wood density strategies among woody plants.

How might different wood density strategies confer advantages to woody plant species in riparian environments? There is little direct evidence from riparian species, however general relationships between wood density and other ecological traits have been recognised in a variety of different systems and can provide some insight into the importance of variation in wood density in riparian systems. Dense wood confers mechanical stiffness, but requires more investment of biomass and is therefore more costly to construct per unit of stem height (Falster, 2006; Niklas and Spatz, 2010). Resources not invested in structural support may be used for purposes that contribute more directly to fitness, such as production of photosynthetic tissues or propagules, or rapid growth.

According to this trade-off, it follows that several relationships between wood density and life-history strategy are apparent. For example, wood density significantly explained variation in survival, fecundity and growth rate in a global dataset of 222 species (Adler et al., 2014). Studies of tropical rainforest species have shown an inverse relationship between growth rate and wood density (King et al., 2006; Kraft et al., 2010; Poorter et al., 2010, 2008; Wright et al., 2010), although no such

relationship was found in a study of New Zealand tree species (Russo et al., 2010). Cohort survival was positively correlated with wood density in the same tropical rainforest studies (King et al., 2006; Kraft et al., 2010; Poorter et al., 2010, 2008; Wright et al., 2010). In a study of 45 rainforest species in tropical Queensland, (Falster and Westoby, 2005) found that wood density increased with plant height along a successional gradient. Following mechanical disturbance caused by a large cyclone in northern Queensland, Australia, wood density of rainforest trees was indicative of both damage sustained and subsequent recovery of biomass. Trees with dense wood were more likely to have experienced only minor damage. Of those trees that experienced major stem and branch damage, lower wood density trees were more likely to resprout and recover biomass faster post-disturbance (Curran et al., 2008). If the links observed in tropical rainforest communities between wood density, growth rate, successional status and recovery from mechanical disturbance hold true for riparian communities, the trade-off between rapid growth in response to high light and water availability, and construction of defences against flooding disturbance may be characteristic of woody plant ecological strategy in riparian zones.

In addition to influencing mean values of wood density, hydrological disturbance may also influence the dispersion of trait values within riparian communities. Niche diversity in riparian environments is promoted by fluvial geomorphic processes (Corenblit et al., 2007), and intermediate levels of disturbance have been theorised to promote divergence of disturbance-response strategies, resulting in a quadratic distribution of variance in associated trait values (Grime, 2006; Sonnier et al., 2010). While riparian plants potentially have the best access to water in a landscape, dramatic fluctuations in soil moisture are often characteristic of riparian environments (Nilsson and Svedmark, 2002). Ecological strategies for coping with unpredictable water availability may therefore be adaptive under these conditions. The relationship between wood density and precipitation-driven patterns

of soil moisture is unclear. Some studies (Swenson and Enquist, 2007; Weimann and Williamson, 2002) found little relationship between wood density and mean annual rainfall while others found that wood density was correlated with mean annual rainfall across a transcontinental gradient (Martínez-Cabrera et al., 2009) and with soil moisture (Preston et al., 2006). High wood density, along with low specific leaf area (SLA) and low maximum height, has been linked with environmental stress tolerance and conservative use of resources (Reich and Wright, 2003; Swenson and Enquist, 2007; Westoby, 1998). Fluctuations in soil moisture driven primarily by hydrological conditions therefore should be an important driver of variation in wood density in riparian plant communities.

Given the extent to which flooding disturbance and fluctuations in water availability dominate riparian landscapes, woody tissue responses to these conditions are likely to be a primary indicator of riparian woody plant ecological strategy. Here we consider variation in wood density of dominant woody riparian plant species over a broad range of hydrological conditions, across 15 riparian sites within south-eastern Australia. As the most hydrologically variable continent on the planet (Finlayson and McMahon, 1988; Peel et al., 2004), Australia provides an ideal system to develop insight into the possible effects of increased hydrological variability in other regions under future climates. We sought to address the following questions: (1) does wood density increase with increasing frequency and magnitude of flood disturbance? (2) does wood density increase with increasing unpredictability of water availability in the riparian zone? (3) does dispersion of wood density peak at intermediate levels of hydrological disturbance?

2.2 Materials and methods

Study site selection

Fifteen riparian sites were selected along gauged rivers within the South-East Coast and south-eastern Murray Darling drainage basins of Australia (Fig. 1.1) (see Appendix 1 for further detail). To differentiate rivers according to ecologically relevant components of hydrology, (Olden and Poff, 2003) described a statistical method for determining a minimally redundant set of hydrological descriptors. Kennard et al. (2010) followed this method to define a set of 120 hydrological metrics relevant to Australian rivers, which included metrics of central tendency and dispersion in all five dimensions of hydrological variation (magnitude, frequency, duration, timing, and rate of change) (Kennard et al., 2010). These metrics were then used to classify Australian river systems into twelve distinct flow regime classes, providing a foundation for analysing the properties of ecosystems across hydrological gradients. In this study, sites were drawn from rivers corresponding to stable winter baseflow, unpredictable baseflow and unpredictable intermittent hydrological classes, as described by Kennard et al (2010). These are the best represented hydrological classes in eastern New South Wales and Victoria, and combined, span clear gradients of flooding intensity and hydrological unpredictability.

Five sites per hydrological class were selected based on the following criteria: gauged locations were selected that had >15 years of associated continuous hydrological data, and an absence of flow regulation, significant water extraction or catchment urbanisation, following Kennard et al. (2010). To minimise signals associated with human land-use and river type, the following further criteria were used to shortlist possible study sites: all were partly confined valleys with discontinuous floodplain pocket River Styles, *c.f.* Brierley & Fryirs (2005) (Brierley and Fryirs, 2005), had an intact native riparian vegetation cover (a band of native riparian vegetation extending >15 m from the bankfull channel edge), were in

good geomorphic condition (lack of significant human-induced erosional or depositional landforms), minimal vegetation clearing (catchment predominantly covered by native vegetation) and occurred in a catchment smaller than 1000 km². These criteria were assessed using a combination of visual inspection of satellite photography (Google Earth, Microsoft Bing) and information from the NSW Riparian Vegetation Extent dataset and the NSW Office of Water River Styles geospatial dataset (Healy et al., 2012). To select the 15 study sites from this shortlist, accessibility by road, permission from state or private landholders, and proximity of accessible areas to continuous hydrological monitoring stations were taken into account.

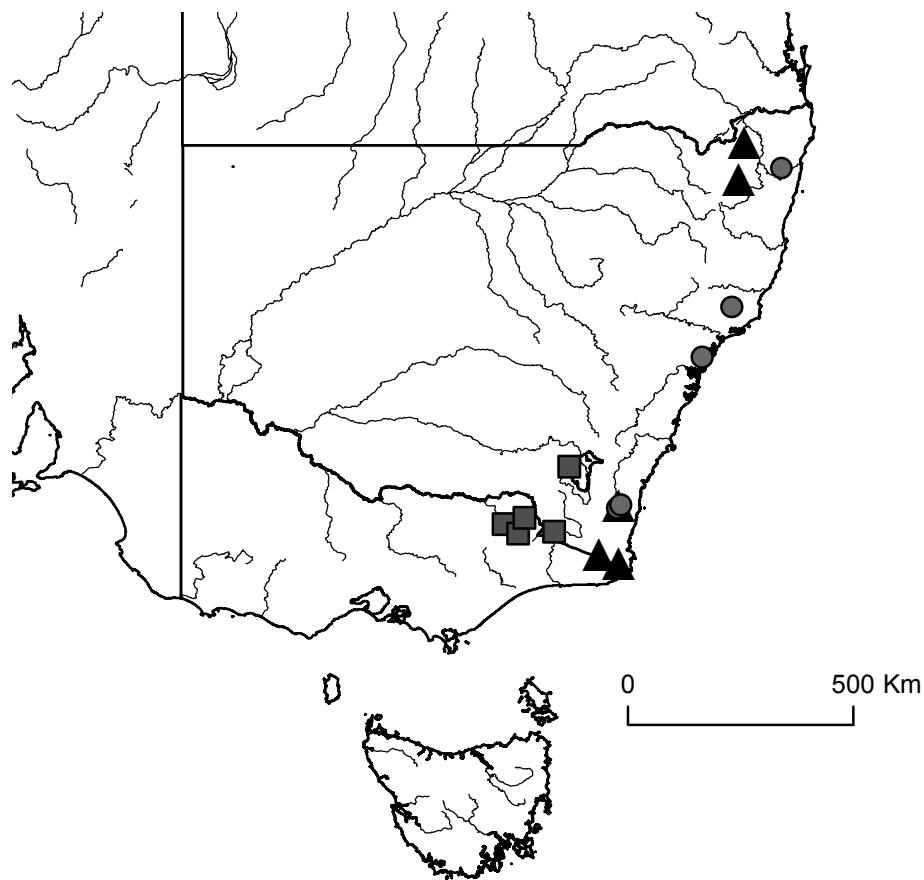


Figure 2.1: Location of fifteen field study sites across south-eastern Australia chosen to represent the three major hydrological classes of south-east Australia. Hydrological class membership is denoted by: ■ stable winter baseflow, ▲ unpredictable baseflow, ● unpredictable intermittent.

Species abundance and trait data collection

Data collection was undertaken between December 2012 and May 2013. At each site, a 10 m by 50 m plot was marked out, with the longest edge abutting the channel edge. Criteria for selection of plot locations were: geomorphic homogeneity (the plot comprising only sloping bank where possible) and lack of anthropogenic disturbance such as built structures, roads or tracks, recent logging or clearing (in the last 20-30 years), herbicide spraying or animal grazing. Variation in the maximum height above the channel edge between plots was kept to within approximately 1.5 m.

Proportional cover of all woody species was assessed within three strata: shrub (1-4 m), sub canopy (4-8 m) and canopy (>8 m). Species were identified using appropriate field guides, and were verified against herbarium specimens at the Macquarie University Herbarium. Some specimens were identified by staff at the Royal Botanic Gardens, Sydney.

Wood samples were collected from woody species present within the plot at >1% cover in shrub, sub canopy or canopy strata, and which had trunks robust enough to core. A 100 mm wood sample from each of two individuals per species was extracted using a 5.15 mm diameter, triple threaded increment borer (Haglf Sweden). Samples were extracted from the base of the main trunk, 10 cm above the leaf litter level, and air-dried at 20-45 °C. On return to the laboratory, samples were rehydrated to saturation in deionised water and 10 mm sections of mature heartwood were cut flush with a razor, using visual inspection of vessel occlusion as an indicator of maturity. Sections were measured (x, y and z dimensions) to the nearest 0.01 mm with callipers (Mitutoyo America, Illinois USA) to calculate wet volume, then oven-dried at 80 °C for 48 hours and weighed using a microbalance (Mettler Toledo, Greifensee, Switzerland). Wood density was then calculated as the ratio of oven dry mass to wet volume (g/cm³).

Species which were present in plots but which could not be cored due to small size were assigned averaged values of wood density from the same species measured at other sites, where possible. Remaining species were assigned values from peer-reviewed literature sources. Appendix 1a contains further details about the dataset, including data density information.

Hydrological analysis

Daily discharge data pertaining to each field site were collated from the PIN-NENA CW 10.1 database (NSW Office of Water, Department of Primary Industries) and the NSW Office of Water Continuous Water Monitoring network website (<http://realtimedata.water.nsw.gov.au/water.stm>) for NSW sites, and the Victoria State Governments Water Measurement Information System website (<http://data.water.vic.gov.au/monitoring.htm>) for Victorian sites. Where possible, 30 year time series were obtained, spanning years 1983–2012. Records were truncated for three sites, spanning 15, 19 and 28 years. Missing data were approximated using the Time Series Manager module in River Analysis Package (Marsh et al., 2003). Consistency of the resulting outputs were checked by visual inspection of hydrographs. For Mammy Johnsons River, Mann River, Sportsmans Creek and Wallagaraugh River, multiple linear regression was chosen as the most appropriate method for estimating missing data values. Linear interpolation was used for Jilliby Creek data. Daily discharge data for the remaining sites were complete.

A set of 24 hydrological metrics was pared from the full set described by Kennard et al. (2010). These metrics were chosen to be representative of variability in high flow magnitude and frequency as well as predictability and consistency of water availability in the riparian environment (see Table 1.1 for a description). We used the Time Series Analysis module in River Analysis Package to generate

these metrics. Means and coefficients of variation were calculated for most metrics to indicate central tendency as well as spread within the data. Low and high spell metrics were thresholded at the 5th and 95th percentiles, respectively, with a flood independence criterion of 7 days between peak events. Twenty year average return interval (ARI) flood magnitude was also calculated with a flood independence value of 7 days between peaks. Colwell's Indices were calculated using mean flow values over monthly time periods and a class distribution of 11 flow classes. Metrics of flow magnitude which had units ML / day were normalised by mean daily flow to allow for comparison between different sizes of river. Some metrics were correlated (see Appendix 1a for correlation analysis).

Table 2.1: Hydrological parameters used as metrics of variability in high flow magnitude and frequency and predictability and consistency of water availability in the riparian environment. * - normalised by mean daily flow (ML/day)

<i>Variable</i>	<i>Abbreviation</i>	<i>Units</i>	<i>Description</i>
Flood frequency and magnitude			
Mean magnitude of high spells *	HSPeak	dimensionless	High spells are periods of flow above the 95th percentile on the flow duration curve. We were interested in how frequently these conditions occurred over the time series as well as the mean magnitude of peak flows during these periods. 20 year average
CV of all years' mean high spell magnitude	CVAnnHSPeak	dimensionless	magnitude of peak flows during these periods. 20 year average
20 year ARI flood magnitude *	AS20YrARI	dimensionless	return interval (ARI) floods are extreme flow events that have
Mean of all years' number of high spells	MDFAnnHSNum	year ⁻¹	the potential to re-work the fluvial landscape. Together, these
CV of all years' number of high spells	CVAnnHSNum	dimensionless	metrics indicate the intensity and frequency of mechanical stress experienced by plants in the riparian zone.
Rise and fall rates			
Mean rate of rise *	MRateRise	day ⁻¹	Rise and fall rates represent flow flashiness. Fast rise rates are
Mean rate of fall *	MRateFall	day ⁻¹	associated with flood waves and intense mechanical stress to plant stems. Slow fall rates keep exposed substrate moist for
CV of all years' mean rate of rise	CVAnnMRateRise	dimensionless	longer periods, which may produce favourable conditions for germination. Historical discharge records are unfortunately limited to daily resolution, so are unable to fully capture flood discharge shapes. High variability between years indicates the occurrence of extreme events which may not have been captured by the mean value.
CV of all years' mean rate of fall	CVAnnMRateFall	dimensionless	

<i>Variable</i>	<i>Abbreviation</i>	<i>Units</i>	<i>Description</i>
Baseflow index			
Baseflow index	BFI	dimensionless	
CV of all years' Baseflow Index	CVAnnBFI	dimensionless	Baseflow index is calculated using the ratio of flow during average conditions to total flow. It is a useful metric of consistency of water availability, in that it is maximised when average flow conditions dominate, and minimised when total flow is dominated by above average flow events. Intra-annual variability in baseflow index measures how predictable baseflow index is between years.
Low flow magnitude, frequency and duration			
CV of all years' mean low spell magnitude	LSPeak	dimensionless	
Mean magnitude of low spells	CVAnnLSPeak	dimensionless	
Mean of all years' number of low spells	MDFAnnLSNum	year ⁻¹	
CV of all years' number of low spells	CVAnnLSNum	dimensionless	Low spells are periods of flow below the 5th percentile on the flow duration curve. We were interested in how frequently these conditions occurred over the time series as well as the mean and interannual variability in magnitude and duration of low flows.
Mean duration of low spells	LSMeanDur	days	
CV of all years' low spell mean duration	CVAnnLSMeanDur	dimensionless	
Mean flow during driest week of the year *	MA.7daysMinMean	dimensionless	
Mean days per year under 0.1ML/day flow	MDFAnnUnder0.1	days/year	
CV of all years' days per year under 0.1ML/day flow	CVAnnMDFAnnUnder0.1	dimensionless	

<i>Variable</i>	<i>Abbreviation</i>	<i>Units</i>	<i>Description</i>
Colwell's indices			
Constancy of monthly mean daily flow	C_MDFM	dimensionless	Colwell's indices provide a measure of the seasonal predictability of flow events and therefore water availability within the riparian zone. Constancy (C) measures uniformity of flow across seasons, and is maximised when flow conditions do not differ between seasons.
Contingency of monthly mean daily flow	M_MDFM	dimensionless	Contingency (M) is a measure of interannual uniformity in seasonal flow patterns, and is maximized when seasonal patterns of flow are consistent between years. We generated Colwell's indices for both average flow conditions and minimum flows conditions.
Constancy based on monthly minimum daily flow	C_MinM	dimensionless	
Contingency based on monthly minimum daily flow	M_MinM	dimensionless	

Wood density analysis

All statistical analyses were performed using the R statistical programming environment (R Core Team, 2015). The R code used for these analyses can be retrieved from <https://github.com/jamesrlawson/riparian-WD/tree/master/scripts>. Statistical significance was interpreted at alpha = 0.05.

Characterising community-level variation in wood density

To investigate variation in wood density across hydrological gradients at the community level, community weighted means (CWM) of wood density were generated for each site. Species relative abundance was compiled from records of percent cover at the shrub (1-4 m), sub canopy (4-8 m) and canopy (>8 m) strata. Wood density values were then weighted according to species relative abundance and summed to produce the CWM. This method integrates particular trait values with their real world abundance as a measure of performance, while providing a useful reduction in data dimensionality. Wood density varies only over one order of magnitude, while exhibiting relatively high intra-species plasticity. As such, CWMs work well for environmental gradient studies of wood density because the focus is maintained on the functional characteristics of the community, rather than on species *per se*.

We also calculated community weighted variance (CWV) in wood density for each site to characterise the dispersion of wood density values within communities. CWV describes divergence from the mean trait value of a community (Schleuter and Daufresne, 2010). When trait values of abundant species are clustered towards the mean, divergence is low. Conversely, divergence is high when abundant species are distributed towards the extremes of the trait range (Villéger et al., 2008). Variance could not be calculated for Site 2 (Wallagaraugh River, unpredictable baseflow category) as only a single woody species was found at > 1 % cover at

this site. This site was therefore omitted from subsequent analyses of CWV.

Testing relationships between wood density and hydrological conditions

Ordinary least-squares regression models were generated for selected metrics to determine relationships between hydrological gradients and CWMs. Linear models were used except where non-linear relationships were obvious. Wood density data was normally distributed and did not require transformation. To reduce the occurrence of Type 1 statistical error, we adjusted the resulting p values using the Benjamini - Hochberg (BH) procedure for controlling family-wise error rate (stats package) (R Core Team, 2015). Although ecological rationale supported inclusion of each subgroup of hydrological metrics, a number of these metrics were correlated. The BH procedure has been shown to control the false discovery rate for positively dependent test statistics (Benjamini and Yekutieli, 2001).

We identified ecologically relevant axes of variation in hydrological conditions by running a principal components analysis (stats package), (R Core Team, 2015) for hydrological metrics which had significant relationships with site mean wood density values. Having established the dominance of a single relevant axis of variation in hydrology (refer Fig. 1.5), we tested the fit of a quadratic model relating extent of hydrological disturbance (as characterised by site scores from the resulting first principal component) to CWV in wood density.

Spatial autocorrelation in CWM and CWV values was assessed using Moran's I (ape package), (Paradis et al., 2004).

2.3 Results

How does mean wood density change over hydrological gradients?

Below we describe patterns of community weighted mean wood density in relation to the hydrological variables divided into two groups: those describing frequency and magnitude of flood disturbance, and those describing predictability of water availability in the riparian zone. Regression statistics for all models are given in Table 1.2.

Community mean wood density varied by 50 % between sites. The largest, most intense flood events throughout a rivers hydrological record were found to show a strong positive relationships with mean wood density (Fig. 1.2a, 1.2b). Flooding frequency had no influence on wood density. Mean flood rise rate (Fig. 1.2c) as well as interannual variability in flood rise and fall rates (Fig. 1.2d, 1.2e) were positively related to wood density; this relationship was considerably stronger for interannual variability in flood rise rate than mean flood rise rate ($R^2 = 0.549$ vs 0.360).

Table 2.2: Statistics for regression models comparing hydrological metrics with site mean wood density. P.adj denotes p values adjusted by the Benjamini-Hochberg method. Significant results are shown in bold. Models used are either quadratic or linear, as shown in Fig. 1.2 and Fig. 1.3. For non-significant relationships, statistics shown are for linear models.

<i>Variable</i>	<i>P</i>	<i>P.adj</i>	<i>R</i> ²
CVAnnBFI	0.008	0.031	0.549
CVAnnMRateRise	0.008	0.031	0.549
C_MinM	0.009	0.031	0.542
C_MDFM	0.012	0.031	0.522
HSPeak	0.004	0.031	0.485
AS20YrARI	0.005	0.031	0.467
LSPeak	0.006	0.031	0.447
CVAnnMRateFall	0.007	0.031	0.435
BFI	0.012	0.031	0.397
M_MDFM	0.013	0.031	0.388
MA.7daysMinMean	0.017	0.036	0.368
MRateRise	0.018	0.036	0.360
MDFAnnLSNum	0.030	0.055	0.314
MRateFall	0.053	0.091	0.258
M_MinM	0.062	0.100	0.242
CVAnnHSPeak	0.117	0.175	0.178
LSMeanDur	0.230	0.325	0.109
CVAnnLSPeak	0.390	0.493	0.057
CVAnnHSNum	0.390	0.493	0.057
CVAnnLSNum	0.454	0.545	0.044
MDFAnnUnder0.1	0.487	0.556	0.038
MDFAnnZer	0.553	0.603	0.028
CVAnnLSMeanDur	0.732	0.747	0.009
MDFAnnHSNum	0.747	0.747	0.008

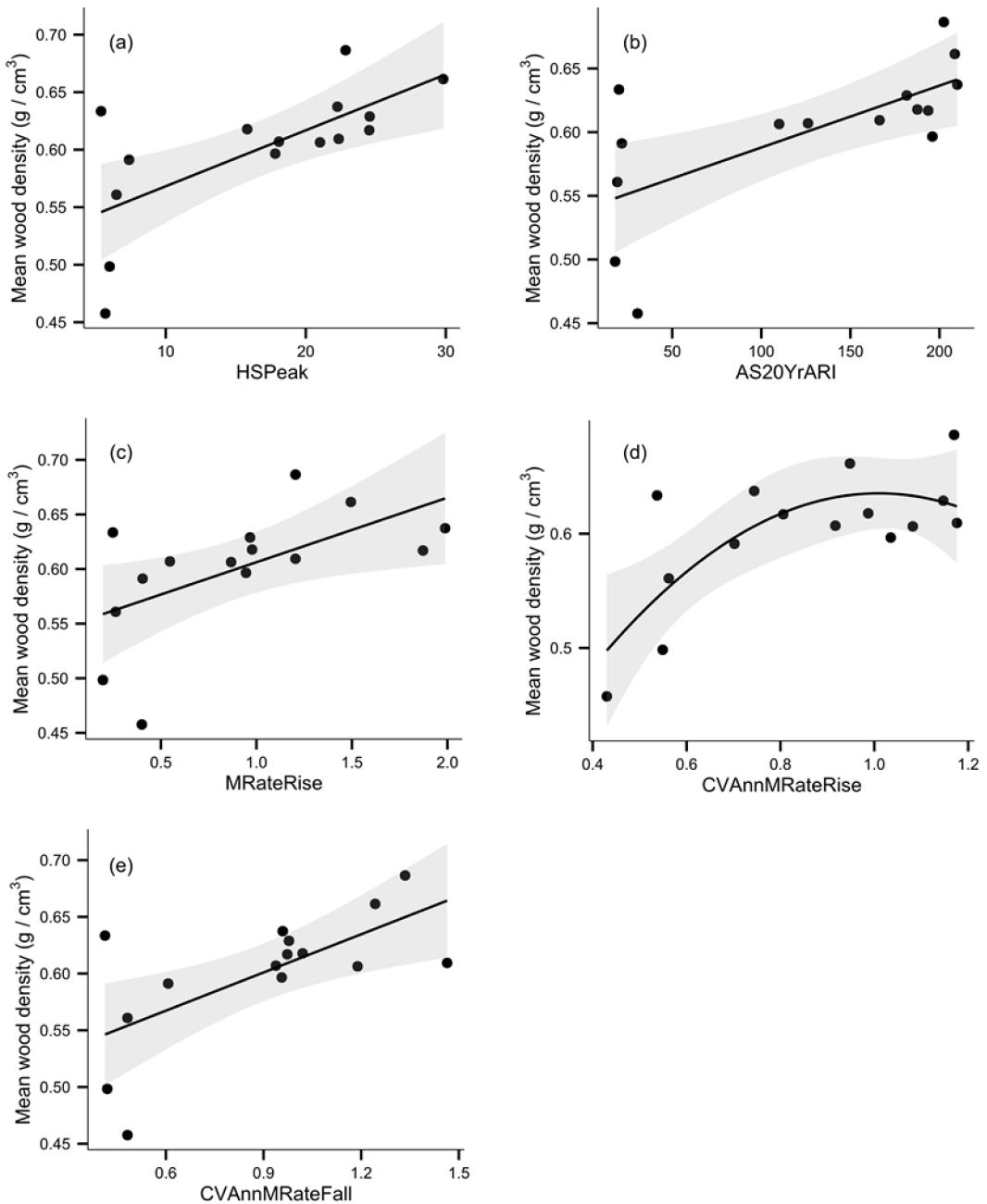


Figure 2.2: Relationships between community weighted mean wood density and hydrological metrics describing a.) mean high flow magnitude (HSPeak), b.) magnitude of the 20 year average return interval flood (AS20YrARI), c.) mean rate of flow rise (MRateRise), d.) interannual variability in flood rise rates (CVAnnMRateRise), e.) interannual variability in flood fall rates (CVAnnMRateFall). Fitted lines depict ordinary least squares regression models. d. is a quadratic fit, all other models are linear fits. Shaded areas depict the smoothed 95 % confidence interval around the regression model.

We found denser woody tissues were increasingly favoured as baseflow index decreased (Fig. 1.3a). Wood density increased as patterns of average flow conditions became a) less uniformly distributed across seasons (Fig. 1.3b), and b) less uniformly distributed year to year (Fig. 1.3c). Thus mean wood density is maximised when average flow patterns are highly seasonal, but the season with which they are associated is not consistent throughout the record. A similar relationship was observed for inter-seasonal (Fig. 1.3d) but not inter-annual uniformity of minimum flows. In other words, wood density was highest where minimum flows were not associated with any particular season. Mean wood density also increased with increasing interannual variability in baseflow index (Fig. 1.3e), pointing to a strong effect from years in which baseflow deviated from the mean. Wood density also decreased with mean low spell flow (Fig. 3f), and with the mean 7-day minimum flow (Fig. 1.3g). For both metrics, higher values indicate wetter minimum flow conditions. Mean wood density also increased with low flow frequency (Fig. 3h). Metrics of low flow duration were not significantly associated with wood density.

No significant pattern of spatial autocorrelation was detected within values of CWM ($P = 0.228$).

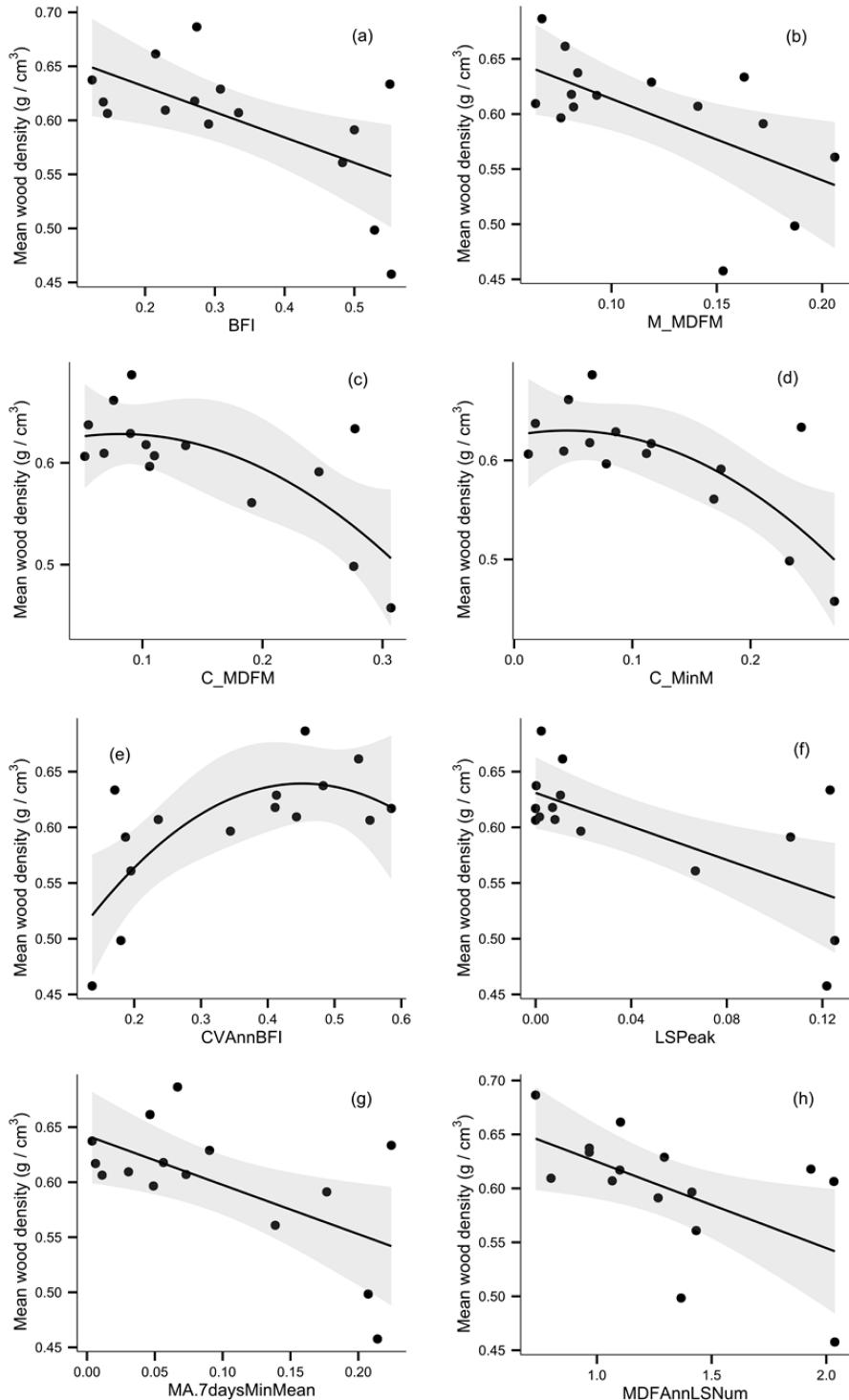


Figure 2.3: Relationships between community weighted mean wood density and hydrological metrics describing a.) baseflow index (BFI), b.) contingency of monthly mean daily flow (M_MDFM), c.) constancy of monthly mean daily flow (C_MDFM), d.) constancy of monthly minimum daily flow (C_MinM), e.) interannual variability in baseflow index (CVAnnBFI), f.) mean low flow magnitude (LSPeak), g.) mean flow during driest week of the year (MA.7days.MinMean), h.) annual frequency of low flows (MDFAnnLSSNum). c. - e. are quadratic fits, all other models are linear fits. Shaded areas depict the 95 % confidence interval around the regression model

What are the principal components of variation in hydrological conditions that explain variation in wood density?

Hydrological metrics that significantly explained site mean wood density were highly correlated in our dataset. Principal Components Analysis (PCA) identified one dominant axis within these metrics, representing 80.3 % of variation (Fig. 1.4). The remaining variation was split between several minor axes; PCA2 represented 6.3 % of variation and the remaining axes each represented less than 3 % of variation.

PC1 represents a gradient of environmental harshness that integrates baseflow characteristics, seasonality and flooding intensity. Metrics which are maximised under conditions of weak seasonality, high predictability and low variability of water availability were loaded towards the positive end of the PC1 axis, while metrics that are maximised under conditions of high interannual baseflow variability and high intensity flooding were loaded towards the negative end. Stable winter baseflow rivers exhibited lower site mean wood density, and were clustered at the mild positive end of the PC1 gradient. Unpredictable baseflow and unpredictable intermittent rivers overlapped across PC1 and were located distally towards the harsh negative end, and were associated with higher site mean wood density. The results of the PCA analysis illustrated that variation in wood density is largely described by a single axis of variation from low to high variability in flow.

Is there a relationship between hydrological disturbance and within-community dispersion of wood density?

No individual metrics describing hydrological disturbance showed significant relationships with CWV following p-value adjustment. The relationship between the PC1 axis and CWV in wood density could be significantly explained by a quadratic model, however ($R^2 = 0.450$, $P = 0.037$) (Fig. 1.5). The fitted curve

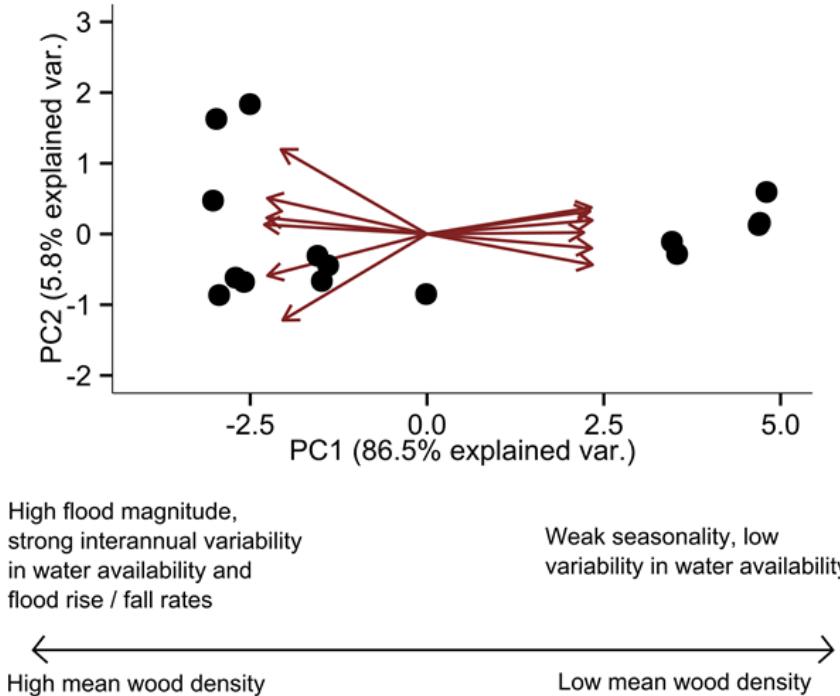


Figure 2.4: Biplot of sites ordinated across the first two principal components as determined from Principal Components Analysis of hydrological metrics displaying significant relationships with mean wood density across 15 sites in south eastern Australia. Points represent individual sites. PC1 explains 80.3 % of the variation in hydrology among the sites and represents a gradient of harshness of environmental conditions.

shows a peak in CWV at intermediate values of PC1, which correspond to intermediate values of hydrological disturbance and variability. No significant pattern of spatial autocorrelation was detected within values of CWV ($P = 0.786$).

2.4 Discussion

We sought to understand how hydrology might influence wood density, a key plant functional trait. We asked whether mean wood density could be explained by the degree of flooding disturbance or hydrological unpredictability in the riparian zone, and whether dispersion of wood density peaks in intermediately disturbed communities. To summarise, we found evidence that mean riparian wood density is

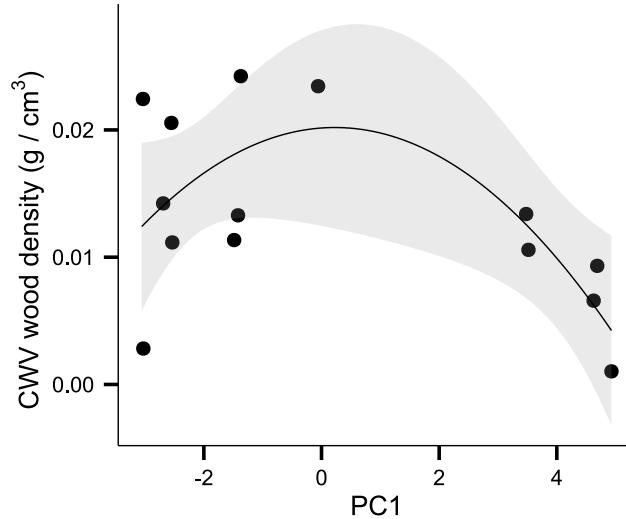


Figure 2.5: Quadratic relationship between community weighted variance in wood density and site scores for the first principal coordinate (PC1) of a Principal Components Analysis of hydrological metrics displaying significant relationships with mean wood density (see Fig. 4), ($R^2 = 0.450$, $P = 0.037$). Variance peaks at intermediate values of hydrological disturbance, as described by the PC1 axis. Shaded areas depict the 95 % confidence interval around the regression model.

positively related to flood magnitude and flow rise and fall rates, as well as to unpredictability in flow conditions over daily, seasonal and annual timescales. We also found evidence for divergence in wood density strategy at intermediate levels of disturbance. While wood density is a complex trait that integrates trade-offs between multiple selection pressures, we believe the strong relationships between mean wood density and hydrology demonstrated here are evidence that hydrological conditions powerfully influence plant ecological strategy in the riparian environment.

Strong relationships with measures of interannual variability point to years in which the environment was extreme as favourable towards high wood density. Several relationships were described best by quadratic models, indicating a maximum above which variation in hydrology ceases to be associated with changes in mean wood density. Predictable hydrologies and weak flooding disturbance intensity were associated with a greater range of mean wood density values. This variabil-

ity may be driven by other environmental factors, which become less influential as hydrological forcing increases. We also found that for *Casuarina cunninghamiana*, a common riparian species in SE Australia, intraspecific variation in wood density responded strongly to hydrology (see Appendix 1, Fig. ??).

Specific aspects of high flow hydrology drove variation in wood density. Mean wood density was not correlated with the frequency of high flow spells, which individually may not correspond to significant disturbance events, depending on the hydrological characteristics of the given river. Rather, it was the actual magnitude of flow during high flow periods that was important. High rates of flow rise and fall, which may be associated with entrainment of large debris into the flood channel and subsequent bank deposition (Cadol and Wohl, 2010), were also associated with high community wood density. Interannual variability in rate of flow rise was a substantially stronger predictor of wood density than the mean value, suggesting a greater influence of flow rise rates in extreme years than the general mean. A pattern is apparent then, in which mean wood density in riparian communities is driven by powerful but relatively rare flow events (e.g. 10 to 20 year average return interval flood). The abundance of high wood density strategies in these environments indicates that infrequent but high-stakes events may be a greater selective pressure in riparian plant communities than average conditions. For densely wooded species, persistence may be more influential on population dynamics than individual growth rates or fecundity (Adler et al., 2014). We therefore suggest that a brick house ecological strategy is favoured in riparian environments that experience intense flooding. This suggestion concurs with findings that trees on windy slopes tend to overcompensate for mechanical stress, with investment in defences increasing cumulatively in response to rare, extreme events (Cohen and Mangel, 1999; Telewski, 1995).

We can extend the observation about the influence of intense pulse flow events on wood density: plants living in environments where flow occurs unpredictably

and largely within specific events, rather than being evenly distributed throughout time, are likely to experience more intense pulses of water stress (i.e. low soil moisture). High wood density may be symptomatic of wood anatomy strategies that allow plants to tolerate water stress (Hacke et al., 2001; Jacobsen and Ewers, 2005; Jacobsen et al., 2007). Numerous studies have discussed the role of various anatomical components of woody tissue in stabilising xylem against cavitation when plants are under severe water stress, but the exact role that woody fibres play in stabilising xylem vessels appears to be inconsistent (Martínez-Cabrera et al., 2009). Overall, resistance against cavitation emerges from complex interactions between wood anatomical traits (Lens et al., 2011; Zieminska et al., 2013) and/or aboveground biomass production traits, both of which are tangentially related to wood density. With the exception of ephemeral dryland rivers, riparian environments tend not to be severely water limited, so specifically constructing woody tissue to deal with constant water stress may not be advantageous. For plants that are habituated to plentiful soil moisture, however, having no backup strategy for surviving drought conditions may be risky.

A more compelling rationale for our findings is that riparian woody plants are again overcompensating for the possibility of rare, life-or-death stress events. In the absence of predictable cues about timing of watering flows, conservative resource-use phenotypes such as higher wood density would be favoured (Valladares et al., 2007). Environmental unpredictability may act as a modifier which shifts ecological strategy in favour of conservative resource use (for which wood density acts as a proxy, in this case). We can observe this effect in intraspecific variation (see Appendix 1, Fig. 1) in wood density for the rheophytic (i.e. confined to frequently flooded substrates) species *C. cunninghamiana*: interannual variability in baseflow index, contingency of monthly minimum daily flow (M_MinM) and contingency of monthly mean daily flow (M_MDFM) describe interannual variability in water availability and all show strong relationships with intraspecific

variation in *C. cunninghamiana* wood density. Traits associated with conservative resource use and better recovery following periods of extreme stress may actually confer as much or greater fitness than traits associated with coping with the stress itself (Gutschick and BassiriRad, 2003).

Conservative resource use and heavy investment in structural strength fit within the resister category of riparian plant strategies described by Naiman & Decamps' (1997) classification of riparian plant life history strategies. Invader strategies with which species avoid harsh hydrological conditions by achieving sexual maturity as fast as possible are also common to the riparian environment (Naiman and Decamps, 1997; Woolfrey and Ladd, 2001). For pioneer species employing a fast relative growth rate, low wood density ecological strategy would be benefitted by repeated setbacks to early successional conditions (Westoby, 1998). Co-existence at intermediate disturbance intensities of a broad spectrum of strategies between invading and resisting may be responsible for the observed peak in wood density CWV, but this suggestion is difficult to substantiate using our dataset, as only a few sites were present in the middle range of the PC1 axis.

Under our argument, where hardy rheophytic species use high wood density ecological strategies to cope with powerful floods and unpredictable watering regimes, we would expect species such as *Casuarina cunninghamiana* and *Tristaniopsis laurina* (two of the most common riparian species in our study region) to have the highest wood density in our dataset. However both species exhibited highly variable trait values, ranging approximately between the median value and the 75th percentile. As with *C. cunninghamiana*, *T. laurina* is a light-demanding coloniser of within- and near-channel landforms (Webb et al., 2002). By establishing in close proximity to the channel, seedlings of these species must balance the risks of flooding with the advantages of growth unencumbered by competition for light or space. Maintaining a high relative growth rate, at least until the trees are physically large enough to endure flooding, allows these species to quickly fill space

and build photosynthetic tissue (i.e. invading) (Melick, 1990). If parallels with tropical rainforest species hold (King et al., 2006; Kraft et al., 2008; Poorter et al., 2010, 2008; Wright et al., 2010), this strategy will not be conducive to setting down dense wood (i.e. resisting). In addition to morphological adaptations in *T. laurina* such as multi-stemmedness, narrow leaves and growth streamlined against the direction of flow (van Steenis, 1981; Webb et al., 2002), the trade-off between flood resistance and rapid resource acquisition and growth during establishment serves to explain why the optimal wood density for rheophytic species might occupy a central position along the axis of wood density. Nonetheless, the wide plasticity in wood density shown by *C. cunninghamiana* and *T. laurina* suggests that intraspecific variation contributes to the species capacity to track hydrological gradients.

Notably, it is the tall, facultative riparian species from rainforest sites that had the highest wood density in our dataset. Lacking the morphological adaptations required to thrive directly along the channel edge, these species may rely solely on generating mechanically strong stems to withstand flooding. High wood density species tended to occur further up the bank, so would be subject to only the more intense flooding events. Since succession typically advances with elevation above the channel edge (Tabacchi et al., 1998), this observation agrees with previous work showing increasing wood density along a successional gradient (Falster and Westoby, 2005). Further parallels in the existing wood density literature are also evident here, where high wood density individuals were much less likely to experience major wind damage following a cyclone (Curran et al., 2008).

The gradient identified by principal components analysis integrates predictability of water availability, seasonality and flood intensity into a single axis of hydrological variation. It is not possible to tease out individual drivers of variation in mean wood density, as the conditions associated with both environmental unpredictability and mechanical disturbance act in unison to drive community wood

density towards higher mean values.

Community weighted variance in wood density showed a quadratic distribution across this gradient of hydrological harshness. Previous work has described a negative relationship between community-level variance in wood density and abiotic stress (using high latitude and elevation as proxies for stressful environments) (Swenson and Enquist, 2007). Rather than constricting trait values, intermediate levels of pulsed fluvial disturbance may promote trait diversity by retarding competitive exclusion (Huston, 1979; Naiman and Decamps, 1997), whilst simultaneously generating structurally heterogeneous habitat (Corenblit et al., 2007). While the fit of our model is statistically significant, the paucity of values through the middle range of the PC1 axis gives rise to error around the peak of the fitted curve; interpretation of this result therefore necessitates some caution.

Damming and water extraction, and changing climatic conditions are altering hydrology globally (Nilsson and Berggren, 2000; Stocker et al., 2013). Artificial flow modification by damming and water extraction reduces overall flow volume and the magnitude and frequency of high flow events, while increasing flow predictability, altering seasonality and limiting channel-floodplain connectivity (Graf, 2006; Maheshwari et al., 1995). In these altered conditions, terrestrial species with softer wood and faster growth rates may encroach on what was once the province of rheophytic assemblages adapted to flooding and less predictable hydrological conditions. The converse of this situation is presented by predictions of future climatic conditions: in Australia, warming of 0.4 - 0.7 °C has occurred since 1950 (Hennessy et al., 2007), associated with a reduction in rainfall across southern and eastern regions of the continent (Smith, 2004), and an increase in intensity and frequency of droughts (Hennessy et al., 2008). Extreme rainfall events are predicted to become more prevalent, even in areas where the trend is towards mean reductions in annual or seasonal rainfall (Chiew et al., 2009). River discharge in Australia is known to be particularly sensitive to the El Nino-Southern Oscillation (ENSO)

phenomenon that is an integral driver of the continents climate patterns (Nicholls, 1989; Ward et al., 2010). Projected increases in climatic variability (Hennessy et al., 2008) may therefore overlay the already strong natural variability induced by ENSO to produce significant alterations to streamflow. Under such conditions, near-channel abundance of opportunistic terrestrial species (with their broad diversity of wood density strategies) may decline in favour of rheophyte-dominated assemblages whose ecological strategies are optimized to harsh hydrological conditions. If changes in spatial extent of climate zones can be related to changes in runoff - a complicated but progressing area of research in hydroclimatology (Peel and Bloschl, 2011) - functional approaches to ecohydrology can give insight into likely changes in riparian plant assemblages and associated changes in ecosystem function.

Conclusion

Our study emphasises the importance of hydrological conditions, particularly disturbance and environmental unpredictability, as determinants of ecological strategy in riparian plant communities. These relationships may be generalisable to diverse biomes, given the strong constraints imposed by flooding and fluctuating water availability on woody plant ecological strategies in many riparian environments. The marked influence of rare, high intensity floods on wood density is likely to have significant ecological consequences for riparian plant communities in a south-east Australian context, and potentially in other regions where increasing climatic variability and frequency of extreme events are hallmarks of climate change predictions.

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Data availability

Data are available through DataDryad, doi:10.5061/dryad.72h45 (Lawson et al., 2015).

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3 Heterogeneous flows foster heterogeneous
assemblages: relationships between functional
diversity and hydrological heterogeneity in
riparian plant communities

Abstract

Riparian ecosystems are biophysically complex and highly diverse taxonomically, structurally and functionally. While many environmental factors determine the structure and function of riparian vegetation communities, hydrology is thought to be the master variable. Flooding and variability in water availability are known to be key drivers of taxonomic diversity, but their influence on the functional trait diversity of riparian vegetation communities remains largely unexplored.

We collected data on species abundance, quantitative plant functional traits and hydrology from 15 sites distributed across south-eastern Australia to address the following questions: (a) is functional trait diversity related to frequency and magnitude of flooding disturbance? (b) is functional trait diversity related to variability in seasonal water availability within the riparian zone?

We confirm that metrics describing both flooding disturbance and patterns of water availability exhibit strong relationships with functional trait diversity in riparian vegetation communities of south-eastern Australia. Our key finding is that functional trait diversity in these systems tends to be positively associated with variability in hydrological conditions and the intensity of rare, high magnitude flooding events, rather than average patterns of flow.

Our study highlights the importance of extreme flooding events and temporal patterns of water availability as determinants of diversity in riparian vegetation communities. These relationships may have significant consequences for plant communities experiencing alterations to hydrology caused by anthropogenic flow modification and the changing climate.

3.1 Introduction

Riparian ecosystems are biophysically complex and highly diverse taxonomically, structurally and functionally (Naiman et al., 1993; Nilsson and Svedmark, 2002; Poff, 2002). Extensive flow regulation of river systems and changing patterns of runoff under future climates are likely to produce dramatically different future flow regimes, with significant consequences for the diversity and functioning of riparian assemblages. Riverine conservation and rehabilitation efforts must therefore be informed by general understanding of the processes that generate patterns of diversity and drive ecosystem functioning in riparian ecosystems.

The prevailing paradigm in riparian ecology holds that heterogeneity in the riparian patch mosaic results from the sculpting action of hydrological processes across the biogeomorphic template (Bornette et al., 2008; Corenblit et al., 2007; Palmer and Poff, 1997; Tabacchi et al., 1996). In riparian environments, it is this intrinsic environmental heterogeneity that fosters structural, taxonomic and functional heterogeneity within vegetation communities (Bornette et al., 2008; Corenblit et al., 2007; Naiman et al., 1993). Local hydrology (river flow regime) is widely considered to be the most important determinant of community composition and functioning in riparian plant assemblages, as it dictates patterns of disturbance by flooding, as well as soil moisture availability (Arthington et al., 2010; Poff et al., 1997).

Flooding may retard competitive exclusion by resetting the patch structure of parts of the landscape and thereby enhance diversity (Huston, 1979; Naiman et al., 1993), or constrain assemblages to species that have ecological strategies adapted to flooding, thereby decreasing diversity (Díaz et al., 1998). General support has been found for the intermediate disturbance hypothesis (Connell, 1978) with respect to the relationship between flooding intensity and taxonomic diversity (e.g. Bendix (1997), Bendix and Hupp (2000), Lite et al. (2005), Corenblit et al. (2007)).

This support is not equivocal however (Baker, 1990; Nilsson et al., 1989) and at within-reach scales the geomorphic template is also a strong control on diversity (Bendix, 1997; O'Donnell et al., 2014).

In regions where riparian plants experience periodic water stress, soil moisture availability may be driven largely by hydrology (Castelli et al., 2000; Nilsson and Svedmark, 2002). Seasonal and interannual variability in patterns of disturbance and water availability are also known to influence species richness (Catford et al., 2012, 2014; Greet et al., 2011) and this effect may be exacerbated for summer flows in hot or dry regions (Garssen et al., 2014). A study investigating drivers of riparian vegetation community structure and composition in subtropical eastern Australia identified variability in dry season flows as the hydrological variable that was most strongly associated with variation in species richness (Arthington et al., 2012).

Conservation and restoration activities increasingly aim to preserve the ecosystem functions associated with biological communities (Aerts and Honnay, 2011; Cadotte et al., 2011; Montoya et al., 2012). Quantitative functional traits (such as specific leaf area, wood density, seed mass, etc.) can form the basis for mechanistic assessments of diversity that describe the range and distribution of ecological strategies in a community and their associated environmental effects. Such metrics of functional trait diversity (hereafter referred to as functional diversity) are substantially more powerful than taxonomic metrics as indicators of ecosystem functioning, ecosystem resilience and capacity to provide ecosystem services (Díaz et al., 1998; Hooper et al., 2005; Tilman et al., 1997). Reduced abundance of functionally unique species may gradually undermine ecosystem resilience or functioning, and assessment of functional diversity can be useful to diagnose degradation before species loss occurs (Mouillot et al., 2013). Assessments of ecosystem service production have also begun to give functional diversity priority over taxonomic metrics (Díaz and Lavorel, 2007).

Numerous metrics of functional diversity have been described in the literature (Mouillot et al., 2013; Schleuter and Daufresne, 2010). These aim to quantify 'the distribution of species and their abundances in the functional space of a given community' (Mouillot et al., 2013) and typically process multidimensional trait data to output a single value describing various properties of these data. The framework described by Villéger et al. (2008), consisting of functional richness (the volume of the convex hull circumscribing the range of trait values), functional divergence (divergence in the distribution of abundance within trait space) and functional evenness (the evenness of this distribution in trait space), has been commonly used to describe functional diversity (e.g. Biswas and Mallik (2010), Pakeman (2011), Savage and Cavender-Bares (2012), Clark et al. (2012)). Functional dispersion (FDis), defined as the abundance-weighted mean distance in multivariate trait space of individual species to the centroid of all species in the community, represents an improvement on this framework (Laliberté and Legendre, 2010). FDis allows for consideration of species abundances while integrating functional richness and functional divergence and is formulated to be independent of species richness, alleviating concerns that it merely tracks patterns of species richness (as is possible with functional richness). FDis is also known to be more robust to bias due to missing trait data than metrics such as functional richness, evenness or divergence (Pakeman, 2014). In an empirical assessment of specific functional diversity metrics as indicators of ecosystem functioning in a Minnesota grassland, FDis was a useful predictor of three measures encompassing above and belowground biomass production and light capture, and compared favourably with other metrics (Clark et al., 2012).

Considerably less is known about drivers of functional diversity than of taxonomic diversity in riparian plant communities. Catford et al. (2011) analysed univariate functional trait distributions to show how flow impoundment along a large river system in south-eastern Australia was associated with greater cover of

exotic species and reduced functional diversity in riparian wetlands. Support for the intermediate disturbance hypothesis with respect to functional diversity has been described in communities along a gradient of disturbance associated with management for logging (Biswas and Mallik, 2010). Similarly in agricultural systems, land-use intensification has been linked with lower functional diversity across an international dataset (Laliberté and Legendre, 2010) and the authors associated this effect with a reduced ability of communities to respond to disturbance. On the west coast of Scotland, increasing anthropogenic disturbance in arable fields, grazed grasslands, moorlands and woodlands was associated with reduced functional richness and increased functional evenness (Pakeman, 2011). A trend is apparent from these studies where functional diversity is inversely associated with human-induced environmental homogenisation.

Environmental heterogeneity is increasingly regarded as a key factor governing species richness gradients (Stein et al., 2014). To date, however, advances in quantitative ecology based on functional traits have been sparsely applied to riparian systems. Describing the influence of hydrological heterogeneity on quantitatively derived measures of riparian functional diversity would represent a significant advance for riparian ecology and ecosystem-oriented riparian conservation.

We hypothesised that the environmental heterogeneity induced by repeated floods and fluctuating soil moisture levels should be reflected in the functional diversity of plant communities adapted to the riparian environment. We investigated the relationship between hydrologically driven environmental heterogeneity and functional diversity in riparian plant communities, using south-eastern Australia as a case study where a broad spectrum of hydrological heterogeneity is present within a relatively compact, contiguous landscape (Finlayson and McMahon, 1988; Peel et al., 2004). Specifically, we asked the following questions: (1) Is functional trait diversity related to the frequency and magnitude of flooding disturbance? (2) Is functional trait diversity related to variability in seasonal water

availability in the riparian zone?

3.2 Methods

Study sites

Fifteen riparian sites were selected along gauged, partly confined rivers in the South-East Coast and south-eastern Murray Darling drainage basins of Australia. These sites were distributed across clear gradients of ecologically relevant dimensions of hydrological variation: specifically, the magnitude, frequency, duration, timing and rates of change of flow events and patterns. The study area spanned latitude -29.467 to -37.371°S and longitude 147.413 to 152.217 °E. Sites spanned an altitudinal range of 23 - 732 m above sea level. Site-specific details can be found in Appendix 2a. Full description of site selection criteria and vegetation survey methods can be found in (Lawson et al., 2015), as this study was undertaken simultaneously and at the same sites.

Rationale for trait selection

Data for the following traits were collected: specific leaf area, maximum canopy height, seed mass, wood density, flowering period length and leaf narrowness. These traits were chosen to encapsulate the key axes of variation and trade-offs relevant to ecological strategies employed by riparian plants (see Table 1.1 for justification and further description of functional traits).

Table 3.1: Justification for inclusion of traits in the functional diversity analysis.

<i>Trait</i>	<i>Definition</i>	<i>Ecological strategies and trade-offs captured by trait</i>
Specific leaf area	Ratio of one-sided leaf area to oven dry mass ($\text{cm}^2 \text{ g}^{-1}$).	Indicates species position along the leaf economics spectrum (Wright et al., 2004). Associated with trade-off between rapid leaf construction and ability to tolerate stress (Reich and Wright, 2003).
Maximum canopy height	Height above ground of apical meristem (m).	Integrates trade-off between competition for light and cost of construction and maintenance of support structures (Falster 2006).
Seed mass	Combined mass of the seed coat, endosperm and embryo (g). Does not include dispersal structures.	Indicates maternal investment in individual offspring (Leishman et al., 2000). Influences hydrochory (via seed buoyancy) (Carthey et al., 2015), and ability to establish in different soil moisture conditions (Leishman et al., 2000).
Wood density	Oven dry mass divided by green volume (g cm^{-3})	Confers mechanical strength to stems but costly to construct. Associated with slower relative growth rates (Chave et al., 2009) but greater ability to tolerate water stress and disturbance (Lawson et al., 2015; Preston et al., 2006; Telewski, 1995).
Flowering period length	Proportion of the year spent in flower (proportion, dimensionless)	Indicates species ability to respond reproductively to favourable conditions.
Leaf narrowness	Ratio of average leaf width to average length (ratio, dimensionless)	Narrow leaves present less photosynthetically active tissue but can regulate temperature more efficiently and thus maintain photosynthesis in hot, dry or highly insolated (i.e. disturbed) conditions (Cornelissen et al., 2003). Strongly indicative of rheophyt, the trait syndrome shared by plants adapted to growing near swift flowing, frequently flooded streams (van Steenis, 1981).

Trait dataset assembly

The dataset for this study was assembled using measurements recorded in the field (specific leaf area, wood density), supplemented by data from published literature, private and public trait databases and Australian flora texts.. In the case that multiple values were found in the literature or online for a trait, values were excluded if they were measured from sites that were substantially different environmentally to the field site in which they were found in this study. Remaining values were averaged. Single values for each trait were recorded, under the assumption that for our chosen traits, interspecific variation is strong enough to allow differentiation between species despite noise due to intraspecific variation, and that species trait hierarchies are largely conserved across different spatial scales and datasets (Cordlandwehr et al., 2013; Kazakou et al., 2014). Leaf narrowness was not included for grasses, while seed mass and flowering period length were not included for ferns.

Specific leaf area was measured once for each species according to the procedure defined by Cornelissen (2003). A minimum of five new but fully mature leaves from well-lit areas were taken from each of five non-contiguous individual plants. Leaves were pressed in the field to maintain fresh area and allowed to air dry at 20-45C, then scanned and leaf area measurements made using image analysis software (ImageJ 1.48 for Windows). Leaves were then oven dried at 70C for 72 hours and weighed using a microbalance (Mettler Toledo, Greifensee, Switzerland). Specific leaf area was calculated as one-sided fresh area divided by oven dry mass.

Wood density data were collected according to the procedure outlined in Lawson et al. (2015). Site-specific values were available for wood density but for the purposes of this study an overall mean value was calculated for species that occurred at multiple sites. Wood density values for species for which data was not available from the field were obtained from the Global Wood Density Database (Chave et al., 2009).

Hydrological analysis

Daily discharge data for each site were obtained from the PINNNENA CW 10.1 database (New South Wales Office of Water, Department of Primary Industries) and the New South Wales Office of Water Continuous Water Monitoring network website <http://realtimedata.water.nsw.gov.au/water.stm> for New South Wales sites, and the Victoria State Governments Water Measurement Information System website <http://data.water.vic.gov.au/monitoring.htm> for Victorian sites. Thirty year time series spanning 1983–2012 were obtained where possible, although three sites had truncated records of 15, 19 and 28 years. Missing data were approximated by multiple linear regression (4 sites) and linear interpolation (1 site) using the Time Series Manager module in the River Analysis Package (Marsh et al., 2003). We used the Time Series Analysis module in the River Analysis Package to generate a set of 23 hydrological metrics for each site, based on a reduction of the minimally redundant set of ecologically relevant metrics for Australian rivers described by Kennard et al. (2010). These metrics were chosen as descriptors of the frequency and magnitude of flooding disturbance, as well as variability in water availability across seasons and between years (see Table 1.2 for descriptions and rationale for inclusion of individual metrics). Collinearity between these metrics was analysed using principal components analysis (PCA); the results of this PCA as well as summary statistics for hydrological metrics are given in Appendix 2a. Parameters used to generate hydrological metrics were identical to Lawson et al. (2015). Metrics of flow magnitude, which had units mL day^{-1} were standardised by mean daily flow to allow for comparison between different river channel sizes. These metrics therefore represent ratios of flow magnitude to mean daily flow.

Table 3.2: Hydrological parameters used as metrics of variability in high flow magnitude and frequency and predictability and consistency of water availability in the riparian environment. * - normalised by mean daily flow (ML/day)

<i>Parameter</i>	<i>Abbreviation</i>	<i>Units</i>	<i>Description</i>
Flood frequency and magnitude			
Mean magnitude of high spells *	HSPeak	dimensionless	Together, these metrics characterise patterns of flooding intensity and frequency. High spells are periods of flow above the 95th percentile on the flow duration curve. HSPeak describes the mean magnitude of peak flows during high spells throughout the record. MDFAnnHSNum describes the mean annual frequency of high spell periods. The coefficients of variation of these metrics between years characterise hydrological variability as it pertains to patterns of high flows. 20 year average return interval (ARI) floods are larger flow events with the potential to be geomorphically effective and rework the fluvial landscape.
CV of all years mean high spell magnitude	CVAnnHSPeak	dimensionless	
20 year ARI flood magnitude *	AS20YrARI	dimensionless	
Mean of all years number of high spells	MDFAnnHSNum	year ⁻¹	
CV of all years number of high spells	CVAnnHSNum	dimensionless	
Rise and fall rates			
Mean rate of rise *	MRateRise	day ⁻¹	Flow rise and fall rates describe the shape of high flow curves. Interannual variability within these metrics captures the diversity of peak flow shapes within a system. Unfortunately, these metrics are constrained to daily resolution by the limitations of historical discharge records.
Mean rate of fall *	MRateFall	day ⁻¹	
CV of all years mean rate of rise	CVAnnMRateRise	dimensionless	
CV of all years mean rate of fall	CVAnnMRateFall	dimensionless	

<i>Parameter</i>	<i>Abbreviation</i>	<i>Units</i>	<i>Description</i>
Colwell's indices			
Constancy of monthly mean daily flow	C_MDFM	dimensionless	Colwell's indices provide a measure of the seasonal predictability of flow events and therefore water availability within the riparian zone. Constancy (C) measures uniformity of flow across seasons, and is maximised when flow conditions do not differ between seasons. Contingency (M) is a measure of interannual uniformity in seasonal flow patterns, and is maximized when seasonal patterns of flow are consistent between years. We generated Colwell's indices for both average flow conditions and minimum flows conditions.
Contingency of monthly mean daily flow	M_MDFM	dimensionless	
Constancy based on monthly minimum daily flow	C_MinM	dimensionless	
Contingency based on monthly minimum daily flow	M_MinM	dimensionless	
Flow seasonality			
Average mean daily flow for Spring *	MDFMDFSpring	dimensionless	These metrics describe the average magnitude and variability within mean daily flows for each season. Averages and coefficients of variation are calculated across yearly means. Seasonal average mean daily flows were standardised by overall mean daily flow, so actually represent the ratio of mean daily flow in a given season to the total mean daily flow.
Average mean daily flow for Summer *	MDFMDFSummer	dimensionless	
Average mean daily flow for Autumn *	MDFMDFAutumn	dimensionless	
Average mean daily flow for Winter *	MDFMDFWinter	dimensionless	
CV of mean daily flow for Spring	CVMDFSpring	dimensionless	
CV of mean daily flow for Summer	CVMDFSummer	dimensionless	
CV of mean daily flow for Autumn	CVMDFAutumn	dimensionless	
CV of mean daily flow for Winter	CVMDFWinter	dimensionless	

Functional trait diversity analysis

Functional dispersion characterises the distribution of species traits at a site in multivariate trait space. We used the dbFD function from the FD package for R (Laliberté and Legendre, 2010) to calculate abundance-weighted functional dispersion (FDis) from species trait values and relative abundances for each site. This package implements the method for distance-based tests for homogeneity of multivariate dispersions described by Anderson (Anderson et al., 2006). dbFD uses Gower's method (Gower, 1971) to generate the trait dissimilarity matrix, which can account for missing values, and automatically standardises traits by their ranges; Cailliez correction was applied to the matrix (Cailliez, 1983). Simplicons diversity was calculated using the SYNCSA package (Debastiani and Pillar, 2012).

Only species present at >1 % cover in plots were included in the analysis ($n = 126$, from a total of 327 species). Data deficient species lacking values for more than four traits could not be included in the analysis as they produced gaps in the distance matrix used to calculate functional diversity. Thus a final total of 107 species were included in the analysis. Data density exceeded 90 % for all sites and averaged 97 %; full data density information including trait specific values are

shown in the Appendix 2b. All trait values were transformed by log10 prior to analysis. Summary statistics for the trait dataset are also available in Appendix 2b. Following citeptLeps2006, we performed principal components analysis (PCA) (stats package), (R Core Team, 2015) on trait data to check for redundancy. Although not completely orthogonal, traits were well distributed across multiple principal components. Therefore we believe there is both ecological (as previously discussed) and statistical rationale to retain all six traits in the analysis.

All statistical analyses were performed using the R statistical programming environment (R Core Team, 2015). Statistical significance was interpreted at alpha = 0.05.

Relationships between FDis, hydrological metrics and taxonomic diversity

Ordinary least-squares (OLS) regression models were generated for the selected metrics to determine relationships between hydrological gradients and FDis. To reduce the occurrence of Type 1 statistical error, we adjusted the resulting p values using the two-step Benjamini - Hochberg (BH) procedure (Benjamini et al., 2006) for controlling the false discovery rate (mt.rawp2adjp function in multtest package for R) (Pollard et al., 2008).

The utility of functional diversity metrics depends on their ability to provide non-redundant information compared with measures of taxonomic diversity. We further tested relationships (using OLS regression) between FDis and species richness and Simpsons diversity (for species used in the analysis, present at >1 % cover), and species richness for the full set of 327 species identified in the study.

We selected a minimal multiple regression model designed to incorporate descriptors of disturbance frequency and magnitude and variability in seasonal flow. The full set of hydrological metrics was initially screened to remove metrics that

were individually determined to have non-significant relationships with FDis. PCA over the remaining metrics identified one major and two minor axes of variation (PC1 71.4 %, PC2 9.0 % and PC3 - 8.3 % of variance explained). For PC1 there was no clear differentiation in eigenvalues; the metric with highest individual R^2 value (interannual variability in high flows) was selected. PC2 identified mean daily flow in summer and PC3 identified interannual variability in flood frequency as further sources of variability. Models were then built pertaining to all possible permutations of summation and interaction for these three metrics. Values for each metric were centred by subtracting the mean value (after Robinson and Schumacker (2009)). Multicollinearity was tested for according to the variance inflation factor (VIF) score (HH package), (Heiberger and Holland, 2004) and models were compared according to the second order of Akaike's Information Criterion (AIC) (MuMIn package) for R (Barton, 2012; Burnham and Anderson, 2002).

Assessing the influence of other environmental variables

Climatic and edaphic conditions are known to be important abiotic drivers of plant diversity at landscape scales (Laliberté et al., 2013; Vázquez-Rivera and Currie, 2015), and may exhibit strong interdependence with hydrological flow regime. We used a variance partitioning approach to assess the individual contributions of hydrology, climatic and edaphic conditions to modelling variation in FDis. Climate data was taken from eMast/TERN at a resolution of 0.01 degrees (Hutchinson et al., 2014). Bioclimatic variables representing annual trends, seasonality and extremes were then calculated following the BIOCLIM concept (Busby, 1991). Edaphic data were obtained from the CSIRO Soil and Landscape Grid of Australia at a resolution of 3 arc seconds (~ 3 m) (Rossel et al., 2014a,c,d,e,f,g,h,i,j,k; ?). Further details on these climate and edaphic datasets are given in Appendix 2a. Optimal models explaining variation in FDis according to climatic and edaphic

variables were then generated using the same process as for hydrological metrics. Variance explained by these models was partitioned by partial regression following Legendre (2007), using the function varpart in R (vegan package), (Oksanen et al., 2013). Adjusted R^2 , which controls for sample size and number of predictors (Peres-Neto et al., 2006), was used to estimate the proportion of variation jointly and independently explained by each model.

3.3 Results

Below we describe patterns of variation in functional dispersion (FDis) as they relate to the hydrological metrics described in Table 1.2. All models are linear apart from M_MinM and CVMDFSummer, for which a quadratic model ($df = 2, 12$) provided a substantially better fit. Statistics for all univariate regression models are presented in Appendix 2c.

Is functional diversity related to the frequency and magnitude of flooding disturbance?

Functional dispersion was positively associated with metrics describing intense but rare episodes of flooding disturbance. FDis was significantly associated with the magnitude of the 20-year average return interval flood (AS20YrARI, Fig. 1.1a, adjusted $p = 0.0278$, $R^2 = 0.377$). FDis was also significantly associated with interannual variability in high flow magnitude (CVAnnHSPeak, Fig. 1.1b, adjusted $p = 0.0152$, $R^2 = 0.577$) and rates of flow rise (CVAnnMRateRise, Fig. 1.1c, adjusted $p = 0.0278$, $R^2 = 0.403$) and fall (CVAnnMRateFall, Fig. 1.1d, adjusted $p = 0.0278$, $R^2 = 0.390$), whereas relationships with metrics describing average conditions were not significant (mean high flow magnitude, HSPeak, adjusted $p = 0.065$; mean flood rise rate, MRateRise, adjusted $p = 0.156$; mean flood fall rate, MRateFall, adjusted $p = 0.157$). Likewise, while interannual variability in

flood frequency (CVAnnHSNum, Fig. 1.1e, adjusted $p = 0.0360$ $R^2 = 0.296$) was significantly associated with FDis, mean annual flood frequency was not (MD-FAnnHSNum, adjusted $p = 0.727$). These results indicate that functional diversity is higher at sites that experience extreme flooding events and heterogeneous patterns of flow.

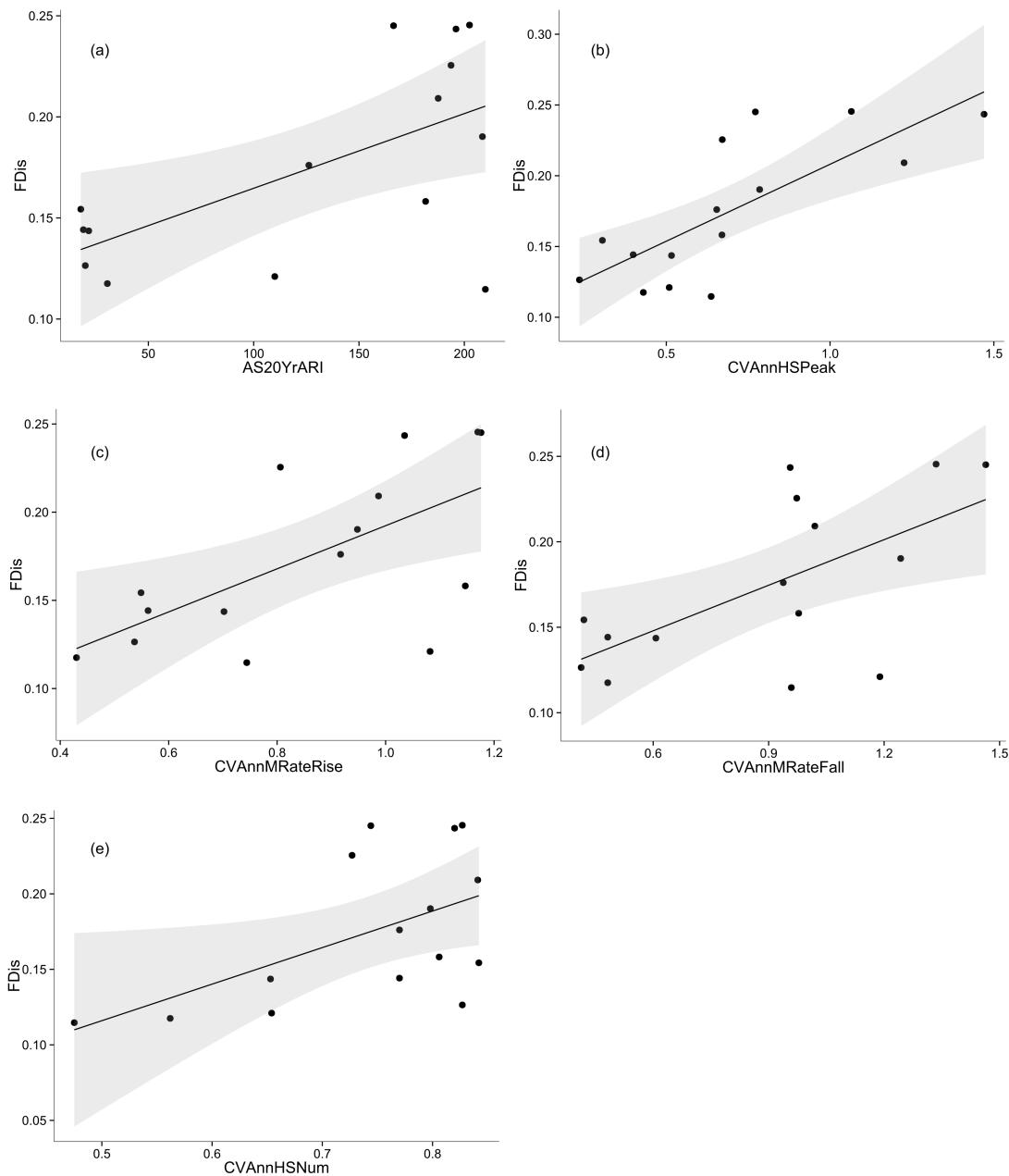


Figure 3.1: Relationships between FDis and hydrological metrics describing (a) magnitude of the 20 year average return interval flood (AS20YrARI), (b) interannual variability in high flow magnitude (CVAnnHSPeak), (c) interannual variability in flood rise rate (CVAnnMRateRise), (d) interannual variability in flood fall rate (CVAnnMRateFall), (e) interannual variability in high flow frequency. Fitted lines depict ordinary least squares regression models. All models are linear fits. Shaded areas depict the smoothed 95 % confidence interval around the regression model. All relationships shown are significant. Units shown in Table 1.2.

Is functional diversity related to variability in seasonal water availability in the riparian zone?

Functional dispersion was positively associated with variability in flow seasonality. FDis was increased when seasonal patterns of minimum (M_MinM, Fig. 1.2 a, adjusted p = 0.0278, R² = 0.540), maximum (M_MaxM, Fig. 1.2b, adjusted p = 0.0325, R² = 0.328) and average (M_MDFM, Fig. 1.2c, adjusted p = 0.0325, R² = 0.347) flows became less uniform (smaller values of M) between years. In other words, at high FDis the season with which these flows were associated was not consistent through the record. FDis was not significantly explained by inter-seasonal uniformity of minimum (Fig. 1.2d, C_MinM, adjusted p = 0.1021, R² = 0.166) or average (Fig. 1.2e, C_MDFM, adjusted p = 0.0861, R² = 0.186) flows, although visual inspection of the scatterplots for these relationships indicates two sites at the lower bound of the x axis (i.e. strongly seasonal patterns of flow), with substantially lower FDis than predicted by the regression model. If we consider these trends, we can infer that functional dispersion was increased when discharge patterns differed strongly between seasons, but the season with which those patterns were associated was not consistent between years.

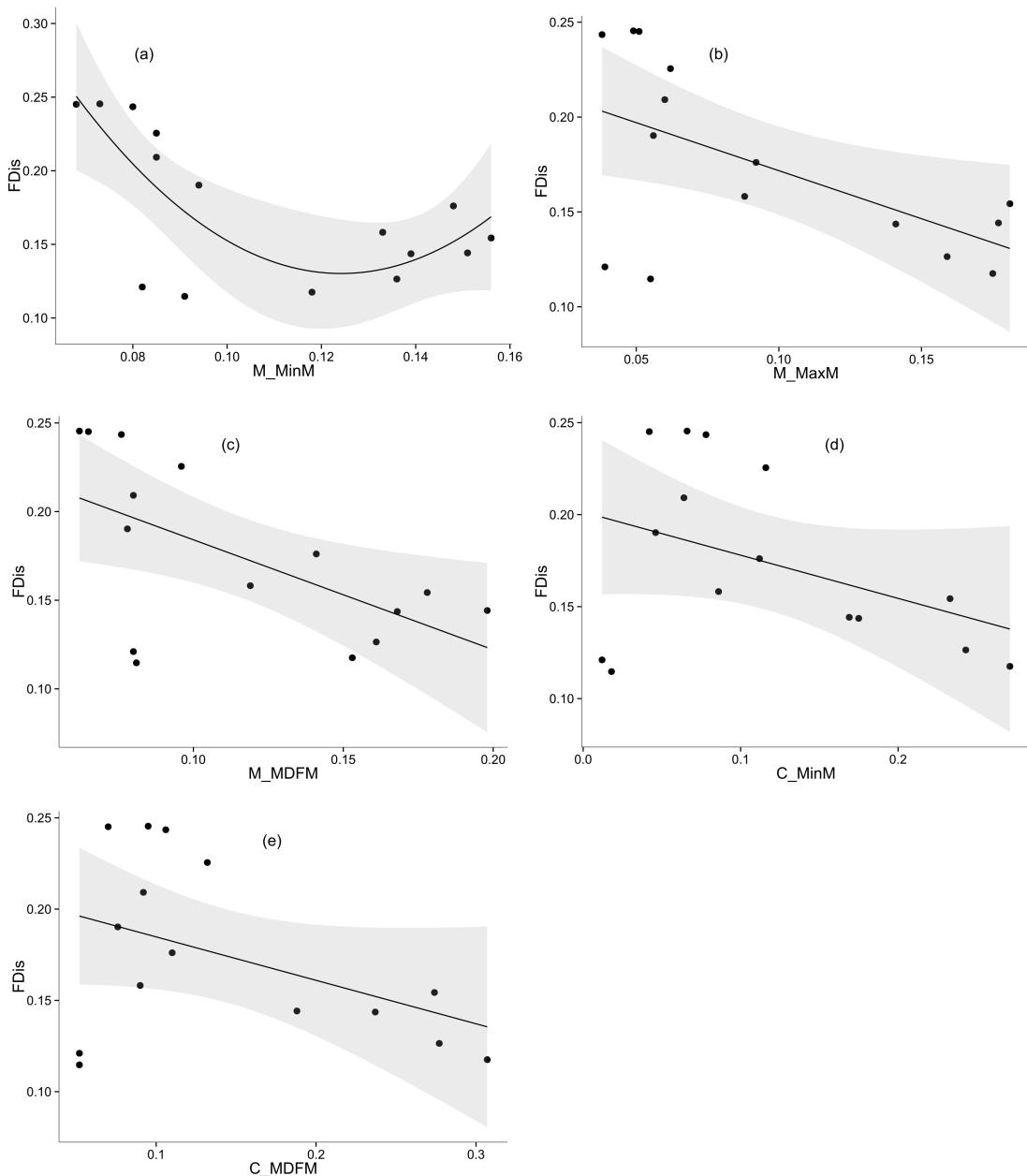


Figure 3.2: Relationships between FDis and hydrological metrics describing (a) contingency of monthly minimum daily flow (M_{MinM}), (b) contingency of monthly maximum daily flow (M_{MaxM}), (c) contingency of monthly mean daily flow (M_{MDFM}), (d) constancy of monthly minimum daily flow (C_{MinM}), (e) constancy of monthly mean daily flow (C_{MDFM}). Fitted lines depict ordinary least squares regression models. (a) is a quadratic fit, (b - e) are linear fits. Shaded areas depict the smoothed 95 % confidence interval around the regression model. (a - c) depict significant relationships. (d - e) depict non-significant relationships (note the strong influence over the regression fit of the two points at the lower bound of FDis). Units are shown in Tables 1.1 and 1.2.

This observation was corroborated by positive relationships between FDis and variability in mean daily flows for autumn (CVMDFAutumn, Fig. 1.3a, adjusted $p = 0.0386$, $R^2 = 0.301$), winter (CVMDFWinter, Fig. 1.3b, adjusted $p = 0.0278$, $R^2 = 0.414$) and spring (CVMDFSpring, Fig. 1.3c, adjusted $p = 0.10325$, $R^2 = 0.327$). Summer flow variability (CVMDFSummer, Fig. 1.3d, adjusted $p = 0.0325$, $R^2 = 0.472$) exhibited a humped relationship with FDis. Mean daily flows for both summer and spring were associated with FDis, however. This association was positive for summer (MDFMDF Summer, Fig. 1.3e, adjusted $p = 0.0230$, $R^2 = 0.503$) and negative for spring (MDFMDFSpring, Fig. 1.3f, adjusted $p = 0.0278$, $R^2 = 0.3862$). Note that this metric actually represents the ratio of seasonal mean daily flow to the general mean of daily flow for a given river. Even though FDis was highest at sites where average flow is not associated with any particular season (low M_MDFM), these sites still had high values for mean daily flow in summer. Pearson correlation confirms a significant negative relationship between M_MDFM and MDFMDFSummer (Pearson's $r = -0.657$, $p = 0.008$) but not C_MDFM and MDFMDFSummer (Pearson's $r = -0.423$, $p = 0.1164$). Summer mean daily flow may have been inflated by exceptional periods where very high average flows occurred during summer. Mean daily flow in spring, conversely, was strongly positively correlated with M_MDFM (Pearson's $r = 0.8357$, $p = 0.0001$) and C_MDFM (Pearson's $r = 0.7839$, $p = 0.0005$), indicating that where mean daily flows in spring are high, this pattern is stable and consistent between years.

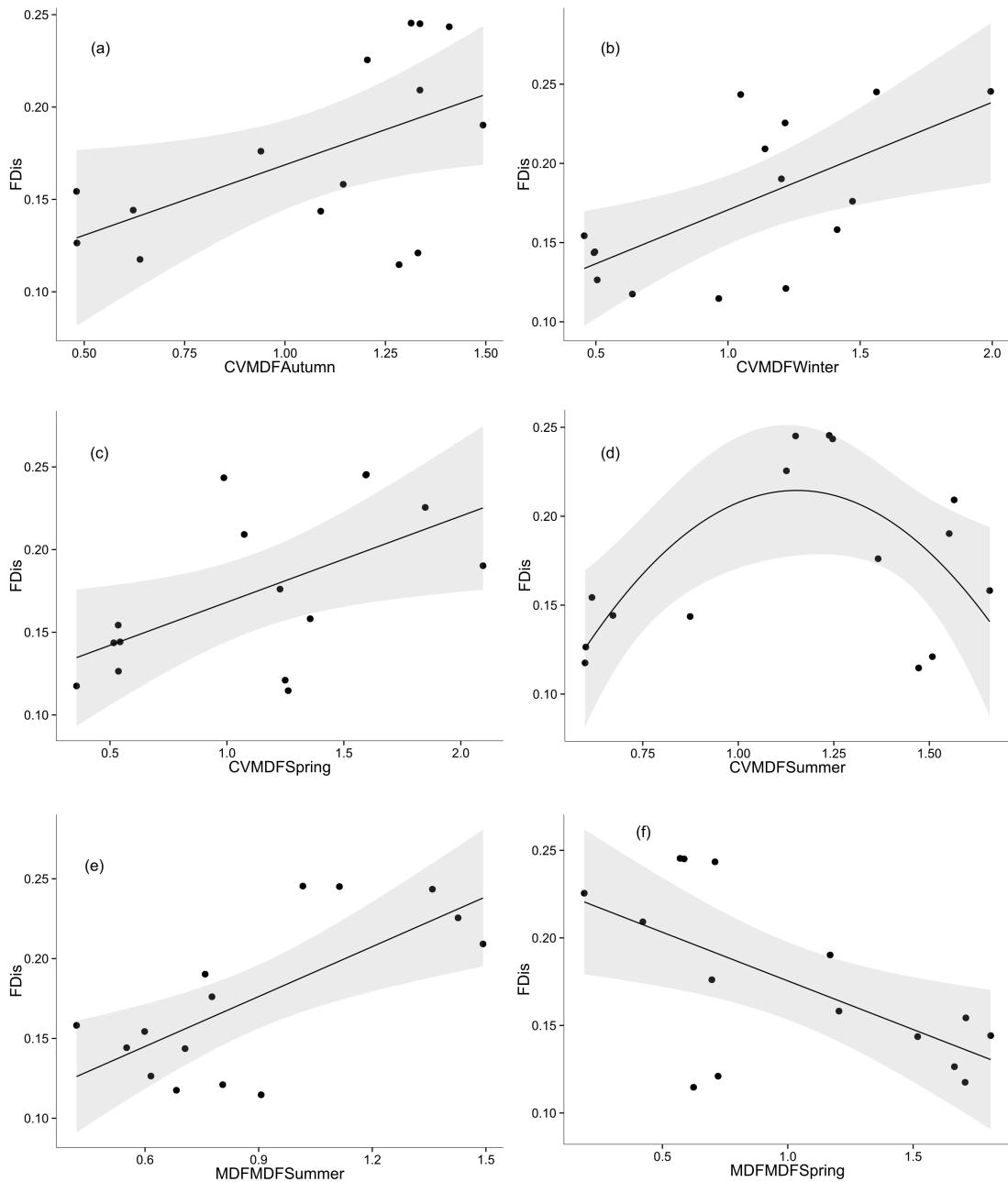


Figure 3.3: Relationships between FDis and hydrological metrics describing (a) variability in autumn mean daily flow, (b) variability in winter mean daily flow, (c) variability in spring mean daily flow, (d) variability in summer mean daily flow, (e) mean daily flow in summer, (f) mean daily flow in spring. Fitted lines depict ordinary least squares regression models. All models are linear fits except in (d), which is a quadratic fit. Shaded areas depict the smoothed 95 % confidence interval around the regression model. All relationships shown are significant. Units are shown in Tables Tables 1.1 and 1.2.

Comparisons with measures of taxonomic diversity

Across the species used in the functional diversity analysis (i.e. present at >1 % plot cover), FDis was independent of species richness ($p = 0.274$, $F(1,13) = 1.302$) and Simpkins diversity ($p = 0.513$, $F(1,13) = 0.454$) for species included in the functional diversity analysis, but significantly associated with species richness for the full set of 327 species ($p = 0.030$, $F(1,13) = 5.957$, $R^2 = 0.314$).

A minimal multiple regression model to explain functional diversity according to hydrology

We used an information theoretic procedure to select the best fitting, most parsimonious multiple regression model from the factorial set of possible models which included FDis as the dependent variable and the following independent variables: interannual variability in high flow frequency (CVAnnHSNum), interannual variability in high flow magnitude (CVAnnHSPeak) and mean daily flow during summer (MDFMDFSummer). This set of models is described in Table 1.3.

Table 3.3: Multiple regression models with associated fitting parameters. * in the model formula denotes both summation as well as interaction between variables. R^2 values have been adjusted for multiple regression for models using more than one variable. The optimal model according to $AICc$ is indicated by bold typeface.

#	<i>Model</i>	<i>adj. R^2</i>	<i>AICc</i>	<i>delta AIC</i>
1	$FDis \sim CVAnnHSNum$	0.296	-46.14	12.78
2	$FDis \sim CVAnnHSPeak$	0.577	-53.79	5.13
3	$FDis \sim MDFMDFSummer$	0.503	-51.37	7.56
4	$FDis \sim CVAnnHSNum + CVAnnHSPeak$	0.636	-54.52	4.40
5	$FDis \sim CVAnnHSNum + MDFMDFSummer$	0.681	-56.50	2.42
6	$FDis \sim CVAnnHSPeak + MDFMDFSummer$	0.561	-51.71	7.21
7	$FDis \sim CVAnnHSNum * CVAnnHSPeak$	0.655	-51.95	6.97
8	$FDis \sim CVAnnHSNum * MDFMDFSummer$	0.665	-52.40	6.53
9	$FDis \sim CVAnnHSPeak * MDFMDFSummer$	0.566	-48.54	10.39
10	$FDis \sim CVAnnHSNum + CVAnnHSPeak + MDFMDFSummer$	0.704	-54.25	4.68
11	$FDis \sim CVAnnHSNum * CVAnnHSPeak + MDFMDFSummer$	0.709	-50.14	8.79
12	$FDis \sim CVAnnHSNum + CVAnnHSPeak * MDFMDFSummer$	0.838	-58.92	0
13	$FDis \sim CVAnnHSNum * CVAnnHSPeak * MDFMDFSummer$	0.944	-48.62	10.30

Model 12 was determined to be the optimal model according to AICc. Models 4, 5 and 10 were close to optimal but offered lower explanatory power according to the adjusted R^2 of the model. Although Model 13 offered higher explanatory power, it was less parsimonious according to AICc and exhibited multicollinearity. Multicollinearity was determined not to be of importance for Model 12 according to variance inflation factor scores (all <3 on centred variables). All terms in Model 12 were individually significant; a full summary of the model is given in Table 1.4. Notably, the coefficient of the interaction term was negative, indicating a diminishing influence on FDis when values of CVAnnHSPeak and MDFMDFSummer are both high.

Table 3.4: Regression summary for Model 12. Beta values are regression coefficients (B) standardised by the standard deviation of the term.

	B	SE	beta	t	p
CVAnnHSNum	0.240	0.054	0.540	4.414	0.001
CVAnnHSPeak	0.071	0.026	0.498	2.773	0.020
MDFMDFSummer	0.074	0.024	0.506	3.056	0.012
CVAnnHSPeak * MDFMDFSummer	-0.190	0.060	-0.459	-3.186	0.001

Table 3.5: Partitioning of variance in FDis as explained by optimal hydrological and climatic models. The | symbol denotes controlled for; that is, variation explained non-redundantly by a fraction.

Combined fractions:	<i>df</i>	<i>adjusted R</i> ²
a + b (hydrology)	4	0.838
b + c (climate)	2	0.629
a + b + c (hydrology + climate)	6	0.854
Individual fractions:		
a (hydrology — climate)	4	0.226
b (shared variation)	0	0.612
c (climate — hydrology)	2	0.016
d (unexplained variation)		0.46

Do climatic or edaphic conditions explain variation in FDis that is unaccounted for by hydrological metrics?

Of the 19 climatic variables examined, a number exhibited statistically significant univariate relationships with FDis; the quadratic function of isothermality was determined by AICc to be the optimal regression model. Of the 12 edaphic variables examined, no significant univariate relationships with FDis were found. Variance partitioning showed that while the dominant fraction of variation explained by the two models was shared (0.612), the climatic model explained a minimal amount of non-redundant information (0.016) compared with the hydrological model (0.226), indicating a dominant influence of hydrological flow regime on functional dispersion in this study. Table 1.5 shows the partition table generated from this analysis.

3.4 Discussion

We surveyed vegetation communities along partly confined river systems across south-eastern Australia and found that functional diversity, as characterised by functional dispersion, exhibited strong relationships with local patterns of hydrology. To our knowledge this is the first study to examine relationships between hydrological conditions and the diversity of ecological strategies within riparian vegetation communities using multiple quantitative functional traits. The overarching pattern across these relationships can be summarised as heterogeneous flows foster heterogeneous communities.

This pattern is consistent with existing understanding of the processes that generate and maintain biological diversity in the riparian environment. Briefly stated, this paradigm holds that riparian biodiversity is a function of landscape complexity generated by hydrogeomorphic processes, overlain by feedback interactions between these processes and biotic components of the riparian environment

(Bornette et al., 2008; Corenblit et al., 2007; Palmer and Poff, 1997; Tabacchi et al., 1998). Because we surveyed geomorphically homogeneous sections of sloping bank, our argument is presented under the assumption that functional diversity is a property of riparian communities at the reach scale. Influx of species from more physically complex adjacent patches, then, is responsible for the diversity we observed on these geomorphologically homogeneous sloping bank sections.

The sites surveyed in this study spanned a spectrum of flooding intensity: the 20-year average return interval (ARI) flood ranged from 18 times the mean daily flow to 210 times the mean daily flow. Higher magnitude flow events are more likely to be geomorphically effective in partly confined river systems (Huang and Niemann, 2006). The strong positive relationship between functional diversity and 20-year ARI flood magnitude supports the supposition that disturbance retards competitive exclusion as a diversity limiting process *sensu* Huston (1979). Notably, no significant relationships were found between functional diversity and metrics describing mean high flow conditions, whereas metrics describing variability had high explanatory power. Interannual variability in high flow magnitude showed the strongest relationship with functional diversity in this study. If a causal relationship exists, it could be because the average high flow magnitude determines what proportion (in terms of elevation above the main channel) of the riparian zone experiences flooding in a given year. Variability in high flow magnitude, combined with geomorphic heterogeneity, will produce variability in the time since last inundation (without significant disturbance), or combined inundation and disturbance, for a given patch of vegetation. Since flood flows also function as an important dispersal pathway for propagules (Merritt et al., 2010), variability in high flow magnitude should influence recruitment processes in a similar manner. Likewise, variability in the frequency of flood flows also results in variable time since last inundation or disturbance. Interannual variability in flood rise and fall rates was also positively associated with functional diversity. Overall, the combination of occasional high

intensity flooding disturbance with year-to-year variability in patterning of high flow events results in a heterogeneous patch mosaic. This environmental heterogeneity provides a broad range of niches, facilitating the success of a diversity of ecological strategies (Bornette et al., 2008).

We can extend this framework to account for the observed relationships between functional diversity and variability in seasonal water availability. Our sites spanned a gradient of flow seasonality: at one end, rivers exhibited weak but stable patterns of seasonality; at the other, rivers were characterised by high interannual variability and modal, seasonally inconsistent distributions of flow. Once again, communities with higher functional diversity tended to be located towards the variable end of the spectrum. South-eastern Australian plants do exhibit characteristic species-level responses to seasonality, although there is no general coordination of growth and reproduction phenologies as in the northern hemisphere (Ford et al., 1979). Flowering times within the Myrtaceae (a dominant family in riparian plant communities of south-eastern Australia) are often staggered where species are sympatric (Beardsell et al., 1993), and growth and reproduction of riparian plants are commonly associated with the arrival of favourable conditions (Robertson, 2001; Siebentritt et al., 2004; Woolfrey and Ladd, 2001). High coefficients of variation in seasonal mean daily flows may therefore act to temporarily provide species with favourable conditions according to their seasonal biology.

Exceptions to these patterns included the quadratic fit for variability in summer mean daily flows, with high values being associated with a reduction in functional diversity, and mean daily flow for summer, which was positively associated with functional diversity and broke the trend of associations with seasonal means being either non-significant or negative. A meta-analysis of the effect of drought on riparian vegetation showed reduced species richness and a shift towards drought-tolerant species following climate-induced increases in the intensity and duration of drought, an effect that was exacerbated by high temperatures (Garssen et al.,

2014). Higher temperatures in the absence of drought were associated with higher rates of primary production. Higher mean daily flows in summer, then, potentially alleviate the water stress induced by hot weather while stimulating plant growth. We did investigate whether sites at subtropical latitudes simply had higher functional diversity than temperate sites, according to well-known latitudinal patterns of species richness (Willig et al., 2003), and found no relationship between latitude and FDis (data not presented).

It was notable that while FDis is statistically independent of species richness, in this study functional dispersion was significantly associated with total species richness (as opposed to richness of the set of species used in the FDis analysis that were present at >1 % abundance). A broad species pool therefore appears to facilitate higher functional dispersion within the dominant flora of a community, even though the richness of the dominant group of species does not necessarily determine functional diversity. It is difficult to interpret this finding, however, as adding data for rare species to the analysis would necessarily render the new value of FDis independent of total species richness.

The multiple regression model selected according to AICc explained a high proportion of variation in FDis. This model described functional diversity as a function of variability in flood frequency and magnitude, and in summer mean daily flow. The combination of flow heterogeneity with extra watering during summer appears to provide optimal conditions for functionally diverse communities. The coefficient of the interaction term between variability in flood magnitude and summer mean daily flow was significant but negative, indicating that the additive effect is subject to diminishing returns at high values of both terms. The key finding here is that these three metrics of hydrological conditions are able to account for most of the variation in FDis; data on climatic conditions and edaphic properties add very little non-redundant information to our model. We used traits in our analysis that capture a broad spectrum of ecological strategies, rather than

solely traits associated with riparian specialist strategies, which might be expected to bias results towards flow response. We caveat, however, that this model does not account for the effect of plot-scale geomorphic variability on diversity, as this was controlled for in the site selection process.

Two sites had anomalous values for FDis that do not fit within this conceptual model of disturbance and flow variability providing high niche heterogeneity. These sites experience highly variable flows but had low functional diversity. We experimentally adjusted the abundances of dominant species at these sites and found that the low values for FDis appear to result from dominance of a single species at each site (the medium sized tree *Acmena smithii* at Mammy Johnsons Creek, and the liana *Ripogonum album* at Jilliby Creek). These sites may represent cases in which species with variability specialist strategies have become dominant. *Acmena smithii* has a relatively large seed and is shade tolerant (Melick, 1990), but once established, develops a lignotuber and is highly resistant to drought and disturbance (Ashton and Frankenberg, 1976). With respect to *Ripogonum album*, there is evidence to suggest that abundance of lianas may be associated with disturbance (Laurance and Pérez-Salicrup, 2001) and that lianas have a competitive advantage over trees in dry conditions (Cai et al., 2009; Swaine and Grace, 2007) (but see Nepstad et al. (2007)).

Our survey covered approximately half of the range of hydrological variability present within the Australian continent; much of the lower range and middle range was captured, but highly variable dryland systems were not included (Peel et al., 2004). Our results mostly show monotonic relationships between FDis and hydrological heterogeneity, and as such do not support intermediate disturbance associated patterns found in other studies of taxonomic (Bendix, 1997; Bendix and Hupp, 2000; Corenblit et al., 2007; Lite et al., 2005) and functional diversity (Biswas and Mallik, 2010) of riparian plant communities. This finding is consistent with the assertion of Mouillot et al. (2013) that metrics of functional diversity

should show monotonic rather than unimodal relationships with disturbance intensity. It is difficult to be conclusive on this point, however, as it is possible that we have found only the ascending half of a unimodal curve. To this end, it would be useful to survey communities that experience more extreme hydrologies, such as those in Australias arid regions or the monsoon tropics. Disturbance intensity and hydrological heterogeneity may not necessarily be connected in such systems. Arid zone rivers characterised by all or nothing flow regimes may not experience the moderate flood events that generate and maintain diversity at the patch scale; for monsoonal rivers, disturbance may be similarly intense, but seasonal and inter-annual patterns of flow are relatively predictable (Kennard et al., 2010). In large tropical riverscapes, hydrological rhythmicity (i.e. the opposite of hydrological heterogeneity) has in fact been associated with greater richness of fish and bird taxa, and greater production in riparian forests (Jardine et al., 2015).

Unlike anthropogenic disturbances associated with agricultural land use, which have been shown to be associated with lower functional richness (Pakeman, 2011) and lower functional redundancy (Laliberté and Legendre, 2010), recurring hydrological disturbance appears to promote riparian plant functional diversity in this study. A similar response to natural fire regimes in the Patagonian steppe has also been observed (Sottile et al., 2015). It seems reasonable to assume that the generative effect of natural disturbance on niche heterogeneity is not reproduced by typical anthropogenic disturbances.

Our findings are important from an applied river management and conservation perspective. Widespread anthropogenic river modification has altered the hydrology of river systems throughout the world, and the changing climate has the potential to exacerbate the impacts of flow modification as well as affecting unaltered river systems. A key issue with river modification is that it reduces flow heterogeneity. Dams flatten flood hydrographs (and peaks), alter seasonality and increase predictability of flows (Graf, 2006; Singer, 2007). These alterations to flow

have terrestrialised riparian areas and wetlands, reducing functional diversity and facilitating invasion by exotic terrestrial weed species (Catford et al., 2011). Dams also interrupt hydrochorous transport of propagules (Merritt et al., 2010), such that flood flows below dams may cause net removal of propagule material from fluvial substrates, rather than deposition. When designing environmental flows (e.g. Howell and Benson (2000)), river managers typically consider magnitude, frequency and seasonality of flows. The findings in this paper agree with recent suggestions (Naiman et al., 2008) that managers should also attempt to simulate flow regime variability in their designed flows.

Future runoff predictions are regionally specific but similarly include changes to total discharge, flow seasonality and flow variability. In regions with projected increases in climatic variability, changes to the prevalence, intensity and timing of extreme flooding or drought events can be expected (Hennessy et al., 2008). Reductions in mean summer precipitation have already occurred over large areas of Australia, coinciding with a warming of 0.4–0.7 °C since 1950 (Hennessy et al., 2007). Lower average flows during hotter summers may stress riparian communities and constrain functional dispersion. Alternatively, greater climatic variability associated with future climates (Hennessy et al., 2008) may promote hydrological heterogeneity in regions that were previously associated with more stable flow conditions. This may result in opening of niche space to favour opportunistic ecological strategies and promote invasion by exotic species.

Restoring functional diversity to pre-degradation levels may be a useful goal for riparian rehabilitation efforts along regulated or otherwise degraded river reaches. High functional diversity communities encompass a broad range of ecological strategies and should have a greater capacity to adapt to environmental change (Standish et al., 2014; Tilman et al., 1997). By working to restore functional diversity along impacted river systems, managers may increase the likelihood that riparian communities will be able to maintain critical ecosystem functions under future

climates.

The identification of such a strong relationship between environmental variability and functional diversity has significance for lotic ecology (Palmer and Poff, 1997), as well as ecology in general. Our study emphasises the importance of flooding disturbance and hydrological heterogeneity as drivers of functional diversity in riparian plant communities. These findings should be applicable to river systems in other regions and biomes characterised by moderate hydrological variability, given the profound influence of hydrology in shaping the structure of fluvial landscapes and determining the ecological strategies of plants that are able to persist and thrive in the riparian environment. Comparisons with datasets from regions with harsh but highly predictable seasonal patterns of hydrology, for example monsoonal or nival regimes, are needed to confirm this assertion. In the south-eastern Australian context, at least, alterations to flow variability and disturbance regimes by dams and the changing climate may have significant consequences for the diversity and functioning of riparian vegetation communities.

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Data availability

Trait data for all species are available at <http://onlinelibrary.wiley.com/doi/10.1111/fwb.12649/suppinfo>.

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4 Environmental drivers of taxonomic and functional diversity of riparian plant communities in a modified landscape

Abstract

Human populations have a profound impact on the biodiversity of riparian plant communities, and understanding the nature and mechanisms of these impacts is central to river conservation and rehabilitation. Reduction of the inherent environmental heterogeneity in riverscapes by flow modification and land-use intensification is thought to cause degradation of riparian communities.

We sampled vegetation and assembled environmental data for 20 river reaches in south-east Queensland, Australia. Plant functional trait data collated from online databases and the ecological literature were used to characterise diversity in terms of ecological strategy and functional effects. Our aim was to tease apart the environmental factors associated with taxonomic and functional trait diversity and the abundance of exotic species in riparian plant communities. We specifically tested the hypotheses that environmental heterogeneity is the dominant control on taxonomic and functional trait diversity, and that flow modification and land use intensification results in reduced diversity and promotes invasion by exotic plants.

We found flow regime generally to be a useful predictor of diversity, but contrary to our expectations, hydrological metrics of environmental heterogeneity had limited explanatory power. Rivers which experienced seasonal, but temporally consistent flow regimes supported the most species rich communities, and modification of flow regime towards temporal consistency was also associated with greater species richness. Also against expectation, proportional abundance of exotic species increased with hydrological heterogeneity. Functional diversity metrics showed unimodal relationships with some metrics of hydrological heterogeneity, but were only weakly predicted by flow modification and showed no relationship with land-use intensity.

Our observations suggest that temporal consistency in provision of resources and energy by stream flows may be more important than environmental heterogeneity.

geneity in determining patterns of riparian plant diversity in south-east Queensland.

Keywords

Riparian, functional diversity, flow regime, environmental heterogeneity, land use, flow modification, dams

4.1 Introduction

Riparian ecosystems are highly biodiverse, provide important ecosystem services and are the focus of substantial management effort worldwide (Naiman et al., 1993; Palmer et al., 2009). Rapid development of catchments has changed fundamental processes which create and maintain biodiversity within riparian landscapes (Nilsson and Svedmark, 2002), and as such, riparian management often takes place within this context of catchment modification. Wholesale vegetation clearing notwithstanding, regulation of river flow regimes, catchment land-use change and invasion by exotic plant species are considered key drivers of ecological change (Cooper et al., 2013; Nilsson and Berggren, 2000; Stromberg et al., 2007). Maintaining indigenous plant assemblages and their associated ecosystem functions, and controlling invasive species are central goals in river rehabilitation and riparian conservation (Richardson et al., 2007).

Environmental heterogeneity is one of the major factors influencing spatial patterns of species diversity (Costanza et al., 2011; Stein et al., 2014). According to classical niche-based theories of species co-existence (Chesson, 2000), where each niche is associated with an optimal ecological strategy, structural complexity and steep resource and energy gradients between patches promote diversity by extending niche space and reducing niche overlap. More recently, niches have been characterised in trait-space: niches and their interrelationships are described by patterns of clustering of functional traits (any morphological, physiological or phenological feature measurable at the individual level (Violle et al., 2007)), the values of which are optimised to a given set of environmental conditions (Adler et al., 2013). Thus the distribution of functional traits within a community can be expected to be patterned by the degree of heterogeneity in environmental conditions present. Describing communities in traitspace dissolves species distinctions and emphasises ecological strategies: what species do within their community and

how they do it. In turn, metrics of diversity derived from functional traits provide a useful complement to taxonomic diversity metrics, as they allow a mechanistic characterisation of biodiversity-ecosystem functioning relationships (Hillebrand and Matthiessen, 2009).

Much of the riparian ecology literature identifies fluvial hydrology and geomorphology as the dominant abiotic force structuring riparian ecosystems (Bendix and Hupp, 2000; Poff et al., 1997). The spatial and temporal heterogeneity inherent in fluvial processes is considered largely responsible for the complex biogeomorphology of riparian environments (Corenblit et al., 2007; Naiman et al., 2005). Sediments are scoured and deposited, some plants are washed away while others are watered; organic matter and woody debris moves through the system and propagules are dispersed. The spatial distribution of these processes within the fluvial landscape is contingent on the magnitude and frequency of the flow events that drive erosion and deposition processes, and the resultant morphology and sedimentology of fluvial landforms produced (Fryirs and Brierley, 2012). This subsequently determines the extent to which different surfaces/landforms are inundated under a range of different flow conditions (Hughes, 1997). Temporal variability in flooding patterns adds a further layer of complexity by influencing the success of plant ecological strategies for a given patch. More frequently flooded patches are likely to support graminoids and rheophytes, while succession is likely to proceed further on patches which are less frequently disturbed (Corenblit et al., 2009). Soil moisture conditions are also strongly driven by fluvial hydrology in riparian environments, with further implications for plant community assembly (Nilsson and Svedmark, 2002).

Intermediate disturbance-type unimodal relationships between fluvial disturbance and species richness are commonly described, e.g. Bendix (1997), Bendix and Hupp (2000), Lite et al. (2005), Corenblit et al. (2007). Unimodal relationships between environmental heterogeneity and diversity are also hypothesised to

occur as a result of microfragmentation at high levels of heterogeneity (Tamme et al., 2010). Previous work on riparian plant communities has shown strong positive links between functional trait diversity and flow heterogeneity (Lawson et al., 2015b): relationships between functional dispersion and metrics of flow variability were mostly monotonic, with the exception of interannual variability in summertime flows, which showed a unimodal relationship.

Over half the world's large river systems and countless smaller watercourses are affected by dams, weirs and diversions (Nilsson and Berggren, 2000; Nilsson et al., 2005). While the effects of individual dams tend to be idiosyncratic (Mackay et al., 2014), flow regulation typically homogenises hydrographs by removing small-moderate flows, reducing flood peaks, altering seasonality and increasing predictability of flows (Graf, 2006; Singer, 2007). According to the magnitude and form of change to the flow regime, flow modification may result in reduced niche complexity in downstream riparian zones (Lloyd et al., 2004). In a recent comprehensive review of ecological responses to flow modification, Poff and Zimmerman (2010) found that 152 out of 165 studies reported decreased values for recorded ecological metrics. Invasion by exotic plants in response to flood reduction often results in extensive shifts in riparian plant assemblages and reduction of both taxonomic and functional diversity (Catford et al., 2011; Merritt and Poff, 2010; Stokes, 2008). Terrestrialisation of riparian plant communities has also been described in systems where low flow conditions dominate (Poff and Zimmerman, 2010).

Human land use also has a profound effect on diversity and functioning in natural ecosystems. Land transformation for agricultural and silvicultural production, urbanisation and resulting habitat fragmentation have resulted in extensive losses of both alpha and beta diversity (Gerstner et al., 2014; Vitousek et al., 1997). This effect is often exacerbated by the entourage of exotic species brought by humans into the landscapes we occupy (Vitousek et al., 1996), with local extirpation of indigenous species (Davis, 2003) and stifling of successional processes (Catford

et al., 2012) being common outcomes of plant invasion. A recent multi-biome meta-analysis found that land-use intensification was associated with diminished functional redundancy and ability to respond to disturbance (Laliberté and Legendre, 2010).

Environmental homogenisation of riparian landscapes by this triad of flow modification, land-use change and exotic invasion therefore has profound implications for riparian biodiversity. The environmental flows concept posits that given a solid understanding of the hydroecology of a given riparian assemblage, restoration of riparian ecosystems on regulated rivers can be facilitated by releasing engineered flows which support indigenous plant assemblages (Poff et al., 2010). The success of such endeavours in modified landscapes, however, is likely to be contingent on the relative contribution of flow modification and other pressures on riparian ecosystems. Functional trait approaches to characterising diversity provide the means to investigate the independent and combined effects of these pressures on the functional structure of riparian plant assemblages.

To this end, we used a functional trait diversity approach to examine vegetation responses to hydrological alteration in a modified landscape in south-east Queensland, Australia. Our aim was to tease apart the environmental factors associated with taxonomic and functional diversity and the abundance of exotic species in riparian plant communities. A set of hypotheses about environmental heterogeneity diversity relationships guided our approach: 1a.) species richness and functional diversity increase and abundance of exotic species decreases monotonically with increasing hydrological heterogeneity; 1b.) species richness, functional diversity and abundance of exotic species show unimodal relationships with hydrological heterogeneity; 2.) species richness and functional diversity decrease and abundance of exotic species increases along gradients of increasing flow modification and catchment land-use intensity.

4.2 Regional setting and hydrology

The study was conducted across seven catchments in coastal south-east Queensland, Australia (25.82 to 28.23 °S, and 152.35 to 153.42 °E, see Fig. 1.1). The dominant land-use in the region is agriculture, with approximately 40 % of the area under livestock grazing, and 4 % used for cropping. Urbanisation is also extensive, particularly along the coast. Native vegetation within conservation estate or state forest comprises 20 % of the study area, and additional native vegetation remnants are common in steep terrain. This study area has a subtropical climate, and is influenced by both tropical and temperate weather patterns. Little variation in temperature is present throughout the region, although mean annual rainfall varies considerably, from 800 mm in the west to 1400 mm in the eastern coastal catchments (Bureau of Meteorology 2009). The majority of rainfall is associated with summer thunderstorms between January and March, although southerly weather systems during autumn and winter are also responsible for a substantial amount of precipitation.

Precipitation patterns are associated with high year-on-year variability, and river discharge regimes in the region are typically unpredictable, with high coefficients of variation in mean daily flow (Kennard et al., 2010; Rustomji et al., 2009). Substantial hydrological variability is represented across coastal south-east Queensland. Four of the twelve hydrological classes identified on the Australian continent by Kennard et al. (2010) are present in the area: perennial, stable baseflow; perennial, unpredictable baseflow; intermittent, unpredictable; and highly intermittent, unpredictable summer dominated.

River flow regimes throughout the study region are modified by dams, weirs, intra- and inter-basin water transfer, and unsupplemented water extraction. The majority of the dams were constructed by the mid-1970s and have a maximum capacity of less than 50,000 ML. Two substantially larger dams (Wivenhoe Dam

1,150,000 ML and Hinze Dam 165,000 ML) in the area were constructed during the 1980s. Mackay et al. (2014) compared historic daily discharge data with modelled predevelopment discharge data and found that flow modification by structures and diversions in south-east Queensland is diverse and system specific. Reduced flow variability is prevalent, and while increased perenniability in drier systems and altered low spell duration are also common, few other generalisations can be made about the effects of regulation on streamflows in the region (Mackay et al., 2014).

4.3 Methods

The current study is an extension of a previous larger study (Arthington et al., 2012); the report describing the original study provides extensive detail not included here. Except where specified, all statistical analyses were performed using the R statistical programming environment (R Core Team, 2015), and statistical significance was thresholded at alpha = 0.05.

Site selection and vegetation sampling

Riparian vegetation was surveyed between August and October in 2008, 2009 and 2010. Twenty river reaches were selected to sample the range of flow regime classes determined by a regional classification of flow regimes (see Mackay et al., 2014). Proximity to flow monitoring gauges with an associated recording history of >25 years was of primary importance. Duplicate surveys were made along each river reach as close as possible to the flow monitoring station (to give a total of 40 sites), but separated by at least 2 km. Sampling sites required 100 continuous metres of relatively intact riparian vegetation, which was not subjected to regular burning and had not been cleared in at least 20 - 30 years. Ideally sites were not currently grazed, although this restriction was relaxed somewhat given the extensive pastoral land use throughout the region.

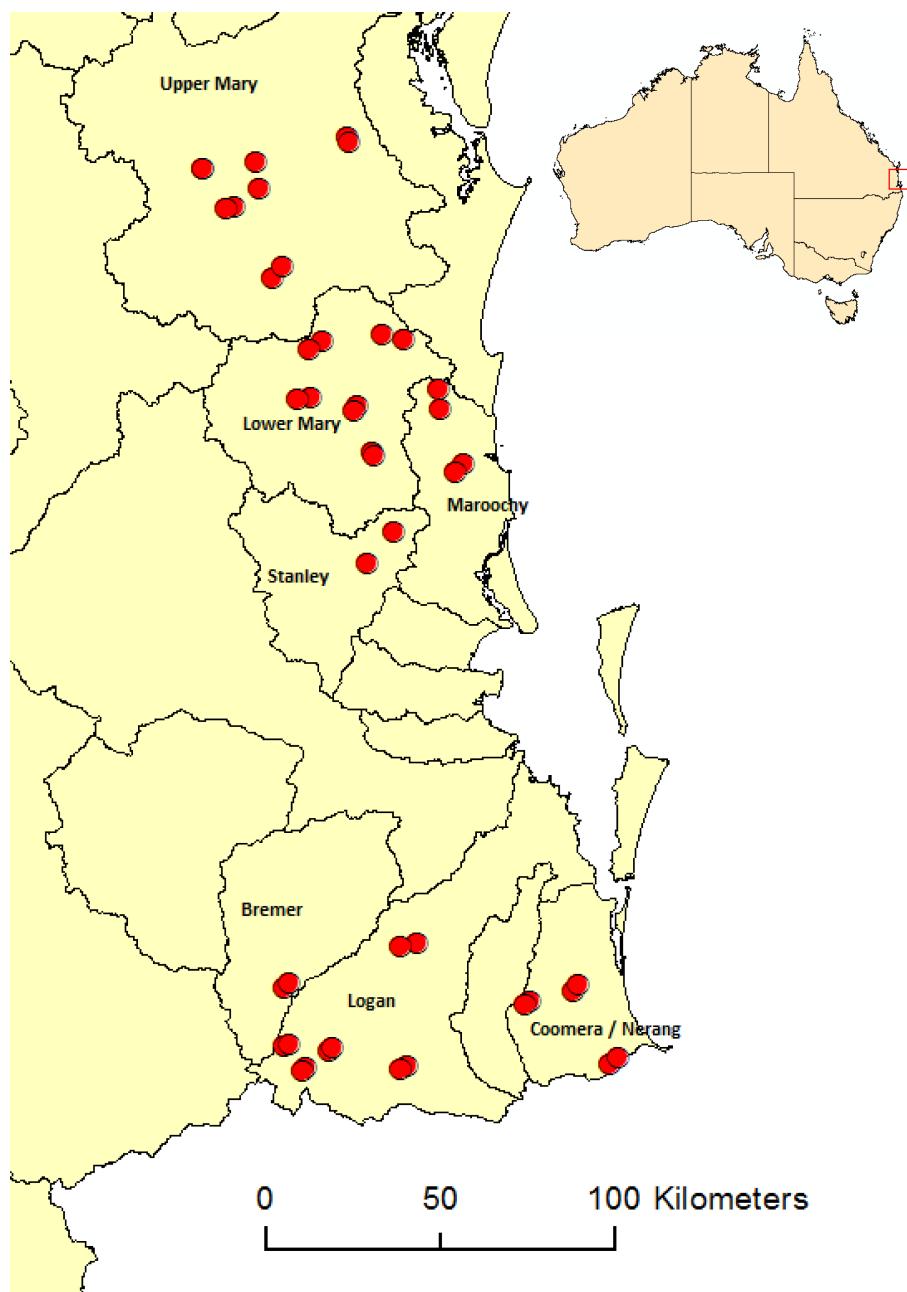


Figure 4.1: Study area (inset), study catchments and locations of field sites in south-eastern Queensland.

Three transects were randomly placed at each site, running perpendicular to the river. Additional transects were conducted at three sites, where low vegetation densities occurred. Transects extended from the waters edge to the macrochannel bank, or to a maximum of 50 m from the waters edge. A standard sampling area was not used due to variability in vegetation structure, channel landforms and

adjacent land uses; sampling area was controlled for in subsequent analyses. Site sampling areas were typically greater than 400 m² but ranged from 260 - 1013 m². All trees, shrubs, ferns rushes, and sedges within a 5 m band centred on the transect line were identified and counted. Species identifications were confirmed by the Queensland Herbarium.

Describing stream hydrology and quantifying flow regulation

Daily discharge data for each reach were obtained from Queensland Government Department of Natural Resources and Mines (DNRM) Water Monitoring Data Portal (<https://www.dnrm.qld.gov.au/water/water-monitoring-and-data/portal>). 35 year time series spanning 1975–2009 were obtained where possible. Missing data were infilled using the Time Series Manager module in River Analysis Package (Marsh et al., 2003), using linear interpolation for periods less than 15 days, or multiple regression using data from adjacent stream gauges. One site (Reynolds Creek) had substantial periods of missing data which could not be infilled by multiple regression, as the flow at this gauge is altered by Moogerah Dam. The record for this site was truncated to exclude the periods where data was missing. The shortest remaining period (34 days) was infilled by linear interpolation. Flow data for one site (Obi Obi Creek at Kidaman) was obtained from Water Quality Accounting (Queensland DNRM) as modelled gauge data derived from a calibration model for the Mary River catchment.

River Analysis Package was used to generate a set of 18 ecologically relevant hydrological metrics for each site, describing mean and interannual variability in the frequency, magnitude and duration and seasonal timing of high and low flow conditions. Table 1.1 provides definitions of these flow regime characteristics and describes their ecological importance and contribution to environmental heterogeneity. As a number of these metrics exhibited collinearity, we have included a

principal components analysis of this data in Appendix 3a. Metrics of flow magnitude which had units ML / day were standardised by mean daily flow to allow for comparison between different river channel sizes. These metrics therefore represent ratios of flow magnitude to mean daily flow.

The extent of flow regulation at a given gauge site was characterised by the percentage deviation of each metric from the same metric generated using modelled pre-development flow data. These modelled pre-development daily discharge data were obtained from a generic integrated water quantity and quality simulation model (IQQM) developed for the region (Simons et al., 1996). IQQM data were available only for the period up to 1999, so data from the timeframe 1975-1999 were used for comparison.

Table 4.1: Hydrological variables used as metrics of fluvially induced environmental heterogeneity in the riparian zone (adapted from (Lawson et al., 2015b))

<i>Variable</i>	<i>Abbreviation</i>	<i>Units</i>	<i>Description</i>
Frequency, magnitude and duration of floods and dry spells			
Mean magnitude of high spells *	HSPeak	dimensionless	
Mean magnitude of low spells *	LSPeak	dimensionless	
CV of all years' mean high spell magnitude	CVAnnHSPeak	dimensionless	
CV of all years' mean low spell magnitude	CVAnnLSPeak	dimensionless	
Mean of all years' number of high spells	MDFAnnHSNum	year ⁻¹	
Mean of all years' number of low spells	MDFAnnLSNum	year ⁻¹	
CV of all years' number of high spells	CVAnnHSNum	dimensionless	Together, these metrics characterise the frequency, magnitude and duration of floods and dry spells. Extreme low or high flows contribute to spatial environmental heterogeneity, in that their effects (flooding disturbance, soil moisture stress) are spatially variable throughout the riparian landscape. High flow spells are periods of flow above the 95th percentile; low flow spells are periods of flow below the 5th percentile.
CV of all years' number of low spells	CVAnnLSNum	dimensionless	HSPeak and LSPeak describes the mean magnitude of highest and lowest flows during high and low spells throughout the record, respectively. MDFAnnHSNum and MDFAnnLSNum describe the mean annual frequency of high and low spells. HSMeanDur and LSMeanDur describe how long flow events last.
High spell mean duration	HSMeanDur	days	
Low spell mean duration	LSMeanDur	days	
CV of all years' high spell mean duration	HSMeanDur	dimensionless	Coefficients of variation (CV) of these metrics between years characterise temporal heterogeneity in flow patterns.
CV of all years' low spell mean duration	LSMeanDur	dimensionless	

<i>Variable</i>	<i>Abbreviation</i>	<i>Units</i>	<i>Description</i>
Baseflow index			
Baseflow index	BFI	dimensionless	Baseflow index is calculated using the ratio of flow during average conditions to total flow. It is a useful metric of perenniability of water availability, in that it is maximised when average flow conditions dominate, and minimised when total flow is dominated by above average flow events. Thus higher baseflow systems experience more homogeneous flows.
CV of all year's baseflow index	CVAnnBFI	dimensionless	
Colwell's indices			
Constancy of monthly minimum daily flow	C_MinM	dimensionless	Colwell's indices provide a measure of the seasonal predictability of flow events, and as such are a direct measure of temporal heterogeneity of flow patterns.
Contingency of monthly minimum daily flow	M_MinM	dimensionless	
Constancy based on monthly maximum daily flow	C_MaxM	dimensionless	Constancy (C) measures uniformity of flow across seasons, and is maximised when flow conditions do not differ between seasons.
Contingency based on monthly maximum daily flow	M_MaxM	dimensionless	Contingency (M) is a measure of interannual uniformity in seasonal flow patterns, and is maximized when seasonal patterns of flow are consistent between years. We generated Colwell's indices for both minimum and maximum flows conditions.
Flow seasonality			
Average mean daily dry season flow *	MDFMDFDry	dimensionless	These metrics describe the average magnitude and temporal variability in mean daily flows for each season (dry = May to October, wet = November to April). Averages and coefficients of variation are calculated across yearly means. Seasonal average mean daily flows were standardised by overall mean daily flow, so actually represent the ratio of mean daily flow in a given season to the total mean daily flow.
Average mean daily wet season flow *	MDFMDFWet	dimensionless	
CV of mean daily dry season flow	CVMDFDry	dimensionless	
CV of mean daily dry season flow	CVMDFWet	dimensionless	

Other environmental variables

Data on upstream land use were obtained via the Queensland Land Use Mapping Program (QLUMP) and dataset (Witte et al., 2006). These data were generated from surveys conducted in 1999 and 2006. Land use was categorised according to the Australian Land use and Management Classification version 6 (BRS, 2002), which differentiates conservation and low impact land uses from intensive land uses. Percentages of upstream land use were calculated as: production from relatively natural environments (forestry, grazing natural vegetation), dryland agriculture and plantations (e.g. cropping, horticulture, grazing pasture), irrigated agriculture (e.g. irrigated cropping, horticulture), conservation and natural environments (e.g. national park) and intensive uses (e.g. residential and industrial uses). We then used inverse distance weighting to weight each land use according to its proximity to the stream, following Petersen et al. (2010).

Climate data were obtained from eMast/TERN, at a resolution of 0.01 degrees (Hutchinson et al., 2014). Bioclimatic variables representing annual trends, seasonality and extremes were calculated following the BIOCLIM framework (Busby, 1991). The resulting set of 19 climate variables were strongly collinear, conse-

quently PCA was used to identify a subset of six variables which represented over 90 % of the variation in the data. Soil data were obtained from the CSIRO Soil and Landscape Grid of Australia, at a resolution of 3 arc seconds (~ 3 m) (Rossel et al., 2014a,b,c,d,e,f,g,h,i,j,k; Wilford et al., 2014).

Trait selection and dataset assembly

We assembled a dataset of six continuous (specific leaf area, leaf area, maximum canopy height, seed mass, wood density and flowering duration) and one categorical (growth form) functional traits with which to calculate functional diversity. These traits collectively describe central trade-offs associated with ecological strategies of riparian plants (functional responses), as well as flow-on effects of species on ecosystem functioning (functional effects). Table 1.2 provides further description of the utility of each of these traits in characterising the functional ecology of riparian vegetation communities.

Data was taken from published literature, private and published trait datasets, and Australian flora texts. Substantial contributions were taken from the following sources: (Fonseca et al., 2000; Gallagher and Leishman, 2012; Gleason et al., 2012; KEW, 2015; Kooyman et al., 2013; PlantNET, 2015; Wright et al., 2000; Zanne et al., 2009) as well as from Ian Wright (pers. comm.) and Cassandra James (pers. comm.). Where multiple records for a trait were found, values were removed if they were measured at sites with an environment substantially different from south east Queensland. With the exception of maximum height, for which the highest value was used, the remaining values were averaged to provide a single value for each species-trait combination. Not all species-trait combinations could be assigned data, so to reduce biases associated with analyses of incomplete trait datasets (Penone et al., 2014), only species with fewer than 3 missing trait values (174 / 260) were retained for the analysis. The remaining missing values were

imputed using a non-parametric random forests approach (missForest package for R) (Stekhoven and Buhlmann, 2012). Dataset density information can be found in Appendix 3a.

Table 4.2: Rationale for selection of functional response and effect traits as descriptors of riparian plant community functional diversity.

<i>Trait</i>	<i>Definition</i>	<i>Functional responses & inherent trade-offs</i>	<i>Functional effects</i>
Growth form	Categorical description of morphology: tree, shrub, woody climber, herbaceous climber, graminoid, herb.	Differential responses to mechanical and biochemical stresses associated with flooding; different strategies for coping with drought and heat stress.	Differential biogeomorphic effects on surface roughness, sediment deposition and fluvial landform cohesion.
Specific leaf area (SLA)	Ratio of one-sided leaf area to oven dry mass (cm^2 / g).	SLA is associated with leaf construction cost, photosynthetic rate and carbon : nitrogen economics. Indicator of ecological strategy under favourable vs. stressful conditions (Wright et al., 2004).	Affects ecosystem productivity and nutrient recycling (Wright et al., 2004).
Leaf area	One-sided leaf area (cm^2).	Shade tolerance (larger leaves) vs. enhanced thermal regulation ability in hot, dry conditions (smaller leaves) (Cornelissen et al., 2003).	May influence flow resistance of vegetation (and therefore fluvial erosion / deposition) when inundated.
Maximum canopy height	Height above ground of apical meristem (m).	Affects ability to tolerate mechanical disturbances such as flooding and maintain xylem integrity in dry conditions (Westoby and Wright, 2006).	Determines coarse physical structure of plant community. Surrogate for competitive ability: taller plants receive more light but must construct and maintain support structures (Falster, 2006).
Seed mass	Combined mass of the seed coat, endosperm and embryo (g). Excludes dispersal structures.	Larger seed mass confers ability to establish in unfavourable conditions (Leishman et al., 2000). Also related to seed buoyancy (Carthey et al., 2015).	Seeds may be an important food source for animals.

<i>Trait</i>	<i>Definition</i>	<i>Functional responses & inherent trade-offs</i>	<i>Functional effects</i>
Wood density	Oven dry mass divided by green volume (g / cm ³)	Dense wood tissue confers mechanical strength, but is energetically expensive to construct. Wood density influences ability to tolerate drought stress and disturbance (Lawson et al., 2015a; Preston et al., 2006; Telewski, 1995).	Regulates decomposition rate; this affects nutrient cycling and determines the residency time of woody debris in the fluvial system Mackensen et al. (2003).
Flowering period length	Proportion of the year spent in flower (proportion, dimensionless).	Indicates species ability to respond reproductively to favourable conditions.	Flowers may be an important food source for animals.

Calculating functional diversity, species richness and proportional abundance of exotics

Functional richness (FRic) and functional divergence (FDiv) are complementary metrics of functional trait diversity, which together, describe the range and distribution of trait values in a community (Villéger et al., 2008). Functional evenness is also included in the framework introduced by Villger et al. (2008) but has since shown limited ability to describe change in functional composition across environmental gradients (Mason et al., 2012; Pavoine and Bonsall, 2011). FRic represents the volume of the convex hull of trait values in a given community while FDiv provides information about the abundance distribution of trait values across this range.

We calculated functional richness and abundance-weighted functional dispersion (FDis) of vegetation communities at each site, using the FD package for R (Laliberté and Legendre, 2010). Gowers method, which scales traits by their range, was used to generate the required dissimilarity matrix, and Cailliez's correction was applied to render the matrix euclidean. We transformed FRic and FDis into standardised effect sizes (SES): $SES = (obs - nullExp) / sd(nullExp)$, where obs is the observed functional diversity value and nullExp and sd(nullExp) are the mean and standard deviation of the expected functional diversity in 999 randomized communities (Gotelli and Rohde, 2002). The null model for comparison with FRic was generated using the trial-swap algorithm (Miklós and Podani, 2004) in the picante package (Kembel et al., 2010) to remove dependence on species richness. The null model for comparison with FDis was generated by randomizing abundances among species but within plots (using the resamp.2s function in spacodiR) (Eastman et al., 2011), to generate a metric of pure functional divergence (FDiv). The resulting indices, FRic.SES and FDis.SES, have greater power to detect community assembly processes than their unstandardised counterparts or the metric

of functional divergence defined by Villger et al. (2008) (Mason et al., 2013).

Where required, trait values were normalised by either \log_{10} (SLA, seed mass) or square root (leaf area, maximum height, flowering duration) transformation prior to analysis. Wood density was not transformed. Summary statistics for the trait dataset are shown in Appendix 3a.

Species richness values were standardised by sampling area to account for differences in sampling effort. Abundance of exotic species was calculated as the number of exotic individuals divided by the total number of individuals counted at each site.

Constructing variance partitioning models

We used a variance partitioning approach to assess the individual contributions of river flow regime, flow modification, land use, climate and soil properties to modelling variation in riparian plant species richness, functional diversity and exotic abundance. Exotic proportional abundance was also included as an explanatory variable for species richness and functional diversity metrics.

The following process was used to derive an optimal set of environment-diversity models for variance partitioning analysis (Legendre, 2007): We first generated minimal multiple regression models for each set of environmental variables (i.e. descriptors of flow regime, flow modification, land use etc.): for each individual dependent variable, the full set of explanatory variables was reduced to the subset which showed statistically significant ($p < 0.05$) linear or quadratic relationships. Second order AIC was used to determine whether the linear or quadratic term better explained variation in the dependent variable (MuMIn package for R) (Barton, 2012; Burnham and Anderson, 2002). For each set of environmental variables, variance explained by significant univariate models was partitioned by partial regression using the varpart function in R (vegan package) (Oksanen et al., 2013).

Multiple regression models were derived from the combinations of variables with the highest adjusted R² values (Peres-Neto et al., 2006). These multiple regression models optimally combine the variation explained by all significant univariate models.

The four best multiple regression models were fed into a second variance partitioning analysis, and adjusted R² was used to estimate the proportion of variation jointly and independently explained by each environmental model.

4.4 Results

Below we describe the patterns of variation in species richness, exotic abundance, functional richness and functional dispersion of riparian plant communities, as they relate to metrics describing river hydrology, flow modification, land use, climate and soil properties. Due to considerable collinearity in the environmental dataset, description of univariate relationships is generally limited here to variables selected by variance partitioning for inclusion in the final multiple regression models. Statistics for the all statistically significant univariate regression models can be found in Appendix 3b. The adj. R² value shown in variance partitioning Venn diagrams (Figs 1.2-1.5b) may not correspond directly to the sum of its fractions as represented in Figs 1.2-1.5a., as negative R² values (not shown in Figs 1.2-1.5a) can result from the adjustment algorithm. All R² values given in the text are adjusted R².

Environmental drivers of variation in species richness

A substantial portion of variation in species richness across the study area (0.787) could be explained by a combination of models describing hydrology, flow modification, climate and soil conditions (Fig. 1.2a,b). Hydrology and flow modification were co-dominant, while climate and soil variables contributed a minor compo-

ment of variation; variation explained by the climate model was almost completely subsumed by the hydrological model. Land use and climate were also associated with species richness but independently explained no variation (not shown in Fig. 1.2a, but see Appendix 3b for regression statistics). Increased species richness in response to these conditions could not be explained by an increased number of exotic species present, and although species richness did decrease with exotic proportional abundance ($R^2 = 0.115$) (see Appendix 3a), exotic abundance did not independently explain variation in species richness.

Species richness was highest when minimum flow conditions were unevenly distributed throughout the year (C_MinM, $R^2 = 0.237$, Fig. 1.2c), and where these seasonal patterns of minimum flows were consistent between years (M_MinM, $R^2 = 0.129$, Fig. 1.2d). Richness declined with increasing duration of high flow periods (HSMeanDur, $R^2 = 0.290$, Fig. 1.2e), but increased somewhat as these high flow periods became more frequent (MDFAnnHSNum, $R^2 = 0.106$, Fig. 1.2f). Increased dry season flows due to flow modification were weakly associated reduced species richness (MDFMDFDry.mod, $R^2 = 0.117$, Fig. 1.2g). Alterations to seasonal consistency of minimum flow patterns had a strong effect (M_MinM.mod, $R^2 = 0.412$, Fig. 1.2h), and corroborated the trend observed in Fig. 1.2d: species richness increased as patterns of monthly minimum flows became more consistent throughout the hydrological record. With respect to climate, species richness was greater at sites which experienced higher rainfall (clim_pwet, $R^2 = 0.390$, Fig. 1.2i) and less variable temperature regimes (clim_tsea, $R^2 = 0.349$, Fig. 1.2j). Soils which contained more organic carbon (soil_soc, $R^2 = 0.202$, Fig. 1.2j) and higher silt content (soil_slt, $R^2 = 0.239$, Fig. 1.2k), lower total phosphorus (soil_pto, $R^2 = 0.110$, Fig. 1.2l) and lower available water capacity (soil_awc, $R^2 = 0.203$, Fig. 1.2m) supported richer communities.

The data did not support hypothesis 1a, that rivers with more heterogeneous flow regimes support communities with higher species richness, or hypothesis 1b,

that there is a unimodal relationship between species richness and flow heterogeneity. Further, these results contradict hypothesis 2 (that species richness and functional diversity should decrease and abundance of exotic species should increase along gradients of increasing flow modification and catchment land-use intensity), given that rivers which experienced more consistent patterns of minimum flows hosted richer plant communities.

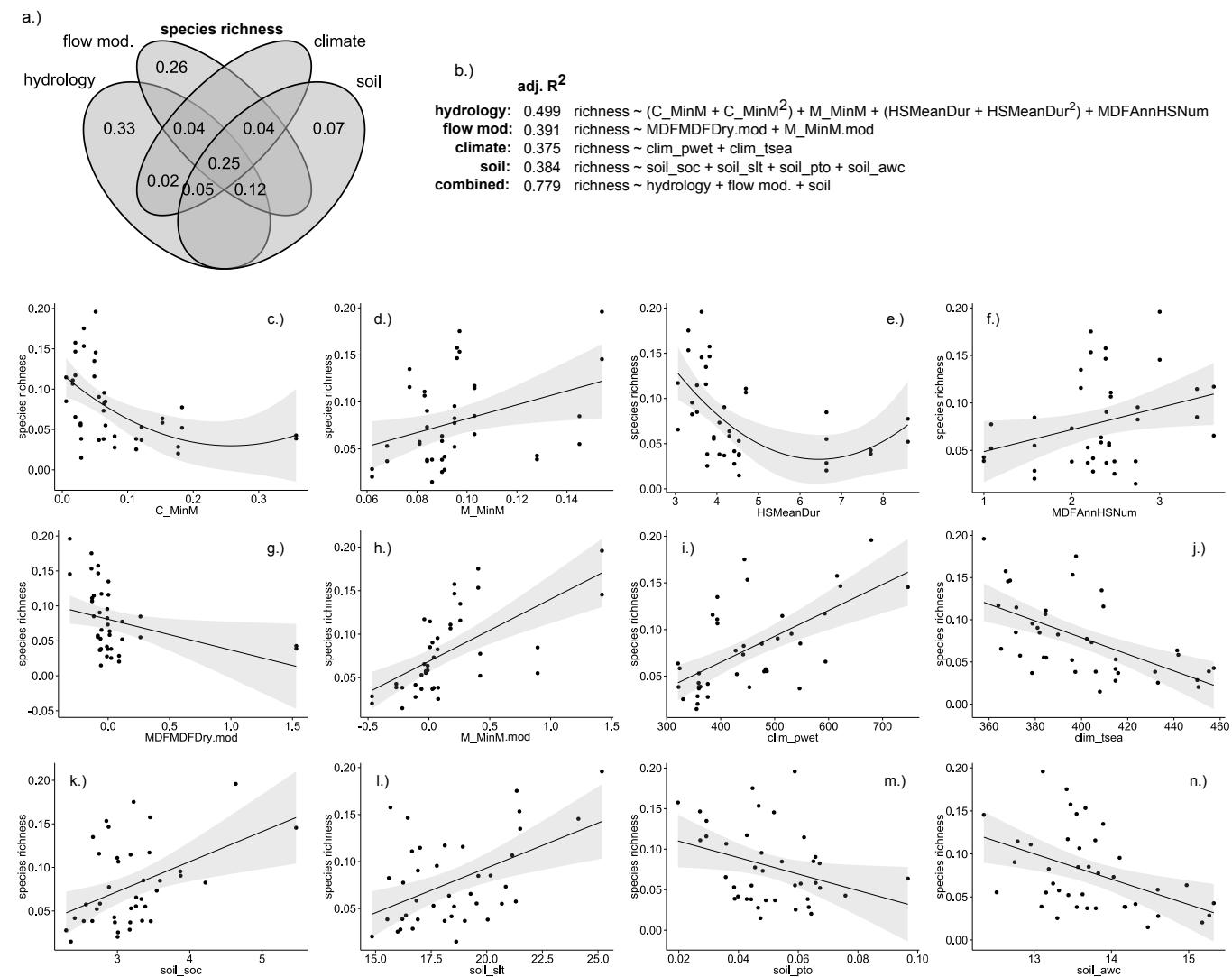


Figure 4.2: Environmental drivers of area-standardised species richness (units = species per m²) in riparian plant communities. a.) variance partitioning Venn diagram. Numbers within the diagram represent adjusted R² (adj. R²) values associated with each fraction of variation; b.) multiple regression models representing each set of environmental conditions, and their optimal combination. Quadratic terms are enclosed in parentheses. Selected univariate relationships between species richness and environmental variables describing c.) constancy of monthly minimum daily flow (C_MinM); d.) contingency of monthly minimum daily flows (M_MinM); e.) mean duration of high flow periods (HSMeanDur, days); f.) mean annual frequency of high flow periods (MDFAnnHSNum); g.) modification of dry season mean daily flow (MDFMDFDry.mod, % change); h.) modification of contingency of monthly minimum daily flows (M_MinM.mod, % change); i.) precipitation in the wettest quarter of the year (clim_pwet, mm); j.) temperature seasonality (clim_tsea, standard deviation * 100); k.) soil organic carbon (soil_soc, %); l.) soil silt content (soil_slt, %); m.) soil total phosphorus (soil_pto, %); n.) soil available water capacity (soil_awc, %). Species richness is presented as standardised by plot area. Fitted lines depict ordinary least-squares regression models. Shaded areas depict the smoothed 95 % confidence interval around the regression model.

Environmental drivers of functional richness (FRic.SES)

Variation in FRic.SES was best explained by a combination of hydrological and soil models (variation explained by the combined model = 0.405) (Fig. 1.3a,b), of which the hydrological model gave the most explanatory power. Soil variables independently explained a small fraction of variation, and while flow modification and climatic variables were also associated with FRic.SES, neither model explained any variation independently.

FRic.SES was distributed unimodally across gradients of interannual variability in baseflow index (CVAnnBFI, $R^2 = 0.170$, Fig. 1.3c); the modelled slope increased steeply at the lower end of the gradient but was only somewhat reduced from the peak by the top of the gradient. Greater frequency of high flow periods was associated with lower functional richness (MDFAnnHSNum, $R^2 = 0.142$, Fig. 1.3d). FRic.SES also declined as rainfall (clim_pwet, $R^2 = 0.246$, Fig. 1.3e), soil total nitrogen (soil_nto, $R^2 = 0.144$, Fig. 1.3f) and soil organic carbon (soil_soc, $R^2 = 0.257$, Fig. 1.3g) increased.

Hypothesis 1a was not supported, given that reduced functional richness was associated with increasing frequency of high flows. Hypothesis 1b was supported by a significant unimodal relationship interannual variability in baseflow (Fig. 1.3c) and functional richness (delta AICc between linear and quadratic models = 3.70). Although not selected for the final hydrological model, mean and interannual variability in duration of high flow periods (HSMeanDur, CVAnnHSMeanDur) also showed significant unimodal relationships with FRic.SES ($R^2 = 0.213, 0.182$, respectively; Appendix 3a). Hypothesis 2 was not supported: we found no effect of either land use or flow modification on functional richness, except a weak relationship with modification of dry season mean daily flow (Appendix 3a).

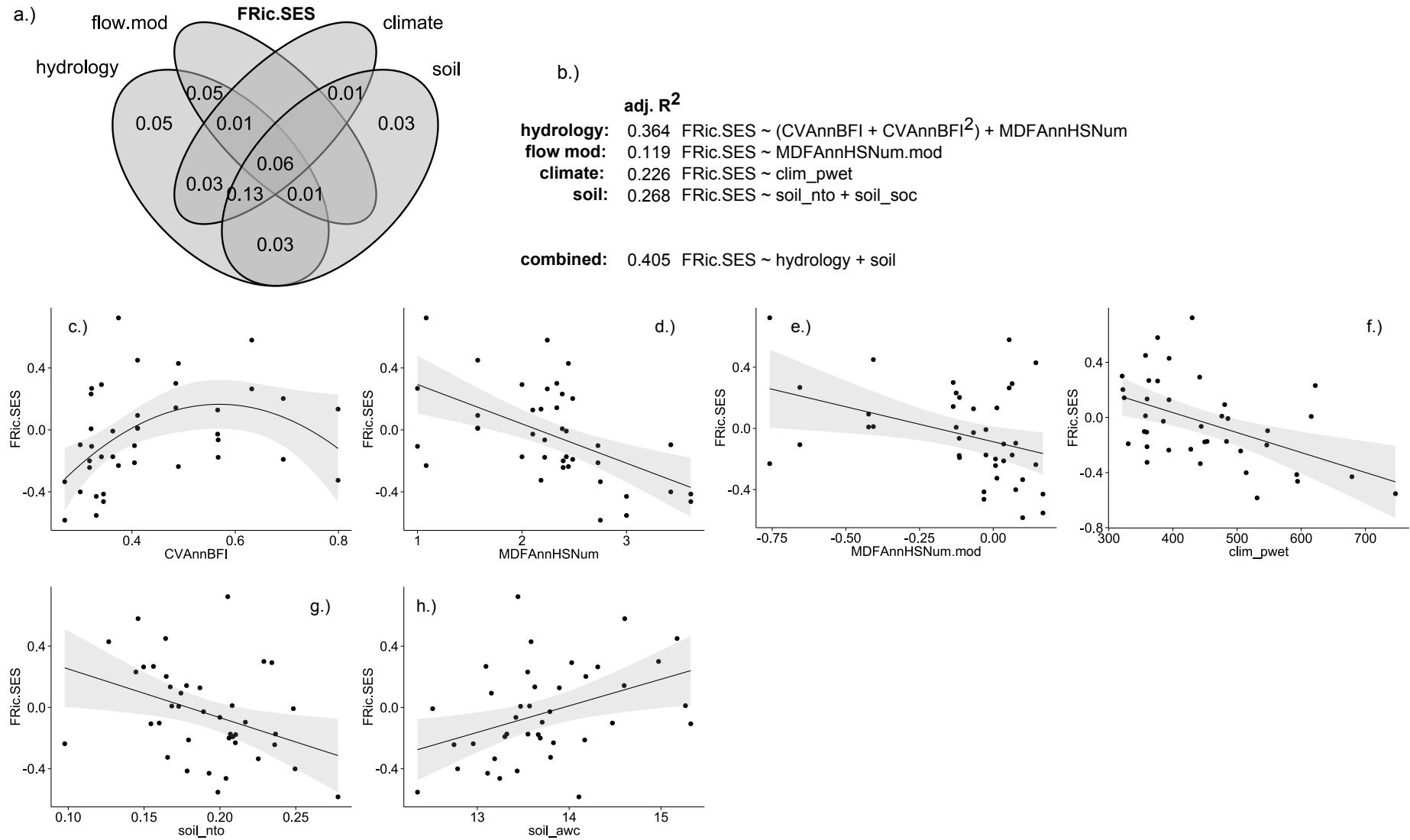


Figure 4.3: Environmental drivers of standardised effect size functional richness (FRic.SES) in riparian plant communities. a.) variance partitioning Venn diagram. Numbers within the diagram represent adjusted R^2 (adj. R^2) values associated with each fraction of variation; b.) multiple regression models representing each set of environmental conditions, and their optimal combination. Quadratic terms are enclosed in parentheses. Selected relationships between FRic.SES and environmental variables describing c.) interannual variability in baseflow (CVAnnBFI); d.) mean annual frequency of high flow periods (MDFAnnHSNum); e.) modification of mean annual frequency of high flow periods (MDFAnnHSNum.mod, % change); f.) precipitation in the wettest quarter (clim_pwet, mm); g.) soil total nitrogen (soil_nto, %); h.) soil organic carbon (soil_soc, %). Fitted lines depict ordinary least-squares regression models. Shaded areas depict the smoothed 95 % confidence interval around the regression model.

Environmental drivers of functional divergence (FDis.SES)

FDis.SES varied substantially across the study area (3.96 standard deviations of the null distribution), and was associated with gradients of hydrology, flow modification, climatic and soil conditions. The soil model explained 0.483 of the variation in FDis.SES; hydrology, flow modification and climatic models did not independently explain further variation (Fig. 1.4a,b).

Rivers with moderate seasonality of maximum flows tended to support communities with high functional divergence (C_MaxM , $R^2 = 0.321$, Fig. 1.4c). The entire range of FDis.SES was represented by rivers associated with highly seasonal patterns of maximum flows (C_MaxM), however. As with functional richness, FDis.SES declined with increasing frequency of high flows ($MDFAnnHSNum$, $R^2 = 0.112$, Fig. 1.4d). Functional divergence also varied with flow modification affecting high flow frequency ($MDFAnnHSNum.mod$, $R^2 = 0.144$, Fig. 1.4e): lower flooding frequency tended to be associated with higher functional divergence. Also tracking trends observed for FRic.SES, FDis.SES declined with increasing rainfall ($clim_pwet$, $R^2 = 0.141$, Fig. 1.4f), soil total nitrogen ($soil_nto$, $R^2 = 0.111$, Fig. 1.4g) and soil organic carbon ($soil_soc$, $R^2 = 0.344$, Fig. 1.4h).

Environmental heterogeneity (as indicated by high flow frequency) was associated with lower functional divergence (Fig. 1.4d,e), opposing the prediction made in hypothesis 1a, while the unimodal relationship with constancy of maximum flows (Fig. 1.4c) provided some support for hypothesis 1b (delta AICc between linear and quadratic models = 10.08). Scant evidence to support hypothesis 2 was found: as with FRic.SES, a weak but significant relationship was present between FDis.SES and dry season mean daily flow (see Appendix 3a).

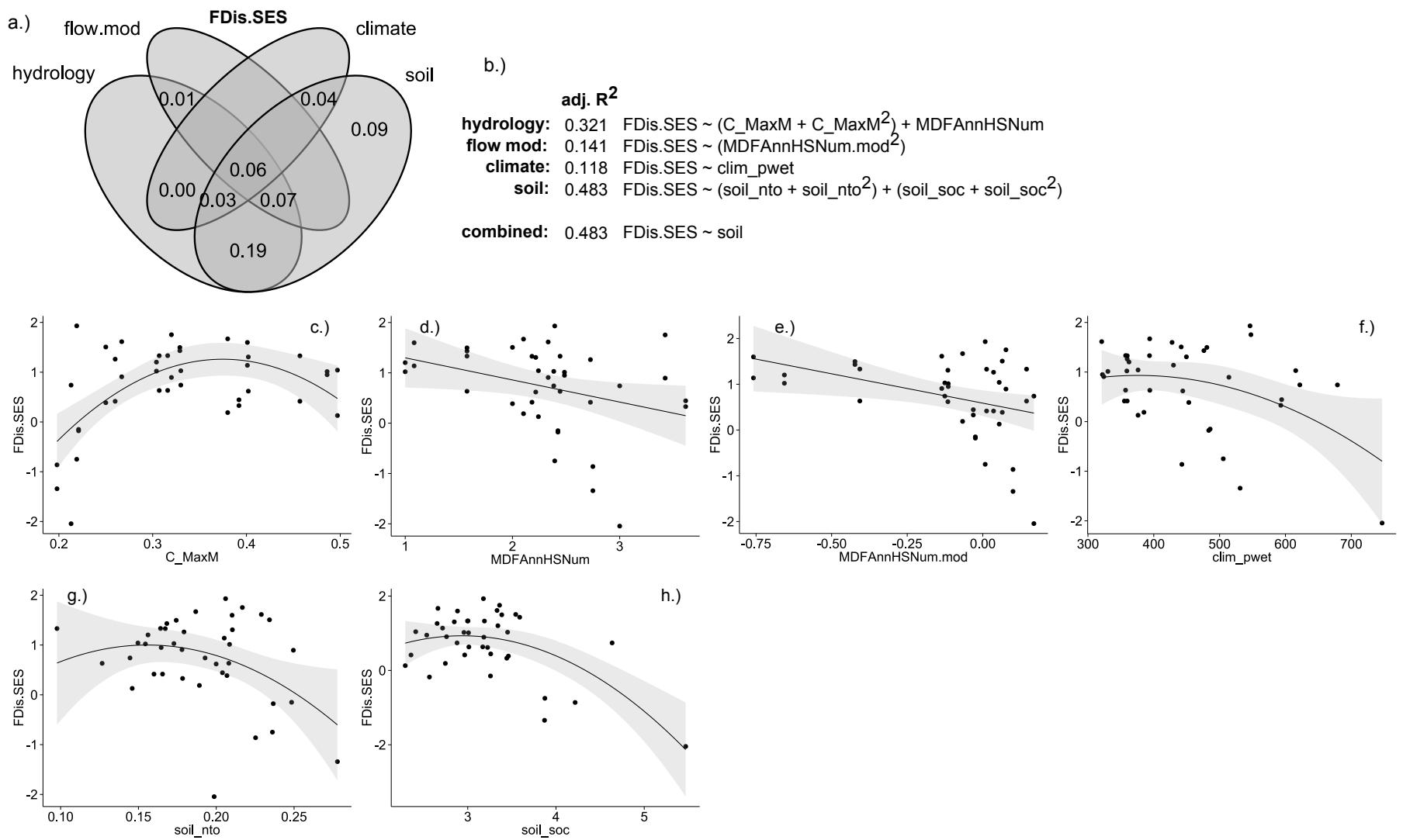


Figure 4.4: Environmental drivers of standardised effect size functional dispersion (FDis.SES) in riparian plant communities. a.) variance partitioning Venn diagram. Numbers within the diagram represent adjusted R^2 (adj. R^2) values associated with each fraction of variation; b.) multiple regression models representing each set of environmental conditions, and their optimal combination. Quadratic terms are enclosed in parentheses. Selected relationships between FDis.SES and environmental variables describing c.) constancy of monthly maximum daily flows (C_MaxM); d.) mean annual frequency of high flow periods (MDFAnnHSNum); e.) modification of mean annual frequency of high flow periods (MDFAnnHSNum.mod, % change); f.) precipitation in wettest quarter (clim_pwet, mm); g.) soil total nitrogen (soil_nto, %); h.) soil organic carbon (soil_soc, %). Fitted lines depict ordinary least-squares regression models. Shaded areas depict the smoothed 95 % confidence interval around the regression model.

Environmental drivers of variation in proportional abundance of exotic species

Variation in exotic species abundance was jointly explained by hydrology, land use, soil and climatic models (0.665 of variation explained by the combined model) (Fig. 1.5a,b). Hydrological models (0.581 of variation explained) and land use (0.515 of variation explained) models were dominant. Two individual metrics of flow modification had significant relationships with exotic abundance (C_MinM.mod, $R^2 = 0.124$; LSPeak.mod, quadratic $R^2 = 0.105$), but these effects were strongly influenced by outlying values and the flow modification model combining these metrics explained no variation independently.

Exotic abundance closely tracked interannual variability in baseflow index (CVAnnBFI, $R^2 = 0.412$, Fig. 1.5c), and also rose as maximum flows became more uniformly distributed across seasons (i.e. a lack of flow seasonality) (C_MaxM, $R^2 = 0.157$, Fig. 1.5d). We found a trough-shaped relationship between interannual variability in dry season flows and exotic abundance (CVMDFDry, $R^2 = 0.412$, Fig. 1.5e), although the lower end of the distribution was data-poor and may have been unduly influenced by values for a single pair of sites. Throughout the centre and upper ranges of the distribution, however, exotic abundance increased strongly with interannual variability in dry season flow. Exotic abundance also increased with interannual variability in high spell duration (CVAnnHSMeanDur, $R^2 = 0.129$, Fig. 1.5f). The proportion of the upstream catchment used for irrigated agricultural production was a strong positive predictor of exotic abundance (production_irrigated, $R^2 = 0.37$, Fig. 1.5g), as was production from relatively natural environments, although somewhat less so (production_natural, $R^2 = 0.232$, Fig. 1.4h). Exotic abundance declined as dry season precipitation increased (clim_pdry, $R^2 = 0.207$, Fig. 1.5i), increased with soil pH (soil_phc, $R^2 = 0.242$, Fig. Xj), and decreased with soil depth to hard rock (soil_der, $R^2 = 0.140$, Fig. 1.5k).

With respect to hypothesis 1a, we found the opposite of expected: hydrological heterogeneity (as measured by CVAnnBFI, CVMDFDry and CVAnnHSMeanDur) appears to be associated with higher exotic abundance. These relationships did not exhibit unimodality. Production land uses were associated with higher exotic abundance, supporting hypothesis 2.

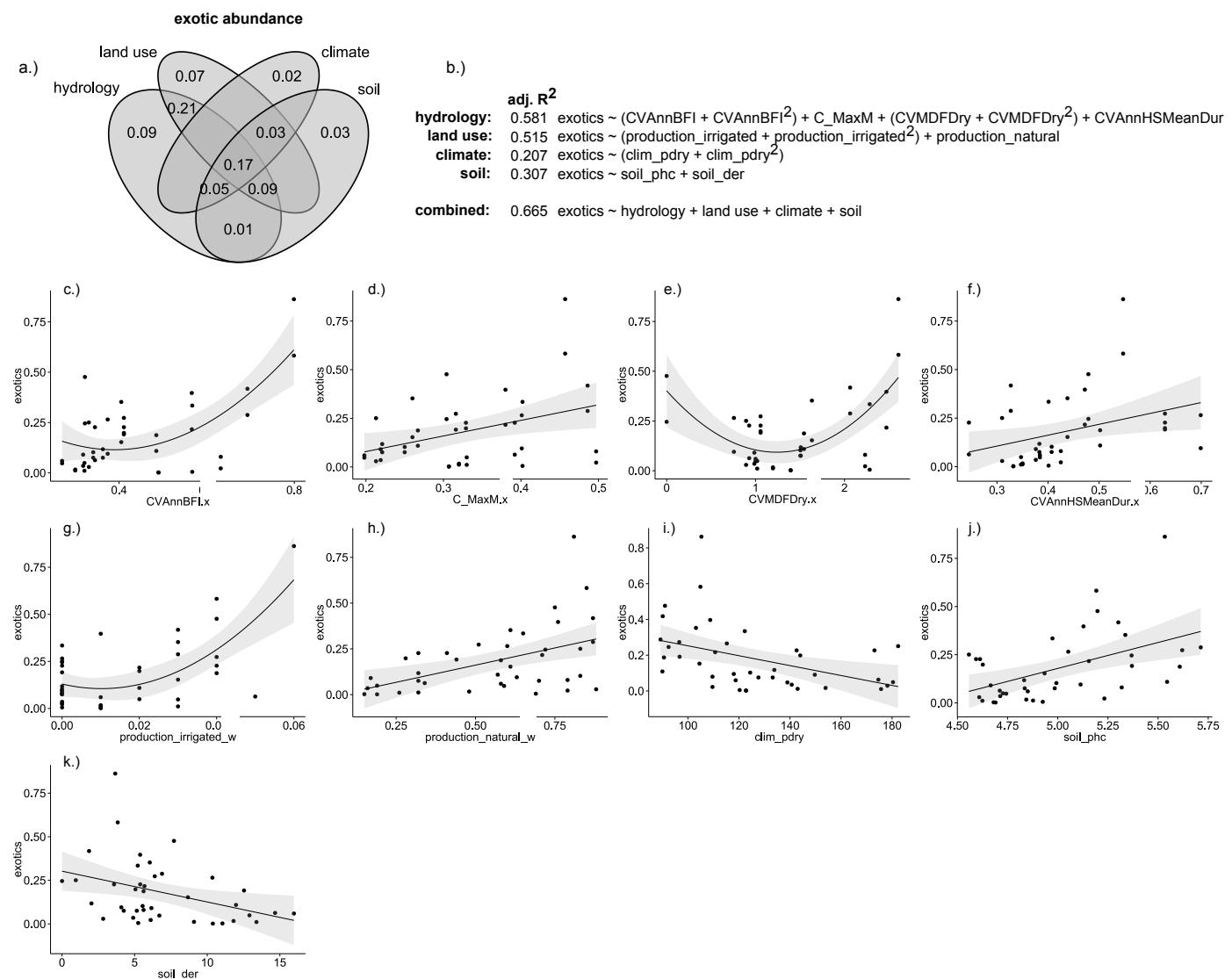


Figure 4.5: Environmental drivers of the proportional abundance of exotic species in riparian plant communities. a.) variance partitioning Venn diagram. Numbers within the diagram represent adjusted R^2 (adj. R^2) values associated with each fraction of variation; b.) multiple regression models representing each set of environmental conditions, and their optimal combination. Quadratic terms are enclosed in parentheses. Selected relationships between exotic abundance and environmental variables describing c.) interannual variability in baseflow index (CVAnnBFI); d.) constancy of monthly maximum daily flows (C_MaxM); e.) interannual variability in dry season mean daily flow (CVMDFDry); f.) interannual variability in mean duration of high flow periods; g.) proportion of catchment used for irrigated agricultural production (production_irrigated, geographically weighted %); h.) proportion of catchment used for production from relatively natural environments (production_natural, geographically weighted %); i.) precipitation in the driest quarter (clim_pdry, mm); j.) soil pH (soil_phc, %); k.) depth of regolith (soil_der, m to hard rock). Fitted lines depict ordinary least-squares regression models. Shaded areas depict the smoothed 95 % confidence interval around the regression model.

4.5 Discussion

We proposed that generation of niche complexity by spatially and temporally heterogeneous environmental conditions is the dominant control on diversity in riparian plant communities. Under this framework, suppression of natural environmental heterogeneity by human modification of river flow regimes and catchment landscapes would result in lower diversity (Poff et al., 1997; Poff and Zimmerman, 2010). This niche-oriented model of riparian plant diversity received mixed support in our study: species richness in fact decreased as hydrological conditions became more heterogeneous, and flow homogenisation by dams was associated with greater species richness. Although abundance of exotic species did increase with the proportion of surrounding land used for agricultural or silvicultural production, there was no relationship between exotic abundance and flow modification, and negative relationships were found with metrics of hydrological heterogeneity. The proportion of variation in functional diversity explained by environmental variables was comparatively lower than species richness or exotic abundance. Functional diversity metrics showed unimodal relationships with some metrics of hydrological heterogeneity, and declined with others. Flow modification was a weak predictor of functional diversity, and we found no effect of land use.

Flow regime was nevertheless the most consistently powerful predictor of diversity in our study. Models derived from hydrological metrics explained more total and independent variation in species richness, exotic abundance and FRic.SES than any other group of environmental variables. Additionally, of the individual environmental variables with significant relationships to FDis.SES, consistency in monthly maximum flows (C_MaxM) explained the most variation. Given that a large proportion of variation in diversity metrics and exotic abundance explained by flow regime was co-explained by soil and climatic variables, is it possible to attribute flow regime as the dominant control on diversity? species richness increased

with contingency of minimum flows (M_MinM, Fig. 1.2d), and also increased when M_MinM was increased by flow modification (M_MinM.mod, Fig. 1.2h). Species richness had no direct relationship with the degree of modification of contingency of minimum flows (i.e. C_MinM.mod) although species richness did increase as dry season flows (MDFMDFDry.mod, Fig. 1.2g) were upregulated, which could be expected to increase constancy of minimum flows. Removal of the outlying pair of sites which had experienced extreme modification strengthened the relationship of MDFMDFDry.mod with species richness ($R^2 = 0.117$ vs 0.283). Likewise, greater high flow frequency (MDFAnnHSNum) was associated with lower FRic.SES and FDis.SES, and communities with altered high flow frequency followed the same trend (Figs 1.3d, 1.4d). Extent of flow modification independently explained variation only in species richness, however, and changes to only a fraction hydrological metrics were important. As such it was not possible to give a conclusive affirmative response to this question; it is possible that relatively shallow extent of flow modification in the region over a relatively short timeframe (~30 years) (Mackay et al., 2014) did not provide the contrast required to find a consistent effect. Correlations between climate and hydrology mean that manipulative experiments are required to confidently determine the influence of flow regime on riparian plant communities. Nevertheless, the importance of hydrological metrics in our optimal models of species richness, exotic abundance, FRic.SES and Fis.SES lends weight to the case that hydrology was an important control on diversity.

Species richness had a more complicated relationship with hydrological heterogeneity than that expected, however. Richness was greatest along rivers which experienced regular seasonal patterns of low flows, and short but frequent flood flows. These short flood flows may enhance diversity by generating habitat complexity (Bendix and Hupp, 2000; Tabacchi et al., 1998), with longer flood durations acting as an environmental filter favouring species with inundation tolerance traits. A global meta-analysis of the ecology of tropical riverscapes showed that consistent,

seasonal flow regimes support communities with higher net primary productivity and higher species richness in bird and fish assemblages than rivers with arrhythmic flow regimes (Jardine et al., 2015). Lundholm found in a meta-analysis of studies describing relationships between species richness, spatial environmental heterogeneity and energy availability, that energy availability was a better predictor of species richness than environmental heterogeneity (Lundholm, 2009). Temporal consistency in patterns of energy and resource availability (water, nutrients, fresh sediment and newly disturbed habitat) appears to compete with environmental heterogeneity as a control on riparian plant diversity in this system.

Further insight into the processes controlling riparian plant community assembly can be derived from patterns of functional diversity assembly across environmental gradients. FRic.SES represents the volume of the convex hull of trait values in a given community, as a fraction of the expected convex hull volume generated from randomized communities (Mason et al., 2013). FRic.SES is not weighted by species abundance and describes only the range of trait values present. FDis.SES, a pure measure of functional divergence (Mason et al., 2013), provides information about the abundance distribution of trait values across this range: functional divergence is maximised when highly abundant species are distant from the community centre of gravity in traitspace (Mouchet et al., 2010). Functional richness was unimodally related to temporal variability in baseflow index. The mechanism behind this is unclear, although following the line of reasoning developed for species richness, the effect of increased niche complexity may be offset by irregular resource availability and habitat microfragmentation as environmental heterogeneity increases (Laanisto et al., 2013). Comparison of patterns of FRic.SES and species richness reveals an interesting effect along gradients of flood frequency and duration: the relationship of mean duration (HSMeanDur) and frequency (MDFAnnHSNum) of high flow periods with FRic.SES was the inverse of that with species richness. Thus community convex hulls retained their volume

in traitspace as environmental heterogeneity increased, but became more sparsely populated.

Most communities had higher functional dispersion than predicted by the abundance-swapped null model, and a similar set of hydrological variables as FRic.SES had significant relationships with FDis.SES. FDis.SES showed a skewed, unimodal distribution across a gradient of constancy of maximum flows (C_MaxM). Strongly negative values for several communities at the lower bound of C_MaxM indicates functional underdispersion (i.e. environmental filtering), although the full range of variation in FDis.SES was present at low C_MaxM (Mason et al., 2013). Variation in FDis.SES constricts as constancy increases, however, so with the exception of communities at this lower bound, communities along rivers with similar C_MaxM tend to have similar species abundance distributions in traitspace. Interestingly, temporal variability in minimum flows (C_MinM, M_MinM) predicted species richness but temporal variability in maximum flows (C_MaxM) predicted functional divergence. Compared with species richness, both FRic.SES and FDis.SES showed the opposite relationships with high flow frequency, climate and soil variables, indicating that trait range is not reduced in concert with species richness. The traits which do remain are clustered towards the edges of the range, producing hollowed-out community trait distributions.

Environmental models in this study accounted for only part of the total variation in functional diversity. In a previous study of relatively unmodified riparian plant communities in south-eastern Australia, 80 % of variation in functional dispersion was explained by a combination of variability in flood frequency, variability in flood magnitude, and mean daily summer flow (Lawson et al., 2015b). A fraction of this variation was independently explained by climate, and none was independently explained by soil variables. In contrast, much of the variance in functional diversity metrics in the current study was jointly explained by hydrological, climate and soil models. The single weak relationship observed between functional

diversity and flow modification suggests that local land management practices and land use histories, which could not be accounted for in this study, may have had a strong influence on diversity (Foster et al., 2003). Additionally, our environmental gradient analyses are based on a niche optimisation paradigm of community assembly, and do not account for neutral processes or biotic interactions (Kraft et al., 2015).

Substantial variation in exotic abundance was jointly explained by hydrological and land use models. The proportion of catchment land-use associated with irrigated agricultural production was typically low, but production from natural environments (forestry etc.) was common and dominated a number of catchments. The rationale for our hypotheses was that environmental heterogeneity should result in structural complexity of habitat and therefore limit competitive exclusion by invasive species. We found that exotic abundance was associated with more hydrologically heterogeneous sites, and a greater proportion of catchment used for forestry. Thus the combined stresses of disturbance from forestry practices and heterogeneous flows may favour novel species assemblages. It is notable that flow modification was not significantly associated with exotic abundance, given that altered flow regimes have been linked to invasion in previous studies of regulated Australian river systems (Catford et al., 2011; Greet et al., 2013). It may be significant that while these studies found flow modification exacerbated invasion primarily by herbaceous species, the most dominant invaders in this study tended to be woody trees or vines (e.g. *Leucaena leucocephala*, *Macfadyena unguis-cati*, *Celtis sinensis*).

Environmental conditions may also have interactive effects on exotic abundance and riparian plant diversity. We originally intended to model a set of competing hypotheses about the effects of interactions between environmental conditions on diversity and exotic abundance, but the analyses described here were performed post-hoc, and the scope of possible models proved too wide to winnow down based

on our limited prior understanding of the system. Future studies which explicitly accommodate tests for interactions into experimental design may provide more insight into environmental controls on diversity. Despite previous findings that ecosystem multifunctionality scales linearly with functional divergence (Mouillot et al., 2011), we caution that communities which are functionally diverse but species poor may have low functional redundancy (i.e. the number of species performing similar ecological roles), which has been associated with diminished resilience to environmental change (Laliberté and Legendre, 2010). Riparian plant communities supported by rivers with highly variable flow regimes may therefore be inherently sensitive to environmental change and exotic invasion.

Our findings also suggest that greater runoff variability predicted to characterise future climates in south-east Queensland (Hennessy et al., 2008) could have deleterious consequences for riparian plant communities. Less defined patterns of seasonality and greater variability in monthly flow patterns between years may shift assemblages towards species more tolerant of environmental variability and promote exotic invasion. Environmental flows designed to alter interannual variability in flow seasonality have the potential to significantly influence species richness in riparian communities, although their potential effects on functional diversity remain unclear. Although evidence for strong links between flow conditions and riparian plant functional diversity has been found in natural catchments of south-eastern Australia (Lawson et al., 2015b), local land use histories are likely to confound the influence of environmental flows on functional diversity in modified landscapes.

Conclusion

This study was motivated by a desire to provide corroboration to previous work showing strong associations between flow heterogeneity and riparian plant func-

tional diversity (Lawson et al., 2015b), and to extend these findings into more modified landscapes. The current study confirms the general importance of flow regime in shaping riparian plant assemblages, but we found little evidence that environmental heterogeneity per se was the key control on diversity in south-east Queensland. Rather, generation of diversity by the flood rhythm appears to dominate here (Jardine et al., 2015). The two processes are likely active together, but it remains unclear how or why one process might become dominant over the other in a given system. An interesting avenue for future research would be to investigate how spatial scale affects the relative influence of flow rhythmicity and environmental heterogeneity on diversity (Lundholm, 2009). Environmental conditions may also have interactive effects on exotic abundance and riparian plant diversity, and explicitly accommodating tests for interactions into experimental design may provide further insight into environmental controls on diversity. Functional ecology is being increasingly used to characterise riparian plant communities, and in the future, a comparative synthesis of different systems may shed light on how the interplay between environmental heterogeneity and flow rhythmicity controls community assembly.

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Authors' contributions

Cassandra James designed and carried out the field component of the original study. Rachael Gallagher provided the majority of the trait data and contributed to the study design and analysis. Kirstie Fryirs and Michelle Leishman advised on the study design and analysis. James Lawson initiated and led the current project, curated the trait dataset, performed the analysis and wrote the manuscript. All authors contributed comments on the manuscript.

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5 Interactive effects of waterlogging and
atmospheric CO₂ concentration on gas
exchange, growth and functional traits of
Australian riparian tree seedlings

Abstract

The ability to survive and thrive in repeatedly waterlogged soils is characteristic of plants adapted to riparian habitats. Rising atmospheric CO₂ has the potential to fundamentally alter plant responses to waterlogging by altering gas exchange rates and stoichiometry, modifying growth, and shifting resource-economic trade-offs to favour different ecological strategies. While plant responses to waterlogging and elevated CO₂ individually are relatively well characterised, few studies have asked how the effects of waterlogging might be mediated by atmospheric CO₂ concentration.

We investigated interactive effects between elevated (550 ppm) atmospheric CO₂ and waterlogging on gas exchange, biomass accumulation and allocation, and functional traits for juveniles of three woody riparian tree species. In particular, we were interested in whether elevated CO₂ mitigated growth reduction under waterlogging, and whether this response was sustained following a refractory recovery period during which soils were re-aerated.

We found inconsistent effects of atmospheric CO₂ concentration and waterlogging status on growth, gas exchange and functional traits between species, and no evidence for a consistent effect of elevated CO₂ in mediating plant responses to flooding. For one species, *Casuarina cunninghamiana*, elevated CO₂ substantially increased growth, but this effect was entirely removed by waterlogging and there was no recovery following a refractory period.

Differential responses to combined waterlogging and elevated CO₂ between species may result in compositional changes to riparian plant communities and associated changes in ecosystem functioning.

5.1 Introduction

Woody plants play an important role in determining the physical structure of many riparian ecosystems (Lawson et al., 2015), and understanding the responses of woody riparian plants to environmental stresses is central to river rehabilitation and riparian conservation efforts. Riparian plant communities are often dominated by keystone species, and responses of such species to environmental change may have important consequences for riparian landscapes defined by their presence. Changing climatic conditions over the next century are expected to cause shifts in hydrological patterns (Stocker et al., 2013), with changes to the prevalence and intensity of extreme flooding events predicted for many regions (Hennessy et al., 2008). Atmospheric CO₂ has also risen substantially over the past century, and a doubling of pre-industrial levels by 2100 is projected (IPCC et al., 2014). Flooding is already a dominant abiotic stress and an important determinant of ecological strategy for woody riparian plants (Blom and Voesenek, 1996; Lawson et al., 2015), but while a significant body of research describes the effects of elevated CO₂ on plants at multiple scales, little is known about how the effects of flooding might be mediated by atmospheric CO₂ concentration.

To thrive near stream channels, plants must navigate a trade-off between ease of access to water and stresses associated with waterlogging or inundation (Colmer and Voesenek, 2009; Naiman et al., 1993). Woody colonists of inset channel features such as bars and benches may experience repeated cycles of soil waterlogging (Corenblit et al., 2009), restricting root access to oxygen (Voesenek and Bailey-Serres, 2015). Maintaining root respiration in low O₂ conditions requires switching to costly anaerobic metabolic pathways (Drew, 1997). The resulting reduction in respiration weakens root function, impairing uptake of water and nutrients (Piedade et al., 2010; Voesenek and Bailey-Serres, 2015) and inducing suberisation (Steudle, 2000). Stomatal closure may also take place following waterlogging,

reducing available CO₂ for photosynthesis (Else et al., 2009; Kozlowski, 1984). Root-zone hypoxia damages roots by disrupting aerobic respiration and causing an energy crisis (Colmer and Voesenek, 2009); reactive oxygen species (ROS) then form as bi-products of anaerobic metabolism (Santosa et al., 2007), and subsequent re-aeration further increases ROS production (Steffens et al., 2013). Production of toxic ions by microbes under anoxic soil conditions causes additional stress to roots (Blom and Voesenek, 1996). Waterlogging may also impair rhizomicrobial nodule formation and activity, resulting in reduced nutrient uptake (Dawson et al., 1989; Shimono et al., 2012). The degree to which this combination of stressors influences plant growth is ultimately determined by species ability to mobilise physiological and morphological responses which mitigate damage Bailey-Serres and Voesenek (2008).

As with waterlogging, atmospheric CO₂ concentration is known to affect plant physiology and growth by altering the fundamental economics of carbon, water and macronutrient uptake and use (Poorter and Navas, 2003; Reich et al., 2014; Wang et al., 2012). Individual species responses are variable, but photosynthetic CO₂ assimilation in C3 plants tends to increase under elevated CO₂ (eCO₂) (Curtis, 1996). Stomatal conductance is also typically reduced (Ainsworth and Rogers, 2007), with attendant gains in water use efficiency (Holtum and Winter, 2010; Keenan et al., 2013; van der Sleen et al., 2014). Biomass accumulation in response to eCO₂ may be enhanced (Wang et al., 2012), but this depends on the availability of water and macronutrients (Körner, 2006; Manea and Leishman, 2014; Reich et al., 2014). Increased allocation of biomass to roots occurs under eCO₂ (Nie et al., 2013) and this effect is interactive with environmental stresses such as drought or low soil fertility (Wang and Taub, 2010). Increased rates of production and turnover of fine roots under eCO₂ have been shown in the field, which has important implications for nutrient cycling and ecosystem functioning (Lipson et al., 2014; Matamala and Schlesinger, 2000; Pregitzer et al., 2000, 1995). eCO₂ is

also known to affect functional traits indicative of positions along economic spectra (*sensu* Reich (2014). Reduction in specific leaf area (SLA) under eCO₂ may be linked to accumulation of non-structural carbohydrates in leaves (Bader et al., 2010; Poorter and Navas, 2003). Alteration of traits reflecting economic trade-offs is of particular significance at the seedling stage, as functional traits of trees are most strongly adapted to the regeneration niche (Poorter, 2007).

Taken individually, waterlogging and elevated atmospheric CO₂ concentration appear likely to exert opposing effects on plant growth. The possibility that eCO₂ may mitigate growth reduction under waterlogging warrants investigation of the interactive effects of these two important environmental variables. Literature describing interactive effects of atmospheric CO₂ concentration and waterlogging or flooding on plant growth is sparse, and findings thus far present an inconsistent picture. eCO₂ stimulated biomass production in waterlogged (water table at -10 cm) but not inundated (water table at +5 cm) juveniles of the flood-tolerant tree species *Taxodium distichum* (Megonigal et al., 2005). Increased photosynthesis under eCO₂ was not reduced by inundation. This effect was attributed to the increased metabolic cost of maintaining roots under low O₂ conditions. In the same study, inundation had no effect on eCO₂ stimulation of photosynthesis or biomass production of the aquatic herbaceous species *Orontium aquaticum*. The opposite response was found for a highly flooding tolerant Amazonian tree: waterlogged *Senna reticulata* grown in open top chambers showed greater increment in biomass under eCO₂ (Arenque et al., 2014). Finally, no evidence for an interaction between CO₂ concentration and waterlogging status was found on growth or stomatal conductance in soybean (Shimono et al., 2012). To our knowledge, no studies have investigated the effects of eCO₂ on recovery from waterlogging. Ability to recover following stress events may be a better indicator of fitness than tolerance of the stress (Gutschick and BassiriRad, 2003), and for waterlogged plants, generation of reactive oxygen species following re-aeration is likely to be a significant

additional stress (Drew, 1997).

The objective of this study was to investigate interactive effects between eCO₂ and waterlogging on gas exchange, biomass accumulation and allocation, and functional traits for riparian tree species. In particular, we were interested in whether eCO₂ mitigated growth impairment under waterlogging, and whether this response was sustained following a refractory recovery period during which soils were re-aerated. We also investigated two hypothesised mechanisms by which such an interactive effect might occur: a.) higher water use efficiency under eCO₂ (Holtum and Winter, 2010) facilitates photosynthesis in plants with anoxia-impaired root functionality by lowering the water cost of carbon assimilation; b.) eCO₂ facilitates biomass recovery by increasing the rate of fine root production during the recovery period (Pregitzer et al., 1995).

5.2 Methods

We selected three riparian tree species native to south-eastern Australia for this study. *Casuarina cunninghamiana* subsp. *cunninghamiana* and *Eucalyptus camaldulensis* subsp. *camaldulensis* dominate many riparian environments in south-eastern Australia; *Acacia floribunda* is also common in this region. Table 1.1 provides further information on the biology and ecology of these species.

Table 5.1: Biological and ecological attributes of study species.

	<i>Acacia floribunda</i>	<i>Casuarina cunninghamiana</i> subsp. <i>cunninghamiana</i>	<i>Eucalyptus camaldulensis</i> subsp. <i>camaldulensis</i>
Family	Fabaceae	Casuarinaceae	Myrtaceae
Distribution	Coastal areas of eastern Australia ¹	Eastern NSW and QLD, Australia. Other subsp. in Gulf of Carpentaria and Papua New Guinea ¹	Inland riparian areas throughout south-eastern Australia. Other subsp. distributed throughout continental Australia ¹
Morphology	Erect or spreading shrub or tree, 38 m high ¹ . Rooting depth 2 m + ²	Erect tree, 15-35 m high ¹ . Rooting depth to 8 m ²	Large, spreading tree, 30+ m high ¹ . Rooting depth 10 m + ²
Habitat	Facultative rheophyte. Found in sclerophyll forest, particularly along watercourses and in sandy alluvial soils. Typically on channel banks and raised within-channel features ¹	Obligate rheophyte. Found along permanent watercourses, on substrates ranging from sand to large cobbles. Often found on bars, benches and channel islands ¹	Obligate rheophyte. Found on deep, rich alluvial soils, on banks and flood plains associated with large, permanent water bodies ¹
Community status	Common ¹	Dominant ¹	Dominant ¹
Nitrogen fixing ability	Nodulated with Rhizobium ³	Nodulated with Frankia ⁴	None
Biogeomorphic effects	Colonist of fresh geomorphic substrates ⁵	Ecosystem engineer. Rapid, en masse colonisation and stabilisation of fresh geomorphic substrates. Established trees stabilise banks and in-channel features ²	Ecosystem engineer. Established trees define physical structure of riparian landscapes. Highly effective at mitigation of flooding-induced landform mass failure ²

¹ PlantNET (2015), ² Hubble et al. (2010), ³ Roughley (1987), ⁴ Dawson et al. (1989), ⁵ J. Lawson personal field observations

Experimental procedure

We used a fully factorial design comprising two CO₂ treatments (ambient and elevated), and three waterlogging treatments (non-waterlogged control, waterlogged and waterlogged then re-aerated for a refractory period), with 8 replicates per treatment combination per species. We measured plant physiology (photosynthetic rate, A; stomatal conductance, G_s; and instantaneous water use efficiency, WUE) as well as biomass, biomass allocation and tissue density traits indicative of ecological strategy and position along economic spectra (Reich, 2014).

Plants were grown individually in pots constructed from 90 mm by 700 mm (4.3 L capacity) sections of PVC pipe with drilled endcaps, containing a commercially sourced 80/20 mixture of river sand and soil (Australian Native Landscapes, North Ryde, NSW, Australia). The bottom 2 cm of each pot was filled with gravel (1 cm particle size) to promote free drainage. 2.5 g L⁻¹ of time-release fertiliser granules (NPK 19.1, 0, 11.9, Yates Australia, Padstow, NSW, Australia) was mixed evenly through the soil medium.

Seeds were obtained from a commercial supplier (Nindethana Seed Service, Albany, WA, Australia) and germinated on moist tissue paper in trays at 20 °C. Following cotyledon emergence, four seedlings were transplanted into each growing pot. Germination was staggered by species to ensure all seedlings were transplanted at the same stage of development (radicle just emerged) within 48 hours. After two weeks of growth, plants were thinned to retain a single, medium sized individual.

Plants were grown in glasshouses at Macquarie University, in Sydney, Australia, between June and November, 2014. Pots were supported by wire mesh on trolleys; pot positioning on trolleys was randomised with respect to species, and trolleys were rotated weekly to offset potential microclimatic effects associated with position within each glasshouse. Two levels of CO₂ treatment (380-400 ppm

and 530-570 ppm) were used in two replicate glasshouses per level. These CO₂ ranges were monitored and maintained using an automated gas delivery system (Canary Company Pty Ltd, Lane Cove, NSW, Australia). The lower range corresponds to the ambient atmospheric CO₂ concentration, while the higher range reflects the predicted atmospheric CO₂ concentration in 2050 (IPCC et al., 2014). Temperature was maintained between 16 and 28 °C. Plants were watered by a misting sprinkler system three times daily and provided with supplementary hand watering every 3-4 days to maintain constant soil moisture levels between pots. Trolleys were swapped between replicate glasshouses monthly.

Waterlogging was initiated after 90 days of plant growth and lasted 24 days, in order to simulate a significant flooding event and to allow time for morphological adaptation to manifest. Plants were randomly assigned to control, waterlogged and recovery treatments. Waterlogged and recovery plants were waterlogged by immersion to within 10 cm of the soil surface in 450 L plastic tubs filled with water. The black tubs were covered with white polythene sheeting to reduce heat absorption. Photosynthetic rate and transpiration rate of plants assigned to the waterlogged treatment were measured at the end of the waterlogging period, after which they were harvested. Tubbs were drained following the waterlogging period, and control and recovered treatment plants were grown for a further 23 days before measurement and harvesting.

Photosynthetic rate (CO₂ assimilation rate), stomatal conductance and transpiration rate of the newest fully developed leaf were measured for four plants per treatment between 9 am and 12:30 pm using a Li-Cor 6400XT infrared gas analyser (Li-Cor Inc., Lincoln, NE, USA). Photon flux was set to 1500 mol m⁻² s⁻¹ and temperature was held at 28°C. For leaves which did not completely fill the cuvette, leaf area was measured by digital analysis (ImageJ 1.48 for Windows) of a photograph of the leaf taken against a 2x3 cm² plastic backdrop, which corresponded to the area of the cuvette. Photosynthetic rate and transpiration rate were deter-

mined by correcting values according to the measured area. Instantaneous water use efficiency was calculated as the ratio of CO₂ assimilation to transpiration rate.

Upon harvesting, roots were washed free of soil and the plant was separated into fine (<1 mm diameter) and coarse (>1 mm diameter, excluding dead root biomass) roots, and aboveground biomass. Five mature (but not senescing) leaves of each individual were selected for determination of specific leaf area (SLA). Fresh leaf area was determined using a LI-3100C Area Meter (Li-Cor Inc., Lincoln, NE, USA); SLA was calculated as the ratio of fresh area to dry mass. A 5 cm section of stem was cut from 1 cm above the root-stem junction for analysis of stem density. The fresh volume of the stem section was measured using the water displacement method and stem wood density was calculated as the ratio of oven dry mass to green volume. Root dry matter content was used as a proxy for root tissue density (Birouste et al., 2013). Dry matter content of fine roots was calculated as the ratio of oven dry mass to fresh mass. Samples were dried in an oven at 70 °C for 72 hours and a microbalance (Mettler-Toledo, Greifensee, Switzerland) was used to determine the resulting mass. Root mass fraction was calculated as the ratio of root dry biomass to whole plant dry biomass. Stunted plants with a shoot length of < 5 cm were excluded.

Data analysis

All statistical analyses were performed using the R statistical programming environment (R Core Team, 2015). We used two-way analysis of variance (ANOVA) to test for main effects of and interactions between waterlogging and CO₂ treatments on physiology (photosynthetic rate, stomatal conductance, water use efficiency), biomass (shoot, total root and fine root) and biomass allocation (root mass fraction), and functional traits (fine root dry matter content, stem density, SLA). Metrics of biomass (total, root biomass, shoot biomass) were compared only

between control and recovered treatment plants, as plants which received the waterlogged treatment were younger at harvest. Post-hoc comparison (Tukeys HSD) was used to determine which combination of treatments were responsible for interaction effects and waterlogging treatment main effects. Type II sums of squares were used where unbalanced analyses resulted from removal of stunted plants from the study, following Langsrud (2003). Data were log₁₀ or square root transformed where appropriate to satisfy assumptions of normality inherent in ANOVA. Statistical significance was thresholded at alpha = 0.1 for photosynthetic rate, stomatal conductance and WUE measurements (n = 4) and 0.05 for all other measurements (n = 8).

5.3 Results

Descriptive statistics and significance of ANOVA and post-hoc tests are shown for all measurements for each combination of treatments in Table 1.2.

	Control eCO ₂	Waterlogged eCO ₂	Recovery eCO ₂	Sig. effect	Post-hoc
	aCO ₂	aCO ₂	aCO ₂		
<i>Acacia floribunda</i>					
Photosynthetic rate (A, $\mu\text{mol m}^{-2} \text{s}^{-1}$)	13.41 (7.58)	19.25 (7.47)	20.9 (6.83)	22.06 (7.68)	17.15 (1.17) C
Stomatal conductance (G_s , $\text{mmol m}^{-2} \text{s}^{-1}$)	0.41 (0.11)	0.41 (0.07)	0.36 (0.16)	0.24 (0.07)	0.27 (0.04) NS
Water use efficiency (A/ G_s)	1 (0.43)	1.22 (0.62)	1.89 (0.53)	2.55 (0.65)	2.02 (0.35) W
Dry root biomass (g)	5.64 (2.35)	6.02 (2.51)			3.74 (0.76) cw, cr
Dry fine root biomass (g)	2.12 (1.5)	2.27 (1.07)		1.01 (0.39)	1.21 (0.35) W
Dry shoot biomass (g)	8.9 (4.17)	10.93 (3.67)		9.29 (1.65)	10.27 (3.13) NS
Root mass fraction	0.4 (0.14)	0.35 (0.07)	0.2 (0.02)	0.24 (0.05)	0.29 (0.03) W
Fine root DMC (%)	0.13 (0.03)	0.16 (0.04)	0.18 (0.07)	0.15 (0.03)	0.13 (0.01) wr
SLA ($\text{cm}^2 \text{ g}^{-1}$)	27.54 (2.12)	28.26 (2.33)	24.83 (2.15)	24.72 (3.12)	29.91 (2.91) cw, wr
Stem density (g cm^{-2})	0.46 (0.07)	0.48 (0.05)	0.49 (0.04)	0.54 (0.07)	0.5 (0.02) NS
<i>Casuarina cunninghamiana</i>					
Photosynthetic rate (A, $\mu\text{mol m}^{-2} \text{s}^{-1}$)	25.3 (6.32)	38.11 (7.8)	26.63 (7.53)	33.53 (3.75)	27.41 (1.81) C
Stomatal conductance (G_s , $\text{mmol m}^{-2} \text{s}^{-1}$)	0.53 (0.14)	0.66 (0.15)	0.64 (0.07)	0.57 (0.07)	0.57 (0.07) NS
Water use efficiency (A/ G_s)	1.5 (0.2)	1.69 (0.08)	1.26 (0.24)	1.72 (0.23)	1.65 (0.18) C x W, C w
Dry root biomass (g)	5.79 (3.1)	10.88 (3.67)			6.31 (2.07) C x W, C c
Dry fine root biomass (g)	1.66 (1.23)	4.11 (1.96)			1.95 (0.73) C x W*, C c
Dry shoot biomass (g)	10.44 (3.75)	17.19 (5.66)			11.97 (3.28) C x W
Root mass fraction	0.34 (0.06)	0.39 (0.04)	0.29 (0.1)	0.27 (0.04)	0.34 (0.03) W
Fine root DMC (%)	0.18 (0.08)	0.25 (0.07)	0.18 (0.08)	0.21 (0.04)	0.15 (0.02) C
SLA ($\text{cm}^2 \text{ g}^{-1}$)	20.82 (2.39)	18.84 (1.76)	20.76 (1.61)	20.57 (2.33)	20.3 (2.19) NS
Stem density (g cm^{-2})	0.4 (0.03)	0.44 (0.02)	0.34 (0.09)	0.4 (0.03)	0.41 (0.02) C

	Control		Waterlogged		Recovery		Sig. effect	Post-hoc
	eCO ₂	aCO ₂	eCO ₂	aCO ₂	eCO ₂	aCO ₂		
<i>Eucalyptus camaldulensis</i>								
Photosynthetic rate (A, $\mu\text{mol m}^{-2} \text{s}^{-1}$)	9.94 (5.88)	15.46 (1.49)	15.46 (1.49)	18.39 (5.11)	17.99 (3.87)	21.09 (2.95)	C, W	cr
Stomatal conductance (G_s , $\text{mmol m}^{-2} \text{s}^{-1}$)	0.14 (0.08)	0.17 (0.10)	0.32 (0.09)	0.28 (0.13)	0.52 (0.17)	0.35 (0.08)	W	cw, wr, cr
Water use efficiency (A/G _s)	2.1 (0.4)	3.26 (1)	1.99 (0.25)	2.65 (0.46)	1.93 (0.21)	2.48 (0.47)	C	
Dry root biomass (g)	14.85 (3.5)	14.32 (2.58)			14.09 (5.73)	13.42 (6.51)	NS	
Dry fine root biomass (g)	2.64 (1.84)	1.73 (0.93)			3.69 (2.73)	3.82 (2.22)	W	
Dry shoot biomass (g)	22.93 (5.31)	22.63 (6.13)			26.49 (10.35)	23.23 (8.49)	NS	
Root mass fraction	0.39 (0.05)	0.39 (0.05)	0.25 (0.02)	0.25 (0.06)	0.35 (0.11)	0.36 (0.05)	W	cw, rw
Fine root DMC (SLA ($\text{cm}^2 \text{g}^{-1}$))	31.7 (8.24)	28.11 (1.74)	31.38 (1.8)	31.82 (3.61)	28.59 (1.59)	28.08 (0.74)	W	cw, wr
Stem density (g cm^{-2})	0.39 (0.02)	0.41 (0.02)	0.38 (0.02)	0.39 (0.04)	0.39 (0.04)	0.39 (0.06)	N	

Table 5.2: Mean and standard deviation (in parentheses) of measured gas exchange rates, biomass and functional traits for each combination of CO₂ level and waterlogging treatments. Significant differences as determined by two-way ANOVA are denoted by the letters NS, C, W or I (NS = no significant effect of either treatment, C = significant effect of CO₂ level, W = significant effect of waterlogging treatment, C x W = significant interaction between CO₂ level and waterlogging treatment). Where interactions were found, waterlogging treatments in which significant differences between aCO₂ and eCO₂ were determined by post-hoc tests are denoted by: c = control, w = waterlogged, r = recovery. Significant differences between waterlogging treatments determined by post-hoc tests are denoted using the following script: cw = difference between control and waterlogged measurements, cr = difference between control and recovery measurements, wr = difference between waterlogged and recovery measurements.

* interaction effect was marginally significant, but post-hoc analysis confirmed significant differences among treatments.

N.B. biomass measurements for waterlogged plants are omitted because these plants were harvested at a younger age than control or recovery plants and are thus not comparable.

Gas exchange and water-use efficiency

Effects of CO₂ level and waterlogging on gas exchange were species specific, and although some significant interactions were found between CO₂ and waterlogging, we found no evidence that interactive effects were maintained following recovery from waterlogging.

Elevated CO₂ significantly increased leaf-level photosynthesis for all three species (*A. floribunda*, p = 0.074, Fig. 1.1a; *C. cunninghamiana*, p = 0.002, Fig. 1.1b; *E. camaldulensis*, p = 0.037, Fig. 1.1c). Photosynthetic rate in *E. camaldulensis* was significantly greater in recovery treatment plants than control plants (p = 0.008). No significant interactions were found between CO₂ level and waterlogging status for photosynthetic rate, although waterlogged *A. floribunda* exhibited only a small difference in mean photosynthetic rate between CO₂ treatments (20.9 and 22.6 mol CO₂ m⁻² s⁻¹, respectively, Fig. 1.1a).

CO₂ level had no effect on stomatal conductance for any species, and waterlogging status influenced stomatal conductance only in *E. camaldulensis*. Control plants had lower stomatal conductance than waterlogged plants (p = 0.042), and recovering plants (p = 0.0002). Waterlogged *E. camaldulensis* also had lower stomatal conductance than recovering plants (0.059).

Water use efficiency in *A. floribunda* was higher in control than waterlogged (p = 0.002), and higher in control than recovery (p = 0.04), but not waterlogged and recovery plants (Fig. 1.1g). WUE increased under elevated CO₂ as a main effect for *E. camaldulensis* (p = 0.002, Fig. 1.1h), and interactively with CO₂ level for *C. cunninghamiana* (p = 0.063); WUE was higher under eCO₂ for waterlogged plants (p = 0.022, Fig. 1.1i) but not control or recovery plants.

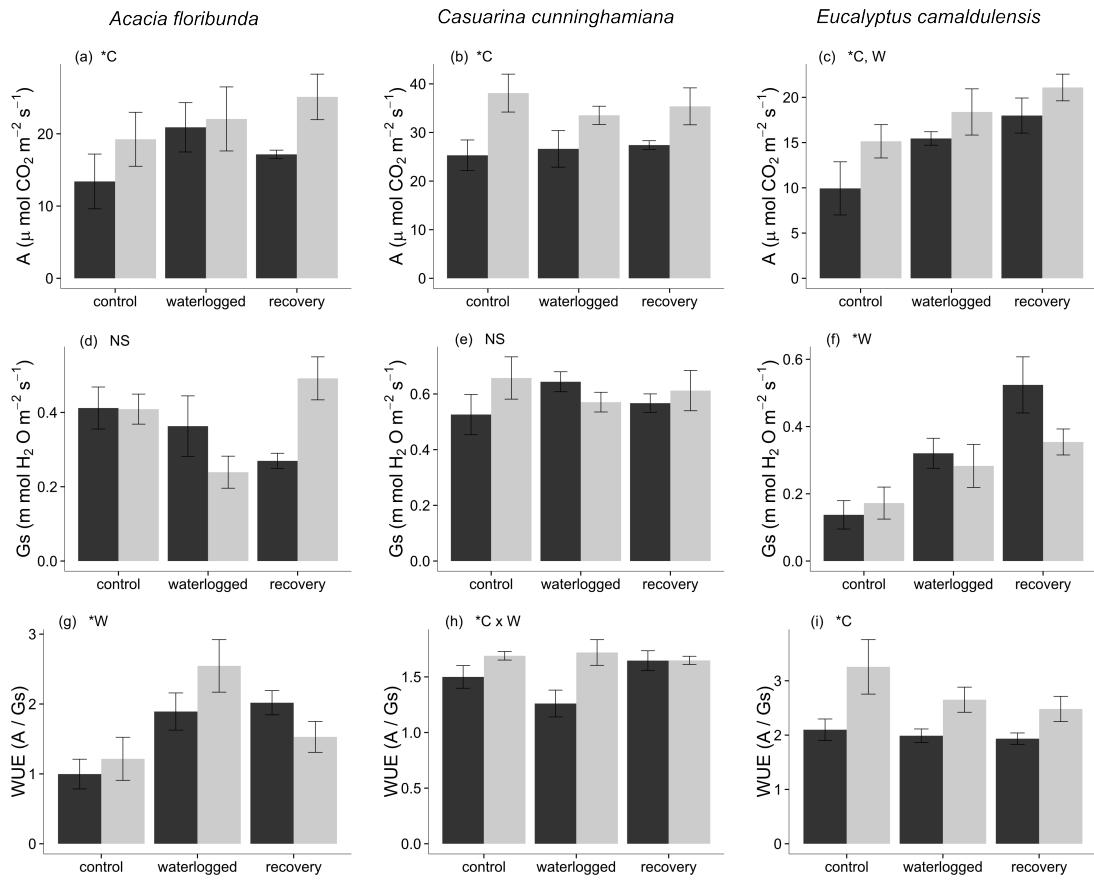


Figure 5.1: Gas exchange measurements under each combination of waterlogging and CO₂ level treatments. Dark shaded columns represent measurements under ambient atmospheric CO₂ concentration (390 ppm), light shaded columns represent measurements under elevated atmospheric CO₂ concentration (550 ppm). Error bars represent the standardised mean error.

* letters denote statistical significance of differences between treatment combinations (NS = no significant difference, C = significant difference between CO₂ level treatments, W = significant difference between waterlogging treatments).

Biomass production and allocation

Waterlogging status and CO₂ level interacted strongly for one species: eCO₂ stimulation of all fractions of biomass production in *C. cunninghamiana* was diminished following recovery from waterlogging.

Total root biomass of plants recovering from waterlogging was lower than control plants for *A. floribunda* ($p = 0.028$, Fig. 1.2a). A significant interaction effect was identified for *C. cunninghamiana* ($p = 0.049$): total root biomass was substan-

tially increased under eCO₂ for control ($p = 0.011$) but not recovery plants (Fig. 1.2b). Neither CO₂ level nor waterlogging had an effect on total root biomass for *E. camaldulensis* (Fig. 1.2c).

Fine root biomass of *A. floribunda* was lower in recovery plants than control plants ($p = 0.005$), with no CO₂ effect (Fig. 1.2d). A marginally significant interaction effect was also present for *C. cunninghamiana* fine root biomass ($p = 0.076$); post-hoc analysis confirmed that control but not recovery plants had significantly greater fine root biomass under eCO₂ ($p = 0.008$) (Fig. 1.2e). Waterlogging stimulated fine root growth in *E. camaldulensis* ($p = 0.046$) but CO₂ level had no effect (Fig. 1.2f).

Neither CO₂ level nor waterlogging had any effect on shoot biomass for *A. floribunda* (Fig. 1.2g) or *E. camaldulensis* (Fig. 1.2i). As with total root biomass and fine root biomass, CO₂ level and waterlogging influenced *C. cunninghamiana* biomass interactively ($p = 0.009$): shoot biomass was higher under eCO₂ for control ($p = 0.015$) but not recovery plants (Fig. 1.2h).

Root mass fraction (RMF) was decreased by waterlogging for all species, but no significant CO₂ or interaction effects were found (Fig. 1.2j-l). RMF of *A. floribunda* was lower in waterlogged than control plants ($p < 0.0001$), and lower in waterlogged than recovery plants ($p < 0.0001$). RMF of *A. floribunda* recovery plants was also lower than control plants ($p = 0.016$). RMF of both *C. cunninghamiana* and *E. camaldulensis* was lower in waterlogged than control plants ($p < 0.0001$), and lower in waterlogged than recovery plants ($p < 0.0001$), but there was no difference between recovery and control plants.

Functional traits

We found no evidence to suggest that CO₂ mediates functional traits in response to waterlogging status.

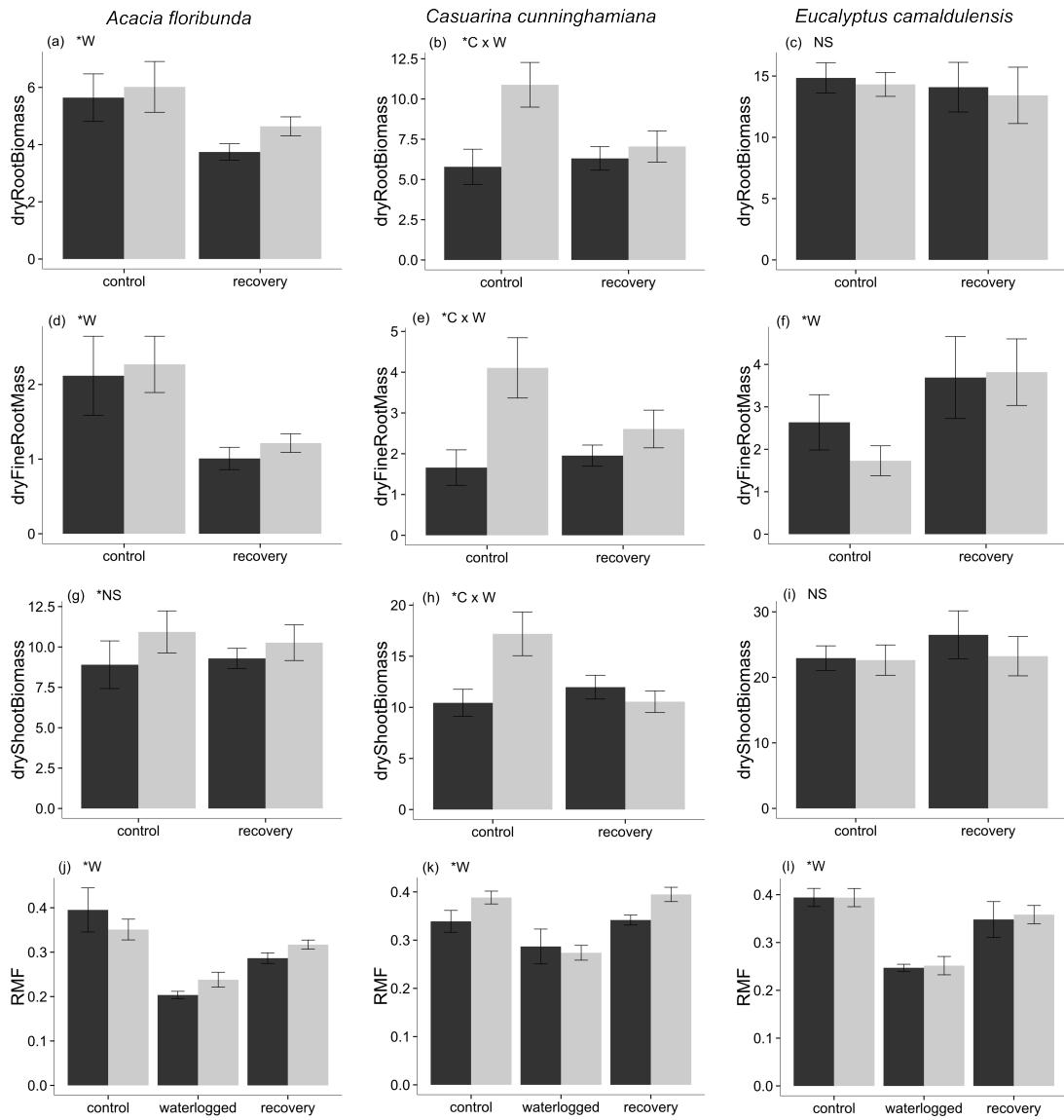


Figure 5.2: Biomass and root mass fraction (RMF) measurements under each combination of waterlogging and CO₂ level treatments. Dark shaded columns represent measurements under ambient CO₂ concentration (390 ppm), light shaded columns represent measurements under elevated CO₂ concentration (550 ppm). Error bars represent the standardised mean error.

* letters denote statistical significance of differences between treatment combinations (NS = no significant difference, C = significant difference between CO₂ level treatments, W = significant difference between waterlogging treatments).

Fine root dry matter content (fRDMC) was higher in waterlogged *A. floribunda* than recovery plants ($p = 0.027$), but not different between control and recovery or control and waterlogged plants. A marginally significant interaction effect was also

present for *A. floribunda* ($p = 0.067$), but no differences were significant upon post-hoc analysis. Waterlogging status also affected *E. camaldulensis* fRDMC (Fig. 1.3b): control plants had higher fRDMC than waterlogged plants ($p = 0.018$), and recovery plants ($p = 0.053$) (marginally significant). eCO₂ was associated with significantly increased fRDMC in *C. cunninghamiana* ($p = 0.013$, Fig. 1.3c), but waterlogging status had no effect.

Waterlogged *A. floribunda* had lower SLA than control ($p = 0.001$), and recovery plants ($p < 0.0001$) (Fig. 1.3 d). Waterlogged *E. camaldulensis* had higher SLA than control ($p = 0.0013$) and recovery plants ($p = 0.0006$) (Fig. 1.3f). Waterlogging status had no effect on *C. cunninghamiana* SLA (Fig. 1.3e). CO₂ level had no effect on the SLA of any species.

Stem density in *C. cunninghamiana* was increased under elevated CO₂ ($p = 0.0177$) (Fig. 1.3h). Stem density was lower in waterlogged *C. cunninghamiana* than control ($p = 0.0167$) or recovery plants (0.050) Neither CO₂ nor waterlogging status had any effect on stem density of *A. floribunda* (Fig. 1.3g) or *E. camaldulensis* (Fig. 1.3i).

5.4 Discussion

We found inconsistent effects of atmospheric CO₂ concentration and waterlogging status on growth, gas exchange and functional traits between species of riparian tree seedlings and no evidence for a consistent effect of elevated CO₂ in mediating plant responses to flooding.

While photosynthesis is the primary means by which plants accumulate biomass, increases in leaf-level photosynthesis may not necessarily translate to biomass gains. Metabolically costly responses to waterlogging tolerance, such as anaerobic catabolism, detoxification of reactive oxygen species and metal ions, and morphological adaptations such as formation of adventitious roots may act as energetic

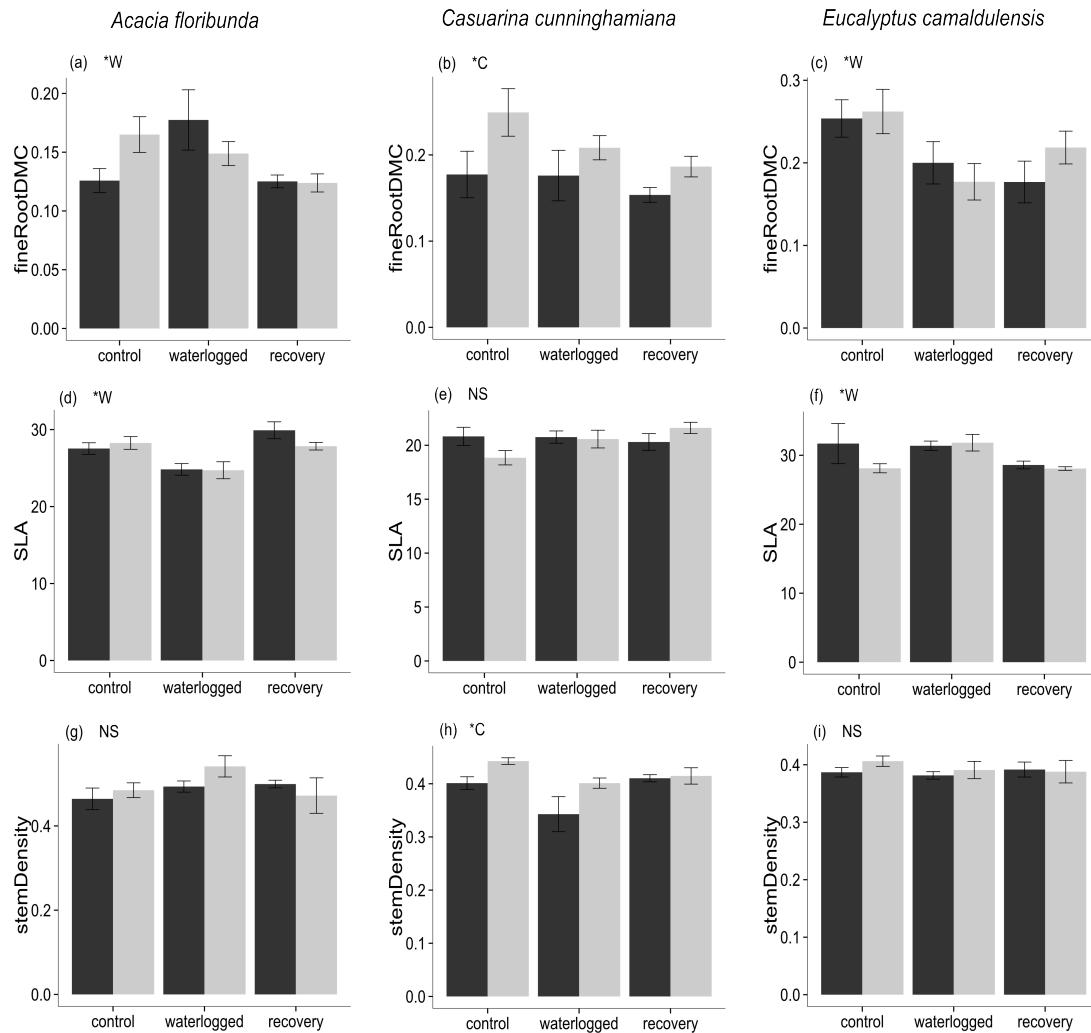


Figure 5.3: Functional trait measurements under each combination of waterlogging and CO₂ level treatments. Dark shaded columns represent measurements under ambient CO₂ concentration (390 ppm), light shaded columns represent measurements under elevated CO₂ concentration (550 ppm). Error bars represent the standardised mean error. * letters denote statistical significance of differences between treatment combinations (NS = no significant difference, C = significant difference between CO₂ level treatments, W = significant difference between waterlogging treatments).

sinks (Colmer and Voesenek, 2009). Relationships between photosynthetic rate and biomass responses to waterlogging and CO₂ level treatments in this study varied widely between species.

For the three species studied here, only for *C. cunninghamiana* was an interactive effect of CO₂ concentration and waterlogging status found. Biomass of shoot, total root and fine root fractions was significantly higher under eCO₂ for control *C.*

cunninghamiana plants, but not for plants which were recovering from waterlogging, despite increased rates of CO₂ assimilation. No significant interaction effect on root mass fraction was found, but visual inspection of the data (Fig. 1.2k) indicates that eCO₂ stimulation of RMF was present in control and recovering, but not waterlogged plants. Re-establishment of pre-waterlogging biomass allocation appears to have occurred despite no differences in total biomass. We found no evidence to support the hypothesis that eCO₂ facilitated biomass recovery by increasing the rate of fine root production in *C. cunninghamiana* after waterlogging. Photosynthesis remained higher in recovering plants under eCO₂, indicating that their ability to convert the extra photosynthate produced under eCO₂ into biomass was impaired by waterlogging.

No increase in any biomass fraction was associated with increased photosynthetic rate under eCO₂ for either *A. floribunda* or *E. camaldulensis*. *A. floribunda* underwent substantial root mortality in response to waterlogging, although the presence of spongy white aerenchymous adventitious roots indicated a degree of morphological adaptation to anoxia (Evans, 2004). Conversely, waterlogging stimulated fine root growth in *E. camaldulensis*. A proliferation of fine aerenchymous roots both below and above the water line was observed in waterlogged and recovered plants, corresponding to increased fine root mass compared with control plants. The strong morphological response of *E. camaldulensis* root systems combined with higher photosynthetic rate in recovering compared with control plants, and higher stomatal conductance in waterlogged plants than control or recovering plants, indicates that *E. camaldulensis* responded favourably to waterlogging in this study. This growth response concurs with the results of previous studies (Marcar, 1993; Sena-Gomes and Kozlowski, 1980), although see Kogawara et al. (2006). No evidence was found to support the hypothesis that higher water use efficiency under eCO₂ might facilitate photosynthesis where waterlogging had caused stomatal closure. WUE was altered by waterlogging only in *A. floribunda*, and by

CO₂ level only in *E. camaldulensis*. WUE was dependent on the combination of waterlogging status and CO₂ level in *C. cunninghamiana*, being higher at eCO₂ than aCO₂ for waterlogged plants only. The lack of stomatal response to waterlogging indicates that higher WUE under eCO₂ is not the mechanism maintaining photosynthetic rate under waterlogging for *C. cunninghamiana*.

Waterlogging and atmospheric CO₂ level also altered functional traits in a species-specific manner, but no interactive effects were found. Traits of *A. floribunda* and *E. camaldulensis* were affected by waterlogging status but not CO₂ level, whereas *C. cunninghamiana* was affected by CO₂. Decreased SLA and increased fine root dry matter content a proxy for fine root tissue density (Birouste et al., 2013) in waterlogged *A. floribunda* indicate a shift towards the slower growth longer lifespan end of their respective economic spectra (Reich, 2014), but this shift was not sustained following the refractory period. A corresponding pattern in water use efficiency corroborates this inference. Higher root dry matter content under waterlogging has been linked to the requirement for structural support of air spaces in aerenchymous root tissue (Ryser et al., 2011). Suberization of root hypodermal tissue often occurs under waterlogging as a means of reducing radial oxygen loss (De Simone et al., 2002; Visser et al., 2000) and may also increase root dry matter content. *E. camaldulensis* responded in an opposite manner, with higher SLA under waterlogging, and lower root dry matter content under waterlogging and after the refractory period. This species appears to employ an opportunistic fast growth ecological strategy in response to waterlogging, involving proliferation of lower density roots, and lower carbon investment in leaf tissue (Reich, 2014; Wright et al., 2004). We found no evidence for decreased SLA under eCO₂ as previously described (Poorter and Navas, 2003). Previous studies report inconsistent effects of eCO₂ on fine root dry matter content in non-riparian species: eCO₂ had no effect on *Liquidambar styraciflua* or *Pinus strobus* fRDMC (Bauer and Berntson, 2001; Iversen et al., 2008), caused a small decrease in *Be-*

tula alleghaniensis (Bauer and Berntson, 2001) and increased fRDMC in cotton (Prior et al., 1994). In this study, eCO₂ significantly increased fine root dry matter content in *C. cunninghamiana* irrespective of waterlogging treatment.

Analysis of gas exchange, biomass accumulation and functional traits after a refractory period provided an opportunity to determine whether responses to waterlogging persisted or were transitory. We were unable to substantiate the hypothesis that eCO₂ would increase the rate of biomass recovery from waterlogging by increasing the rate of fine root turnover. *C. cunninghamiana* was the only species for which eCO₂ altered biomass accumulation, and depression of biomass was observed following the refractory period irrespective of CO₂ level. Although we made no analysis of nodulation rates, nodulation of *C. cunninghamiana* by the nitrogen fixing ascomycete *Frankia* is known to be highest under well aerated soil conditions (Dawson et al., 1989). Reduced nitrogen uptake due to nodule mortality or impairment could account for the constrained biomass response to eCO₂ post-waterlogging (Reich et al., 2006). While eCO₂ did not mitigate growth reduction or mediate changes to functional traits under waterlogging for any species in this glasshouse study, we did observe reduced growth stimulation by eCO₂ in one species. This effect was strong, and evident across all measured biomass fractions. Differential responses to eCO₂ and waterlogging between species in the field could have important ecological consequences. *C. cunninghamiana* is a highly effective agent of biogeomorphic succession in fluvial landscape of south-eastern Australia that is, it facilitates the creation and stabilisation of fluvial landforms (Erskine et al., 2009). Reduction of eCO₂ biomass stimulation by waterlogging could alter spatial patterns of landform stabilisation by *C. cunninghamiana*. Infrequently waterlogged stands on channel banks might be favoured over stands growing on wetter in-channel features such as bars, benches and islands. Differential responses to combined waterlogging and eCO₂ between species notably *C. cunninghamiana* and *A. floribunda*, which are frequently conspecific may also result in composi-

tional changes to riparian plant communities and associated changes in ecosystem functioning.

5.5 Conclusion

Waterlogging and atmospheric CO₂ concentration both have significant consequences for physiological processes, growth and functional characteristics of riparian tree seedlings. The relative importance of these environmental factors varies according to species, as do the specific effects of each on plants. This study adds to the small but growing body of literature describing the interactive effects of waterlogging and CO₂ concentration; notably, the outcome for *C. cunninghamiana* concurs with that found for *Taxodium distichum*, a flood tolerant colonist of alluvial riparian areas in the south eastern United States (Megonigal et al., 2005). Suppression of eCO₂ biomass stimulation in seedlings by waterlogging has the potential to alter demographics and structural dynamics in many Australian riparian communities especially where *C. cunninghamiana* is a keystone species (Woolfrey and Ladd, 2001).

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6 Discussion

In this thesis I explored how natural and altered environmental conditions shape the ecology of riparian plant communities. In this final chapter I aim to summarise the contribution of my thesis to the greater body of riparian plant ecology and river restoration research, outline outstanding questions raised by my work, and present some possible avenues for future work.

6.1 Summary of findings

In Chapter 2, I asked the following research questions: (1) does wood density increase with increasing frequency and magnitude of flood disturbance? (2) does wood density increase with increasing unpredictability of water availability in the riparian zone? (3) does dispersion of wood density peak at intermediate levels of hydrological disturbance? I found evidence for an affirmative answer to all three questions. Community mean wood density was strongly correlated with metrics of frequency and magnitude of flood disturbance, as well as variability of water availability in the riparian zone, and dispersion of wood dispersion indeed peaked at intermediate levels of hydrological disturbance and variability.

In Chapter 3, I asked: (1) Is functional trait diversity related to the frequency and magnitude of flooding disturbance? (2) Is functional trait diversity related to variability in seasonal water availability within the riparian zone? I found strong associations between functional trait diversity and metrics describing frequency and magnitude of flooding disturbance and variability in seasonal water availability within the riparian zone.

In Chapter 4, I investigated relationships between environmental variables and species richness, functional trait diversity, and exotic abundance, with a focus on the role of environmental heterogeneity and modification of river flows and landscapes by human activity. I asked: (1a) do species richness and functional diversity increase and abundance of exotic species decrease monotonically with in-

creasing hydrological heterogeneity? (1b) do species richness, functional diversity and abundance of exotic species show unimodal relationships with hydrological heterogeneity? (2) do species richness and functional diversity decrease and abundance of exotic species increase along gradients of increasing flow modification and catchment land-use intensity? With respect to (1a), patterns of species richness and exotic abundance were opposite to expectation, and findings were inconclusive for functional trait diversity. Our findings were also inconclusive with respect to (1b), with limited evidence that functional diversity is unimodally related to hydrological heterogeneity. Relationships between species richness and exotic abundance with metrics of flow modification opposed our expectation under (2), and while production land use was associated with higher exotic abundance, no effect of land use on species richness was found. I found weak evidence supporting flow modification as a control on functional diversity, and no evidence for an effect of catchment land-use intensity.

In Chapter 5, I tested for interactive effects between eCO₂ and waterlogging on gas exchange, biomass accumulation and allocation, and functional traits in riparian tree seedlings. I found no interactive effects on *Acacia floribunda* or *Eucalyptus camaldulensis*, but strong interactive effects on *Casuarina cunninghamiana*.

6.2 Biogeographic context

The riparian plant communities described here were located primarily along coastally drained rivers in partly constrained valley settings, spanning the temperate southeast and subtropical eastern Australia. Figure 6.1 shows a map of the field sites surveyed in Chapters 2-4. Although no systematic review has summarised ecological knowledge of Australian riparian plant communities, more research attention appears to have been focused on semi-arid, inland-draining systems such as the Murray Darling Basin, or larger tropical rivers, than on these smaller coastal sys-

tems.

Much of the canonical riparian plant ecology literature focuses on alluvial river systems in Europe and North America (Corenblit et al., 2007; Naiman and De-camps, 1997; Naiman et al., 2005; Nilsson et al., 1989; Tabacchi et al., 1998). Flow regimes in south-eastern Australia diverge considerably from this canon: the seasonal regularity which characterises nival European and North American rivers is often absent. In Australia, substantial year-by-year variability is evident and Australian rivers are known for having some of the highest coefficients of flow variability in the world (Peel et al., 2004; Rustomji et al., 2009). South-eastern Australian riparian plants exhibit characteristic species-level responses to seasonality, although there is no general coordination of growth and reproductive phenologies as in the Northern Hemisphere (Ford et al., 1979). As such, Australian riparian plant communities are likely to be adapted to different environmental controls. In common with North American systems, however, the signature of rapid landscape modification has been etched deeply into fluvial landscapes. Many rivers have undergone irreversible transitions in physical and ecological condition following European settlement (Brierley et al., 1999; Fleischner, 1994; Knopf et al., 1988; Wasson, 1994), and the mid-20th century saw the rise of extensive flow impoundment schemes in both continents (Graf, 2006; Lloyd et al., 2004).

This body of work therefore contributes fresh perspective to the global literature, from species pools subject to a different evolutionary history and operating under different environmental conditions to the most commonly described riparian ecosystems.

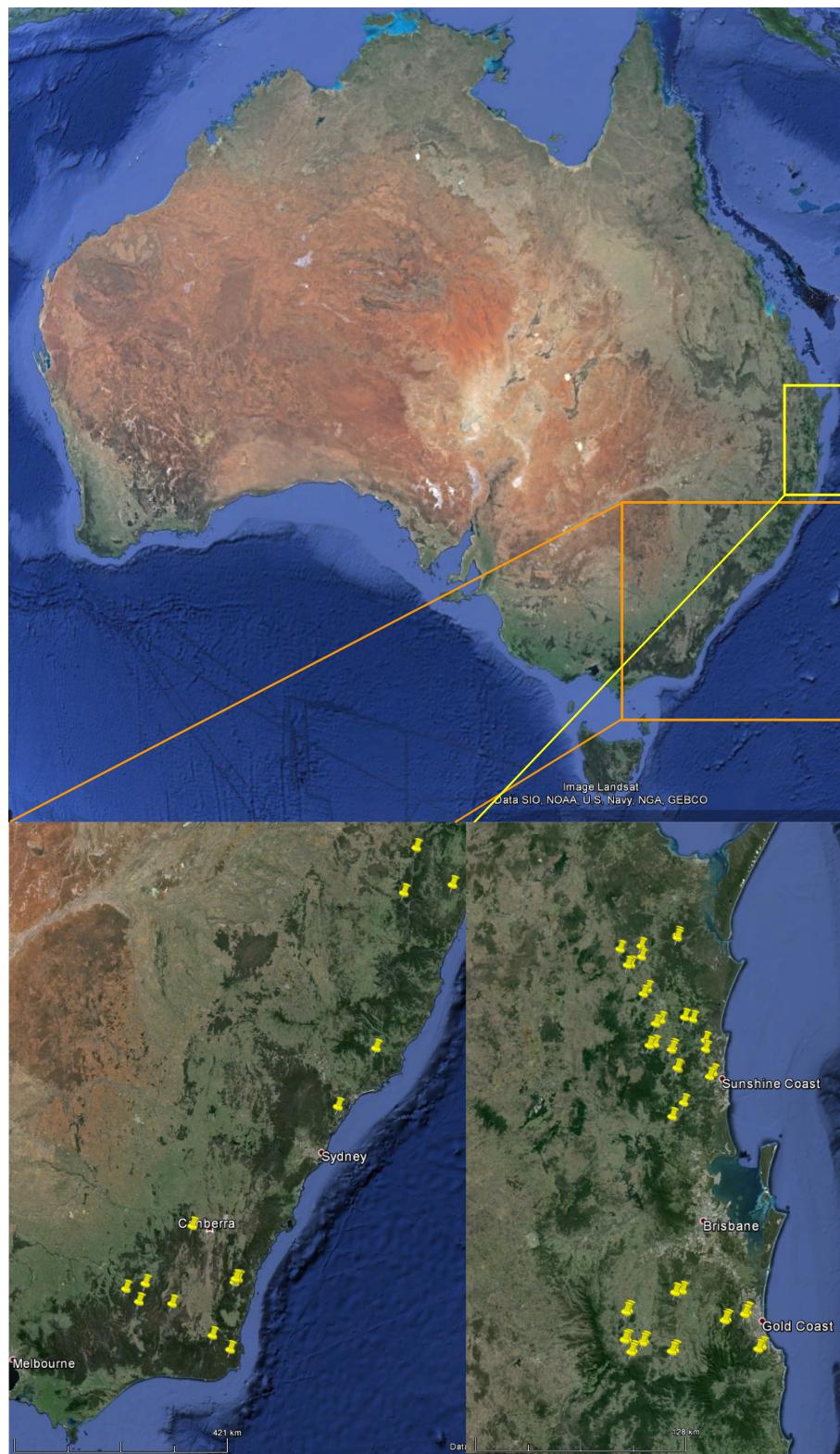


Figure 6.1: Map showing study areas, and geographical distribution of field sites described in Chapters 2 & 3 (lower left) and 4 (lower right) (Google Maps 2015).

6.3 Ecological responses of riparian plant communities to fluvial hydrology

The relationship between environmental heterogeneity and biodiversity has been a key focus of ecologists since the early 1960s (MacArthur and MacArthur, 1961; Stein et al., 2014). Riparian landscapes provide particularly useful model systems for exploring hypotheses about environmental heterogeneity due to strong control of biotic assemblages by fluvial hydrology. In tandem with disturbance, hydrologically-driven environmental heterogeneity has taken a central role in our conceptualisation of how riparian ecosystems function (Naiman et al., 2005; Poff et al., 1997).

Chapters 2, 3 and 4 tested hypotheses derived from this paradigm. Broadly, this work confirms the importance of hydrological heterogeneity and fluvial disturbance in shaping riparian plant assemblages. The specific contribution of these chapters to the riparian literature lies in the mechanistic, functional trait-based approach used. Through the lens of functional traits, I have begun to address questions about how flow regime influences ecological strategies of riparian plants at the community level, and how the functional organisation of communities varies along hydrological gradients.

In Chapter 2, I found that wood density, a functional trait associated with resistance to mechanical disturbance and drought tolerance (Chave et al., 2009; Niklas and Spatz, 2010), varied strongly in response to patterns of hydrology. Community mean values of wood density increased with the intensity of fluvial disturbance and flow heterogeneity; communities which experienced more variable flow conditions were shifted towards the slow, conservative end of the spectrum of resource-economic ecological strategies (Reich, 2014). Wood density in turn influences wood decomposition rates (Mori et al., 2013) which has implications for ecosystem nutrient cycling and energetic fluxes in riparian ecosystems (Harmon

et al., 1986), as well as for the residence time of geomorphically active large woody debris in river systems (Cadol and Wohl, 2010; Gurnell et al., 2002). I also found a humped relationship between community-weighted variance in wood density and the same combined gradient of disturbance and hydrological heterogeneity, lending evidence to general hypotheses (from outside of the riparian literature) that intermediate levels of disturbance should promote divergence in disturbance-response strategies (Grime, 2006; Sonnier et al., 2010). Given the substantial cost to plants incurred in setting down dense woody tissue (Falster, 2006), these findings demonstrate that some of the key trade-offs negotiated by plants in riparian communities are made in response to fluvial disturbance and hydrological heterogeneity.

Plant life forms and qualitatively derived functional groups have been used for some time to describe functional organisation in riparian plant communities (Brinson, 1993; Stromberg, 2013; Stromberg et al., 2010). In Chapters 3 & 4 I derived quantitative, continuous indices of functional diversity from vegetation survey and data for a range of functional traits with the intent of capturing key axes of variation in riparian plant ecological strategy. Using functional traits as descriptors of ecological strategy provides generality across systems (Lavorel and Garnier, 2002; Suding et al., 2008), and negates any requirement for expert knowledge to assign species to qualitative functional groups. These indices of functional diversity also facilitate the use of quantitative modelling methods (Mason et al., 2013), and allow more solid inferences to be made about how individual components of flow regime influence community assembly and ecosystem processes than are possible using taxonomic metrics of diversity (Díaz et al., 1998; Tilman et al., 1997).

Patterns of variation in functional dispersion measured in natural landscapes of coastal south-eastern Australia (described in Chapter 3) showed strong positive relationships with metrics describing hydrological heterogeneity. While I did not systematically describe variation in species richness along hydrological gradients, species richness (but not the number of species used in the functional dispersion

analysis) was significantly positively correlated with functional dispersion. I was able to generate a multiple regression model which explained 80 % of the total variation in functional dispersion using three hydrological metrics. Partitioning of variance between this model and optimal models generated using climatic and soil variables, showed that a substantial proportion of variance explained by hydrology was not co-explained by climate or soil, further demonstrating the dominance of fluvial disturbance and flow variability in shaping the functional structure of these plant communities.

Riparian plant communities in south-eastern Queensland (described in Chapter 4) showed somewhat different responses to hydrology. Several additional environmental variables were taken into account to quantify the degree of anthropogenic modification both to the surrounding catchment and to the flow regime itself. In this study, I found functional richness and functional divergence (as measured by abundance-standardised functional dispersion) were associated with only a limited subset of metrics describing hydrological heterogeneity, and variance partitioning of models showed that relatively little variation in either functional richness or divergence was explained by hydrology when climate and soil properties were taken into account. Flow modification did explain some variation in metrics of functional diversity, but again, not independently. Contrary to our hypotheses, and to patterns commonly described in Northern hydroecological systems (e.g. Naiman and Decamps (1997)), species richness declined as flow regimes became more heterogeneous. The observation that species richness and metrics of functional diversity showed opposite relationships with the same hydrological variables allowed us to determine that communities living under hydrologically heterogeneous conditions were maintaining functional diversity with a reduced species pool.

Outstanding questions about the role of hydrological heterogeneity in structuring communities

Although hydrology was the dominant control on functional traits and functional trait diversity in both regions analysed here, the relative importance of hydrological heterogeneity per se differed. Some of the major outstanding questions in this thesis are why this might have been so, and which aspects of the findings can be generalised or extrapolated to systems in other regions within Australia and across the globe?

It is possible that Australian plant communities in fact have unique relationships with flow heterogeneity, given Australia's title of 'the planet's most hydrologically variable continent' (Peel et al., 2004; Rustomji et al., 2009). A larger comparative study of factors shaping the functional ecology of riparian plant communities would be an essential step towards finding generalities in flow heterogeneity-diversity relationships, and would also provide further opportunity to investigate discontinuities in trends. Riparian researchers are becoming more interested in functional ecology, and it is possible that we will see global syntheses being made over the next decade. Research in regions underrepresented in the riparian ecology literature, such as the tropics and the developing world, would be of particular value in this endeavour.

Absent an exhaustive global comparative synthesis, comparing the specific findings of Chapter 3 and Chapter 4 reveals a possible explanation for their differences. While functional diversity of communities described in Chapter 2 scaled monotonically with most metrics of flow variability, and was positively associated with species richness, functional diversity of communities in south-east Queensland (Chapter 4) was significantly associated with only a small set of metrics describing flow variability (e.g. interannual variability in baseflow index, constancy of monthly maximum flows) and in those cases, relationships were better described

by quadratic models. As noted previously, species richness showed inverted relationships with these metrics. To properly compare the results of these two chapters, a methodological issue must first be addressed: functional dispersion (FDis), *sensu* Laliberté and Legendre (2010), was used in Chapter 3, while standardised effect size FDis (FDis.SES), *sensu* Mason et al. (2013), was used in Chapter 4 as a measure of functional divergence. With the exception of a few outliers, FDis was tightly positively correlated with FDis.SES for the south-east Queensland dataset (Pearson's $r = 0.75$). With respect to species richness, this confirms that standar-dising FDis for abundance was not responsible for inverting the species richness functional diversity relationship.

In our discussion of Chapter 4, I noted that rhythmicity in temporal patterns of energy and resource availability and environmental heterogeneity may both act as controls on riparian plant diversity. I citepd recent work showing that rhythmic seasonal flow activity fosters greater diversity in birds and fishes and greater net primary production in plant communities (Jardine et al., 2015), and that energy (and resource) availability may be more important than environmental heterogeneity in determining patterns of diversity (Lundholm, 2009). Thus differences between the findings of Chapters 3 and 4 could be explained by differences in the influence of these two factors. For this conceptual model to be useful, we need to describe some key components of its structure. Firstly, is it flow rhythmicity *per se* which is important, or simply total energy availability, which happens to be maximised in rhythmic systems? If the former, can flows be both heterogeneous and rhythmic, or are the two factors inherently opposite? For example, can a river with high interannual variability in its baseflow index also experience highly regular summer flood flows? Perhaps cases at extreme ends of each spectrum are less interesting than those at intermediate levels of heterogeneity and energy availability / rhythmicity.

Perhaps a better way of conceptualising environmental control over diversity

might be as a three dimensional relationship, where heterogeneity and energy availability (or flow rhythmicity) are incompletely orthogonal to each other. The curves presented in this thesis would then be two dimensional slices of a three dimensional volume. A challenge for future research in this field is therefore to explicitly include energy availability or flow rhythmicity in hypotheses about flow responses of plant communities, and to attempt to characterise how communities respond to both factors simultaneously.

6.4 Responses of riparian plant communities to anthropogenic environmental change

My interest in the functional ecology of riparian plant communities was initially motivated by the need for new approaches and perspectives towards conserving, rehabilitating and managing riparian landscapes in south-eastern Australia. The 20th century has seen unprecedented change in riverine ecosystems and these changes are likely to intensify over the current century (Hennessy et al., 2008; Nilsson and Berggren, 2000). Compared with Europe and North America, applied river rehabilitation in Australia is somewhat hampered by a lack of basic ecological knowledge (Brooks and Lake, 2007). Thus one of the main aims of this thesis was to inform management with new information about riparian ecology in both natural and modified landscapes.

How might riparian plant communities respond to climate change?

Climate change is predicted to have global impacts on ecosystems in the 21st century (IPCC et al., 2014). Riparian ecosystems are likely to be particularly vulnerable due to their high exposure and sensitivity to changes in climate, in combination with pressures associated with extraction of provisioning ecosystem

services by humans (Capon et al., 2013). Elevated concentrations of carbon dioxide (eCO_2) represent the most direct and obvious change to the atmosphere. The potential influence of eCO_2 on plants and plant communities has been the topic of intensive research over the last two decades. To date, however, the implications for conservation management under high CO_2 regime are highly species and system specific, and are likely to be contingent on a slew of other environmental factors (Norby and Zak, 2011; Poorter and Navas, 2003; Poorter et al., 2011; Reich et al., 2014). Basic research on the ecological effects of eCO_2 is needed for individual systems, and each piece of experimental work contributes to the greater outlook.

Of the three anthropogenic alterations investigated in this thesis, I suggest that elevated atmospheric CO_2 (eCO_2) may have the smallest effect. I showed in Chapter 5 that eCO_2 significantly stimulated growth in only one of three riparian tree seedlings, and this effect was completely negated by inundation. Inundation itself had strong effects on gas exchange, growth and functional traits in all three species. Differential responses between species to combined waterlogging and eCO_2 may have flow-on effects to demographics, competition, and ultimately, community composition.

Chapter 5 contributes to what is currently a very small set of publications investigating the potential for interactive effects between future atmospheric concentrations of CO_2 and inundation or waterlogging events on terrestrial plants (Arenque et al., 2014; Megonigal et al., 2005; Shimono et al., 2012). I included an analysis of functional trait responses, as well as including a recovery phase in the experiment, neither of which have been previously attempted to our knowledge. Fruitful avenues for future work include study of more species, serial waterlogging treatments to better understand how eCO_2 influences on waterlogging recovery, analysis of leaf nutrient concentrations to determine the role of nutrient limitation in suppressing growth stimulation by eCO_2 (Reich et al., 2014), and mesocosm experiments to investigate the implications of eCO_2 waterlogging interactions for

competition.

Greater hydrological variability and intensity of extreme weather events characterise models of high CO₂ climates (Hennessy et al., 2008; Stocker et al., 2013). Our research demonstrates that riparian plant communities vary substantially in their taxonomic and functional composition over gradients of hydrological heterogeneity. As discussed in Chapters 2 and 3 (Lawson et al., 2015a,b), the changing climate is likely to enhance dominance of variability-tolerant ecological strategies associated with traits such as high wood density, and push communities towards more dispersed functional structures. In species-rich communities of south-east Queensland, increased flow heterogeneity may have important consequences for taxonomic diversity, functional redundancy and ecosystem resilience. Greater exotic abundance was associated with more heterogeneous systems in south-eastern Queensland. Despite the lack of association between flow modification and exotic abundance in this study, it remains possible that climate-related increases in hydrological heterogeneity may also result in invasion by exotic species.

Further work is required to integrate observations about riparian plant community responses to hydrological heterogeneity with climate change predictions. Functional trait approaches are likely to be particularly useful in the absence of detailed species-level ecological knowledge (Catford et al., 2012).

Could environmental flows be a useful tool for river rehabilitation in south-eastern Australia?

Hydrology was confirmed as the master variable controlling riparian plant communities (Poff et al., 1997) in both field studies, but flow modification also had a profound influence on species richness in south-eastern Queensland. That homogenised flows were actually associated with increased species richness (and functional diversity, to some extent) runs counter to much of the riparian literature on

flow modification (Lytle and Poff, 2004; Nilsson and Berggren, 2000). As discussed above, increased flow rhythmicity may underlie this unexpected effect. The lack of any association between flow modification and abundance of exotic species also opposes the general body of literature (Catford et al., 2011; Greet et al., 2013). Catchment land use and soil properties explained a substantial proportion of variation in exotic abundance, and may be more important drivers of invasion in this region.

Environmental flows - flows released from dams which are engineered to mimic natural flow events - are the focus of increasing research effort, and may be an important tool in rehabilitation of modified systems (Arthington et al., 2012). Frameworks for developing and using environmental flows, such as Ecological Limits of Hydrological Alteration (ELoHA) (Poff et al., 2010), are predicated on the notion that altered flow regimes are the main cause of degradation in riparian ecosystems. The relationship between flow alteration and degradation is clearly defined in some systems, such as those invaded by *Tamarix spp.* in south-western North America: flood reduction and homogenised flow regimes result in more invasive *Tamarix spp.* and less native *Populus spp.* (Shafroth et al., 2010; Stromberg et al., 2007). Our analysis of patterns of functional diversity in natural landscapes (Chapter 3) led us to conclude that managers should include a component of variability in designed flow regimes to simulate natural flow heterogeneity. In south-east Queensland, the situation is more complicated, and the feasibility of using environmental flows for conservation or restoration depends on the desired outcome. Supporting indigenous biodiversity over exotic species, improving geomorphic condition, generating habitat complexity and maintaining or restoring lost ecosystem processes and services are commonly desired outcomes for environmental flows (Meitzen et al., 2013; Poff et al., 2010; Richter and Thomas, 2007). South-east Queensland communities were particularly sensitive to modification of contingency of monthly minimum flows (year on year variability in monthly minimum flow patterns), suggesting

management efforts aimed solely at maximising taxonomic diversity would do well to increase flow contingency. This approach risks shifting community composition, but may be a reasonable response to offset greater climatic variability under future climates. Our research in south-east Queensland had rather less to say about the potential utility of environmental flows in directing functional diversity and associated ecosystem functionality. Flow modification largely did not have a consistent effect on functional diversity, suggesting that funds and effort may be better spent on local initiatives within catchments, such as improving landholder engagement in rehabilitation projects (McDonald and Williams, 2009).

6.5 Conclusion

Awareness of the economic, societal and intrinsic value of Australian waterways is increasing, and the field of riparian ecology is now progressing rapidly in Australia. We are finding commonalities with more extensively studied river systems in other parts of the world, and also new patterns and processes which give Australian river systems a unique character. I attempted to answer some basic questions about riparian plant communities in south-eastern Australia using methods from modern plant ecology. In my first two studies I was able to clearly validate my hypotheses, while in the third and fourth studies a more complex and unexpected picture arose. Hopefully, I have set a useful stage for further work on the functional ecology of riparian plant communities, and my basic research informs more applied aspects of river management and rehabilitation.

6.6 References

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Appendix 1 (supplementary to Chapter 2)

Table 1: Locations and characteristics of field sites. Hydrological class refers to the classification by Kennard et al. (2010).

Site	Longitude	Latitude	Hydrological class
Snowy Creek	147.413	-36.569	stable winter baseflow
Gibbo River	147.709	-36.756	stable winter baseflow
Goodradigbee River	147.826	-36.444	stable winter baseflow
Nariel Creek	148.731	-36.421	stable winter baseflow
Jacobs River	148.427	-36.727	stable winter baseflow
Tuross River at Belowra	149.709	-36.201	unpredictable baseflow
Genoa River	149.321	-37.174	unpredictable baseflow
Wallagaraugh River	149.714	-37.371	unpredictable baseflow
Mann River	152.105	-29.695	unpredictable baseflow
Cataract Creek	152.217	-28.934	unpredictable baseflow
Jilliby Creek	151.389	-33.246	unpredictable intermittent
Sportsmans Creek	142.981	-29.467	unpredictable intermittent
Mammy Johnsons River	151.979	-32.244	unpredictable intermittent
Wadbilliga River	149.694	-36.259	unpredictable intermittent
Tuross River downstream of Wadbilliga junction	149.761	-36.197	unpredictable intermittent

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Table 2: Summary for Principal Components Analysis across all 24 hydrological metrics described in this study. PC1 here corresponds to the first principal component of variation across metrics which had significant relationships with CWM wood density (Pearson's $r = 0.990$) (see Fig. ?? in the main text for reference).

	PC1	PC2	PC3	PC4	PC5
Standard deviation	3.61	1.86	1.52	1.39	1.04
Proportion of variance	0.543	0.144	0.096	0.080	0.045
Cumulative proportion	0.543	0.688	0.783	0.864	0.909

Table 3: Data density of trait dataset using (a.) site-specific field-sampled values for wood density only; (b.) site-specific field-sampled values combined with averaged values from other sites, and; (c.) (a) and (b) combined with values from wood density databases. For one species (*Eucalyptus camphora* subsp. *humeana*), intraspecific variability was greater than 0.1 g / cm^3 , and the averaged value was deemed not to be representative of the true value. This species was present at 1.4 % cover at site 9.

Site	# species sampled in field (a)	Data density using field sampled values (a)	# species sampled in field at any site (b)	Data density using field sampled values at any site (b)	# species with available trait values (c)	Data density using all values (c)
1	7	0.98	7	0.98	9	1.00
2	1	1.00	1	1.00	1	1.00
3	4	0.97	5	1.00	5	1.00
4	4	0.81	5	0.95	6	0.97
5	5	1.00	5	1.00	5	1.00
6	5	1.00	5	1.00	5	1.00
7	4	0.92	5	0.94	5	0.94
8	7	0.98	8	1.00	8	1.00
9	3	0.63	5	0.70	8	0.84
10	3	0.64	6	0.97	6	0.97
11	4	1.00	4	1.00	4	1.00
12	3	0.62	6	0.88	8	0.98
13	8	0.92	9	0.95	12	1.00
14	4	0.75	5	0.80	8	0.86
15	5	0.92	5	0.92	6	1.00

Table 4: Sources of wood trait values for species which could not be sampled in the field.

<i>Species</i>	<i>Source of wood density value</i>
<i>Guioa semiglaucia</i>	Kooyman & Westoby (2009)
<i>Pittosporum spinescens</i>	Stuart (2011)
<i>Cassinia trinervia</i>	Tng & Bowman (2013)
<i>Bedfordia arborescens</i>	Tng & Bowman (2013)
<i>Prostanthera lasianthos</i>	Tng & Bowman (2013)
<i>Pultenaea juniperina</i>	Tng & Bowman (2013)
<i>Ligustrum sinense</i>	Martnez-Cabrera et al. (2009)
<i>Grevillea robusta</i>	Chave et al. (2009) - averaged value
<i>Notelaea longifolia</i>	Chave et al. (2009)
<i>Trema tomentosa subsp. <i>aspera</i></i>	Chave et al. (2009) - averaged value

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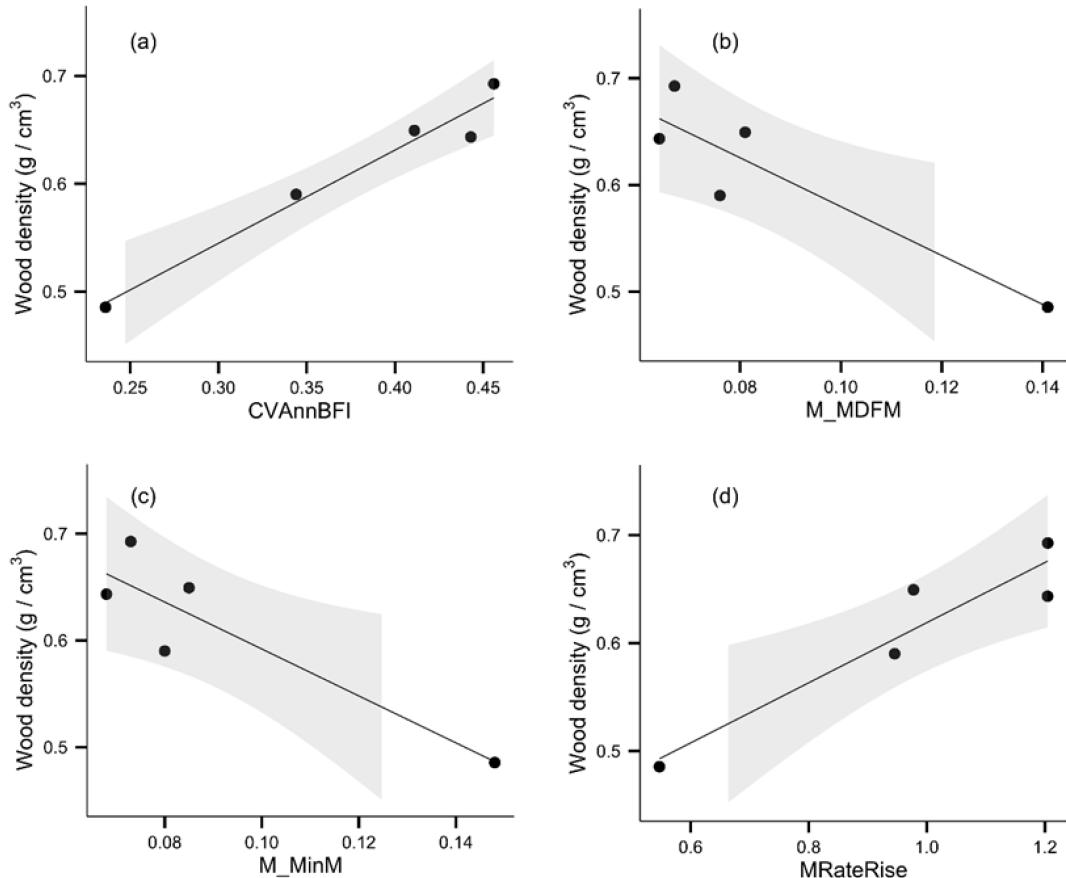


Figure 1: Relationships between wood density of *Casuarina cunninghamiana* and hydrological metrics describing a.) interannual variability in baseflow index (CVAnnBFI) ($R^2 = 0.963$, $P = 0.003$); b.) contingency of monthly mean daily flow (M_MDFM) ($R^2 = 0.826$, $P = 0.033$); c.) contingency of monthly minimum daily flow (M_MinM) ($R^2 = 0.812$, $P = 0.037$); d.) mean flood rise rate (MRateRise)) ($R^2 = 0.885$, $P = 0.017$). Shaded areas depict the 95 % confidence interval around the regression model.

Appendix 2a (supplementary to Chapter 3)

Table 5: Location and characteristics of field sites.

<i>Site</i>	<i>Gauge Name</i>	<i>Longitude</i>	<i>Latitude</i>	<i>Catchment area (km²)</i>	<i>Elevation (m asl)</i>
1	Mammy Johnsons River at Pikes Crossing	151.979	-32.244	158	104
2	Wallagaraugh River at Princes Highway	149.714	-37.371	477	35
3	Genoa River at Bondi	149.321	-37.174	234	417
4	Wadbilliga River at Wadbilliga	149.694	-36.259	126	201
5	Tuross River D/S Wadbilliga Junction	149.761	-36.197	918	79
6	Tuross River at Belowra	149.709	-36.201	564	105
7	Jacobs River at Jacobs Ladder	148.427	-36.727	184	343
8	Nariel Creek at Upper Nariel	147.826	-36.444	261	711
9	Gibbo River at Gibbo Park	147.709	-36.756	390	515
10	Snowy Creek at Below Granite Flat	147.413	-36.569	416	331
11	Mann River at Mitchell	152.105	-29.695	890	401
12	Cataract Creek at Sandy Hill	152.217	-28.934	237	595
13	Sportsmans Creek at Gurranang Siding	152.981	-29.467	205	13
14	Goodradigbee River at Brindabella	148.731	-35.421	432	510
15	Jilliby Creek at U/S Wyong River	151.389	-33.246	93	39

Table 6: Importance of components, from Principal Components Analysis of the set of 23 hydrological metrics used as explanatory variables in this study.

	<i>PC1</i>	<i>PC2</i>	<i>PC3</i>	<i>PC4</i>	<i>PC5</i>
Standard deviation	3.848	1.824	1.377	0.935	0.788
Proportion of variance	0.644	0.145	0.082	0.038	0.027
Cumulative proportion	0.644	0.788	0.871	0.909	0.936

Table 7: Loadings across principal components for the set of 23 hydrological metrics used in this study.

<i>metric</i>	<i>PC1</i>	<i>PC2</i>	<i>PC3</i>	<i>PC4</i>	<i>PC5</i>
HSPeak	-0.24	0.09	0.23	0.13	0.02
MDFAnnHSNum	-0.08	-0.46	-0.08	-0.39	0.03
CVAnnHSNum	0.00	0.40	-0.34	0.43	0.06
CVAnnHSPeak	-0.19	0.06	-0.42	-0.22	0.03
MRateRise	-0.22	-0.18	0.20	0.18	0.12
MRateFall	-0.21	-0.25	0.10	0.22	-0.02
CVAnnMRateRise	-0.22	0.26	-0.02	-0.15	0.02
CVAnnMRateFall	-0.24	0.14	0.08	-0.05	0.22
AS20YrARI	-0.25	0.02	0.01	0.05	-0.02
C_MDFM	0.24	-0.10	-0.14	0.12	0.24
M_MDFM	0.25	0.01	0.02	0.09	-0.30
C_MinM	0.24	-0.07	-0.15	0.19	0.14
M_MinM	0.22	0.11	0.10	0.10	-0.53
C_MaxM	0.02	-0.43	0.33	0.27	0.10
M_MaxM	0.25	-0.02	0.00	0.07	-0.01
MDFMDFSpring	0.24	0.08	0.11	-0.19	0.19
MDFMDFSummer	-0.18	-0.19	-0.44	0.19	0.07
MDFMDFAutumn	-0.23	-0.13	-0.04	0.17	-0.42
MDFMDFWinter	0.14	0.30	0.40	-0.13	0.23
CVMDFSpring	-0.22	0.10	0.20	0.35	0.14
CVMDFSummer	-0.22	0.11	0.14	-0.20	-0.42
CVMDFAutumn	-0.24	0.02	0.01	-0.24	0.09
CVMDFWinter	-0.21	0.22	0.03	0.08	0.06

Table 8: Summary statistics for hydrological variables. From left: minimum, maximum, mean and standard deviation.

<i>metric</i>	<i>min</i>	<i>max</i>	<i>mean</i>	<i>sd</i>
HSPeak	5.38	29.81	16.67	8.34
MDFAnnHSNum	2.8	5.93	4.1	0.96
CVAnnHSNum	0.48	0.84	0.74	0.11
CVAnnHSPeak	0.24	1.47	0.69	0.34
MRateRise	0.2	1.99	0.91	0.57
MRateFall	0.07	0.8	0.34	0.23
CVAnnMRateRise	0.43	1.18	0.85	0.25
CVAnnMRateFall	0.41	1.46	0.9	0.34
AS20YrARI	17.94	209.99	126.13	81.19
C_MDFM	0.05	0.31	0.14	0.09
M_MDFM	0.06	0.2	0.12	0.05
C_MinM	0.01	0.27	0.12	0.08
M_MinM	0.07	0.16	0.11	0.03
C_MaxM	0.19	0.44	0.28	0.09
M_MaxM	0.04	0.18	0.09	0.06
MDFMDFSpring	0.19	1.81	1.02	0.55
MDFMDFSummer	0.42	1.49	0.88	0.33
MDFMDFAutumn	0.28	1.82	1	0.52
MDFMDFWinter	0.64	1.44	1.08	0.25
CVMDFSpring	0.36	2.1	1.12	0.54
CVMDFSummer	0.6	1.66	1.15	0.39
CVMDFAutumn	0.48	1.49	1.07	0.35
CVMDFWinter	0.46	1.99	1.05	0.46

Bioclimatic variables assessed for relationships with FDis:

Annual Mean Temperature

Mean Diurnal Range (Mean of monthly (max temp - min temp))

Isothermality (BIO2/BIO7) (* 100)

Temperature Seasonality (standard deviation * 100)

Max Temperature of Warmest Month

Min Temperature of Coldest Month

Temperature Annual Range (BIO5-BIO6)

Mean Temperature of Wettest Quarter

Mean Temperature of Driest Quarter

Mean Temperature of Warmest Quarter

Mean Temperature of Coldest Quarter

Annual Precipitation

Precipitation of Wettest Month

Precipitation of Driest Month

Precipitation Seasonality (Coefficient of Variation)

Precipitation of Wettest Quarter

Precipitation of Driest Quarter

Precipitation of Warmest Quarter

Precipitation of Coldest Quarter

Edaphic variables assessed for relationships with FDis:

Available Water Capacity

Bulk Density Whole Earth (g cm⁻³)

Clay (%)

Depth of Regolith (m)

Depth of Soil (m)

Effective Cation Exchange Capacity (meq / 100 g)

Total Nitrogen (%)

pH CaCl₂

Total Phosphorous (%)

Silt (%)

Sand (%)

Organic Carbon (%)

Further information on soil variables can be found at:

<http://www.clw.csiro.au/aclep/soilandlandscapegrid> (accessed 09/06/2015)

Appendix 2b (supplementary to Chapter 3)

Table 9: Data density information for trait dataset. Coverage describes the total proportional coverage at a site for which species were included in the analysis. Density values for each trait describe the proportional coverage at a site for which data for that trait were included in the analysis. N.B. leaf narrowness and wood density were not available for grasses or ferns; seed mass and flowering period were also not available for ferns.

<i>site</i>	<i>coverage</i>	<i>wood density</i>	<i>max. height</i>	<i>seed mass</i>	<i>SLA</i>	<i>flowering period</i>	<i>leaf narrowness</i>
1	0.98	0.615	1	0.846	1	0.923	0.692
2	0.959	0.333	1	0.667	1	0.667	0.333
3	0.949	0.455	1	0.727	1	0.727	0.545
4	0.903	0.4	1	0.867	1	0.867	0.6
5	0.968	0.455	1	1	1	1	0.545
6	0.964	0.7	1	1	1	1	0.7
7	1	0.5	1	1	0.9	1	0.7
8	1	0.529	1	0.882	1	0.882	0.765
9	0.988	0.474	1	0.842	1	0.842	0.737
10	0.976	0.583	1	0.917	1	0.917	0.667
11	0.96	0.188	1	1	0.938	1	0.688
12	0.992	0.381	1	0.952	0.952	0.952	0.714
13	0.935	0.55	0.95	0.9	1	0.9	0.7
14	1	0.636	1	1	1	1	1
15	0.963	0.455	1	0.909	0.909	0.909	0.727

Table 10: Summary statistics for trait dataset. From left: minimum, maximum, mean and standard deviation.

<i>trait</i>	<i>min</i>	<i>max</i>	<i>mean</i>	<i>sd</i>
Max. height (m)	0.2	50	10.47	13.18
Seed mass (mg)	0.04	323.99	16.55	45.06
SLA (m^2 / kg)	1.41	63.27	17.93	14
Flowering period length (proportion of year)	0.17	1	0.45	0.24
Leaf narrowness (unitless ratio)	0.59	233.33	9.86	32.53
Wood density (g / cm^3)	0.33	0.95	0.61	0.13

Table 11: Importance of principal components PC1 – PC5 from Principal Components Analysis of trait dataset, using species with data available for all traits (55 species).

	<i>PC1</i>	<i>PC2</i>	<i>PC3</i>	<i>PC4</i>	<i>PC5</i>	<i>PC6</i>
Standard deviation	1.3938	1.0962	1.0827	0.9247	0.7438	0.52457
Proportion of variance	0.3238	0.2003	0.1954	0.1425	0.0922	0.04586
Cumulative proportion	0.3238	0.5240	0.7194	0.8619	0.9541	1

Table 12: Importance of principal components PC1 – PC5 from Principal Components Analysis of trait dataset, using species with data available for SLA, maximum height, seed mass and flowering period length (97 species).

	<i>PC1</i>	<i>PC2</i>	<i>PC3</i>	<i>PC4</i>
Standard deviation	1.4160	1.0016	0.8326	0.54649
Proportion of variance	0.5012	0.2508	0.1733	0.07466
Cumulative proportion	0.5012	0.7520	0.9253	1

Appendix 2c (supplementary to Chapter 3)

Table 13: Statistics for univariate linear regression models comparing FDis with hydrological metrics. *p.adj* represents *p* values which have been adjusted to control the false discovery rate. Relationships which remained significant following adjustment are shown in bold typeface. * All models are linear apart from M_MinM and CVMDFSummer, for which a quadratic model (*df* = 2,12) provided a substantially better fit.

<i>metric</i>	<i>p</i>	<i>p.adj</i>	<i>R2</i>	<i>F(1,13)</i>
CVAnnHSPeak	0.001	0.0152	0.577	17.750
M_MinM	0.0094	0.0278	0.540	*7.0560
MDFMDFSummer	0.0031	0.023	0.503	13.170
CVMDFSummer	0.0218	0.0325	0.472	*5.3560
CVMDFWinter	0.0096	0.0278	0.414	9.194
CVAnnMRateRise	0.011	0.0278	0.403	8.781
CVAnnMRateFall	0.0129	0.0278	0.390	8.299
MDFMDFSpring	0.0134	0.0278	0.386	8.180
AS20YrARI	0.0148	0.0278	0.377	7.879
M_MDFM	0.0209	0.0325	0.347	6.908
M_MaxM	0.0258	0.0325	0.328	6.330
CVMDFSpring	0.026	0.0325	0.327	6.313
CVMDFAutumn	0.0342	0.0386	0.301	5.595
CVAnnHSNum	0.036	0.0386	0.296	5.468
HSPeak	0.0648	0.0648	0.238	4.069
MDFMDFWinter	0.0881	0.078	0.207	3.401
C_MaxM	0.0885	0.078	0.207	3.392
C_MDFM	0.1086	0.0861	0.186	2.968
MDFMDFAutumn	0.1091	0.0861	0.185	2.959
C_MinM	0.1361	0.1021	0.163	2.524
MRateRise	0.1556	0.1072	0.149	2.272
MRateFall	0.1572	0.1072	0.148	2.253
MDFAnnHSNum	0.727	0.4741	0.010	0.127

Appendix 3a (supplementary to Chapter 4)

Table 14: Importance of components, from Principal Components Analysis of the set of 18 hydrological metrics used as explanatory variables in this study.

	<i>PC1</i>	<i>PC2</i>	<i>PC3</i>	<i>PC4</i>	<i>PC5</i>
Standard deviation	2.787	1.995	1.273	1.079	0.996
Proportion of variance	0.431	0.221	0.090	0.065	0.042
Cumulative proportion	0.431	0.653	0.743	0.807	0.862

Table 15: Loadings across principal components for the set of 18 hydrological metrics used as explanatory variables in this study.

<i>metric</i>	<i>PC1</i>	<i>PC2</i>	<i>PC3</i>	<i>PC4</i>	<i>PC5</i>
MDFMDFWet	-0.068	0.127	-0.647	-0.183	0.210
MDFMDFDry	0.261	-0.226	-0.132	-0.141	0.243
CVMDFWet	-0.300	-0.102	0.242	-0.194	0.210
CVMDFDry	-0.331	-0.134	0.043	0.125	-0.046
HSPeak	-0.307	-0.001	-0.272	0.190	-0.018
HSMeanDur	0.261	-0.313	-0.046	0.068	-0.016
CVAnnHSPeak	-0.296	0.063	-0.210	0.082	0.131
CVAnnHSMeanDur	0.141	-0.367	0.150	0.312	0.029
LSPeak	-0.137	0.384	-0.023	0.314	0.257
LSMeanDur	-0.283	-0.193	-0.067	-0.336	0.205
CVAnnLSPeak	0.095	-0.342	0.069	-0.350	0.330
CVAnnLSMeanDur	-0.121	-0.242	-0.199	0.130	0.311
BFI	0.334	-0.020	-0.026	0.205	0.215
CVAnnBFI	-0.250	-0.286	-0.139	0.160	-0.235
C_MinM	0.200	-0.225	-0.403	0.394	-0.045
M_MinM	0.172	0.159	-0.211	-0.233	-0.451
C_MaxM	-0.154	-0.345	-0.155	-0.202	-0.456
M_MaxM	0.259	0.175	-0.246	-0.283	0.066

Table 16: Summary statistics for trait data.

<i>trait</i>	<i>mean</i>	<i>SD</i>
flowering duration (months)	4.72	2.58
leaf area (cm^2)	28.61	28.05
maximum height (m)	19.79	13.98
seed mass (mg)	365.99	2078.8
SLA (cm^2/g)	15.3	7.42
wood density (g/cm^3)	0.609	0.13

Table 17: Proportional abundance of plants represented in the functional diversity analysis at each site.

<i>site</i>	<i>Total cover (individuals Ha^{-1})</i>	<i>Represented cover (individuals Ha^{-1})</i>	<i>Proportion represented</i>
1	8365	8219	0.983
2	13698	13643	0.996
3	28142	22487	0.799
4	9567	8177	0.855
5	3193	3179	0.996
6	25237	25140	0.996
7	14409	12887	0.894
8	9458	9384	0.992
9	16578	15068	0.909
10	12505	11118	0.889
11	42275	35464	0.839
12	9320	9320	1.000
13	25981	23881	0.919
14	12954	12007	0.927
15	11103	10882	0.980
16	20669	16540	0.800
17	25177	18199	0.723
18	4613	4219	0.915
19	3657	3443	0.942
20	27249	23889	0.877
21	23301	23008	0.987
22	15639	13730	0.878
23	10855	6067	0.559
24	17888	15538	0.869
25	3869	2603	0.673
26	14070	11862	0.843
27	17238	14213	0.825
28	13756	9638	0.701
29	7249	7208	0.994
30	21555	21483	0.997
31	7296	7227	0.991
32	5307	5307	1.000
33	19417	19046	0.981
34	9942	9782	0.984
35	8202	8185	0.998
36	3745	3607	0.963
37	13851	13535	0.977
38	18326	15187	0.829
39	8410	5840	0.694
40	5360	5283	0.986

Table 18: Proportion of species included in the functional diversity analysis for which trait values were available.

<i>trait</i>	<i>data density</i>
flowering duration	0.891
growth form	1
leaf area	0.983
maximum height	0.971
seed mass	0.868
SLA	0.661
wood density	0.672

Appendix 3b (supplementary to Chapter 4)

Linear regression model statistics					Quadratic regression model statistics											
metric	P	R2.linear	est	stderr	t	metric	P	R2.adj	est	stderr	t	p.term	est.quad	stderr.quad	t.quad	p.term.quad
C_MinM	0.004	0.202	-0.255	0.082	-3.098	C_MinM	0.003	0.237	-0.688	0.235	-2.927	0.006	1.335	0.683	1.955	0.058
clim_pdry	0.000	0.375	0.001	0.000	4.774	clim_pdry	0.000	0.341	0.001	0.002	0.345	0.732	0.000	0.000	0.137	0.892
clim_pwet	0.000	0.390	0.000	0.000	4.932	clim_pwet	0.000	0.357	0.000	0.000	0.522	0.605	0.000	0.000	0.068	0.946
clim_tcld	0.050	0.098	0.016	0.008	2.027	clim_tcld	0.031	0.126	0.446	0.239	1.869	0.069	-0.015	0.008	-1.805	0.079
clim_tsea	0.000	0.349	-0.001	0.000	-4.514	clim_tsea	0.000	0.341	-0.009	0.006	-1.376	0.177	0.000	0.000	1.223	0.229
CVAnnHSMeanDur	0.013	0.152	-0.156	0.060	-2.609	CVAnnHSMeanDur	0.031	0.127	-0.573	0.445	-1.287	0.206	0.437	0.463	0.944	0.351
						CVAnnHSPeak	0.027	0.133	-0.486	0.223	-2.177	0.036	0.350	0.143	2.445	0.019
exotics	0.032	0.115	-0.087	0.039	-2.224											
FRic.SES	0.050	0.098	-0.048	0.023	-2.029											
HSMeanDur	0.010	0.164	-0.013	0.005	-2.727	HSMeanDur	0.001	0.260	-0.107	0.036	-2.990	0.005	0.008	0.003	2.659	0.012
leaf.area	0.023	0.129	0.015	0.006	2.371	leaf.area	0.016	0.157	0.073	0.033	2.230	0.032	-0.006	0.003	-1.817	0.077
						LSPeak.mod	0.035	0.121	0.085	0.041	2.086	0.044	-0.177	0.066	-2.701	0.010
M_MinM	0.023	0.129	0.740	0.312	2.374	M_MaxM.mod	0.003	0.225	0.073	0.021	3.501	0.001	-0.027	0.007	-3.623	0.001
M_MinM.mod	0.000	0.392	0.071	0.014	4.954	M_MinM.mod	0.000	0.397	0.105	0.026	4.002	0.000	-0.035	0.023	-1.521	0.137
MDFAnnHSNum	0.041	0.105	0.023	0.011	2.114											
MDFMDFDry.mod	0.031	0.116	-0.044	0.020	-2.238	MDFMDFDry.mod	0.000	0.314	-0.228	0.053	-4.271	0.000	0.137	0.038	3.638	0.001
production_dryland	0.010	0.162	0.151	0.056	2.707	production_dryland	0.003	0.237	0.508	0.157	3.239	0.003	-0.806	0.334	-2.414	0.021
						seed.mass	0.022	0.143	0.136	0.047	2.914	0.006	-0.039	0.014	-2.783	0.008
soil_phc	0.000	0.321	-0.080	0.019	-4.241	soil_phc	0.001	0.291	-0.444	0.630	-0.705	0.485	0.036	0.062	0.578	0.567
soil_pto	0.037	0.110	-1.015	0.469	-2.164	soil_pto	0.047	0.107	-3.919	2.166	-1.809	0.079	27.036	19.698	1.372	0.178
soil_soc	0.004	0.202	0.034	0.011	3.100	soil_soc	0.015	0.159	0.027	0.077	0.356	0.724	0.001	0.010	0.091	0.928

Figure 2: Univariate OLS regression statistics for species richness.

Linear regression model statistics						Quadratic regression model statistics									
metric	P	R2.linear	est	stderr	t	metric	p	R2.adj	est	stderr	t	p.term	est.quad	stderr.quad	t.quad
C_MaxM	0.033	0.114	1.155	0.523	2.209	C_MinM	0.045	0.109	3.528	1.669	2.114	0.041	-7.163	4.845	-1.478
C_MinM	0.042	0.104	1.207	0.573	2.104	clim_pdry	0.015	0.161	-0.006	0.016	-0.389	0.699	0.000	0.000	0.075
clim_pdry	0.003	0.203	-0.005	0.002	-3.116	clim_pwet	0.005	0.205	-0.001	0.003	-0.346	0.732	0.000	0.000	-0.076
clim_pwet	0.001	0.246	-0.001	0.000	-3.518	clim_tsea	0.004	0.215	0.069	0.046	1.494	0.144	0.000	0.000	-1.384
clim_tsea	0.002	0.217	0.005	0.002	3.242	CVAnnBFI	0.012	0.170	6.141	2.246	2.734	0.010	-5.396	2.171	-2.486
CVAnnHSMeanDur	0.004	0.200	1.179	0.382	3.084	CVAnnHSMeanDur	0.009	0.182	4.169	2.831	1.473	0.149	-3.137	2.943	-1.066
CVAnnHSNum	0.025	0.125	0.303	0.130	2.326	CVAnnHSNum	0.023	0.141	2.223	1.169	1.902	0.065	-0.726	0.439	-1.652
FDis.SES	0.005	0.191	0.156	0.052	2.994	FDis.SES	0.011	0.175	0.173	0.054	3.193	0.003	-0.048	0.044	-1.108
HSMeanDur	0.007	0.178	0.086	0.030	2.865	HSMeanDur	0.005	0.213	0.551	0.243	2.272	0.029	-0.041	0.021	-1.932
LSPeak	0.010	0.163	-6.065	2.234	-2.715	LSPeak	0.031	0.127	-13.083	11.086	-1.180	0.245	49.502	76.569	0.647
MDFAnnHSNum	0.000	0.292	-0.254	0.064	-3.958	MDFAnnHSNum	0.001	0.284	0.143	0.321	0.446	0.658	-0.088	0.069	-1.262
MDFAnnHSNum.mod	0.017	0.142	-0.457	0.182	-2.507	MDFAnnHSNum.mod	0.039	0.115	-0.824	0.444	-1.854	0.072	-0.658	0.727	-0.905
richness	0.050	0.098	-2.052	1.012	-2.029	MDFMDFDry.mod	0.020	0.147	1.135	0.391	2.906	0.006	-0.712	0.275	-2.584
soil_nto	0.016	0.144	-3.177	1.259	-2.525	soil_nto	0.043	0.110	3.699	9.453	0.391	0.698	-18.071	24.619	-0.734
soil_phc	0.007	0.178	0.391	0.136	2.873	soil_phc	0.019	0.150	4.214	4.528	0.931	0.358	-0.376	0.445	-0.845
soil_soc	0.001	0.257	-0.255	0.070	-3.628	soil_soc	0.004	0.218	-0.362	0.489	-0.741	0.464	0.015	0.066	0.221

Figure 3: Univariate OLS regression statistics for FRic.SES.

Linear regression model statistics						Quadratic regression model statistics									
metric	P	R2.linear	est	stderr	t	metric	p	R2.adj	est	stderr	t	p.term	est.quad	stderr.quad	t.quad
C_MaxM	0.030	0.118	3.287	1.457	2.257	C_MaxM	0.000	0.321	39.627	9.921	3.994	0.000	-52.868	14.316	-3.693
clim_pwet	0.017	0.140	-0.003	0.001	-2.492	clim_pwet	0.028	0.131	0.009	0.010	0.943	0.352	0.000	0.000	-1.256
CVAnnHSMeanDur	0.025	0.126	2.612	1.116	2.341										
CVAnnHSNum	0.038	0.108	0.789	0.367	2.149										
flowering.duration	0.029	0.120	1.598	0.703	2.274										
FRic.SES	0.005	0.191	1.220	0.407	2.994	FRic.SES	0.000	0.334	1.357	0.367	3.693	0.001	-3.118	0.968	-3.219
HSMeanDur	0.028	0.121	0.197	0.086	2.285										
LSPeak	0.011	0.158	-16.695	6.254	-2.670	LSPeak	0.033	0.124	4.252	31.016	0.137	0.892	-147.752	214.215	-0.690
maximum.height	0.000	0.277	-0.573	0.150	-3.813	maximum.height	0.000	0.302	1.220	0.983	1.241	0.223	-0.258	0.140	-1.844
MDFAnnHSNum	0.035	0.112	-0.439	0.201	-2.191										
MDFAnnHSNum.mod	0.016	0.144	-1.284	0.508	-2.524	MDFAnnHSNum.mod	0.023	0.141	-2.802	1.222	-2.293	0.028	-2.726	2.000	-1.363
seed.mass	0.005	0.193	-0.694	0.230	-3.013	seed.mass	0.002	0.245	-2.362	0.802	-2.946	0.006	0.525	0.243	2.164
soil_nto	0.046	0.101	-7.426	3.601	-2.062	soil_nto	0.043	0.111	33.457	26.387	1.268	0.213	-107.448	68.723	-1.563
soil_soc	0.001	0.243	-0.692	0.198	-3.491	soil_soc	0.000	0.344	2.803	1.250	2.242	0.031	-0.477	0.169	-2.826

Figure 4: Univariate OLS regression statistics for FDis.SES.

Linear regression model statistics						Quadratic regression model statistics											
metric	P	R2	est	stderr	t	metric	P	R2.adj	est	stderr	t	p.term	est.quad	stderr.quad	t.quad	p.term.quad	
C_MaxM	0.011	0.157	0.802	0.302	2.657	BFI	0.028	0.131	-4.563	1.628	-2.802	0.008	9.286	3.351	2.771	0.009	
C_MinM	0.008	0.169	0.908	0.327	2.780	C_MaxM	0.043	0.111	0.606	2.404	0.252	0.802	0.284	3.469	0.082	0.935	
C_MinM.mod	0.026	0.124	0.052	0.023	2.319	C_MinM.mod	0.013	0.167	2.153	0.954	2.257	0.030	-3.840	2.770	-1.387	0.174	
clim_pdry	0.006	0.185	-0.003	0.001	-2.939	clim_pdry	0.005	0.207	-0.018	0.009	-2.058	0.047	0.000	0.000	1.758	0.087	
clim_pwet	0.011	0.157	-0.001	0.000	-2.664	clim_pwet	0.005	0.212	-0.005	0.002	-2.493	0.017	0.000	0.000	2.171	0.036	
clim_tsea	0.002	0.219	0.003	0.001	3.260	clim_tsea	0.007	0.193	0.027	0.028	0.979	0.334	0.000	0.000	-0.869	0.390	
conservation	0.039	0.107	-0.448	0.210	-2.138	conservation_w	0.017	0.155	-2.184	0.871	-2.509	0.017	3.296	1.608	2.050	0.047	
CVAnnBFI	0.000	0.329	0.726	0.168	4.319	CVAnnBFI	0.000	0.412	-2.305	1.119	-2.060	0.046	2.958	1.081	2.736	0.009	
CVAnnHSMeanDur	0.023	0.129	0.560	0.236	2.376	CVAnnLSMeanDur	0.005	0.208	0.013	0.910	0.015	0.988	0.335	0.608	0.550	0.585	
CVAnnLSMeanDur	0.001	0.243	0.508	0.146	3.489												
CVAnnLSNum	0.005	0.193	1.189	0.395	3.014	CVAnnLSNum	0.014	0.164	4.016	3.474	1.156	0.255	-3.303	4.033	-0.819	0.418	
CVMDFDry	0.047	0.100	0.089	0.043	2.055	CVMDFDry	0.000	0.412	-0.498	0.128	-3.899	0.000	0.201	0.042	4.767	0.000	
						CVMDFDry.mod	0.040	0.114	0.576	0.247	2.331	0.025	1.421	0.540	2.630	0.012	
HSPeak	0.049	0.098	0.004	0.002	2.037	HSPeak	0.010	0.177	-0.014	0.007	-1.850	0.072	0.000	0.000	2.394	0.022	
intensive	0.038	0.108	-0.443	0.207	-2.146												
leaf.area	0.000	0.325	-0.090	0.021	-4.273	leaf.area	0.000	0.467	-0.441	0.101	-4.357	0.000	0.033	0.009	3.530	0.001	
						LSMeanDur	0.000	0.569	-0.039	0.007	-6.006	0.000	0.001	0.000	6.789	0.000	
						LSPeak.mod	0.048	0.105	-0.345	0.160	-2.151	0.038	0.660	0.257	2.568	0.014	
						M_MaxM	0.006	0.202	-24.821	7.484	-3.317	0.002	161.452	52.104	3.099	0.004	
						M_MinM	0.041	0.113	-24.464	9.471	-2.583	0.014	106.980	42.899	2.494	0.017	
production_dryland	0.047	-0.462	0.225	-2.055	0.100												
production_irrigated	0.000	5.523	1.440	3.836	0.279	production_irrigated	0.000	0.370	-4.759	3.959	-1.202	0.237	233.220	84.597	2.757	0.009	
production_natural	0.002	0.375	0.111	3.388	0.232	production_natural	0.007	0.193	0.154	0.612	0.252	0.803	0.213	0.580	0.367	0.715	
richness	0.032	-1.318	0.593	-2.224	0.115												
soil_der	0.017	-0.018	0.007	-2.487	0.140	soil_nto	0.044	0.109	11.681	5.594	2.088	0.044	-33.185	14.570	-2.278	0.029	
soil_phc	0.001	0.269	0.077	3.485	0.242	soil_phc	0.006	0.201	0.102	2.597	0.039	0.969	0.016	0.255	0.064	0.949	
wood.density	0.000	2.160	0.491	4.403	0.338	wood.density	0.000	0.366	-13.597	8.182	-1.662	0.105	12.371	6.413	1.929	0.061	

Figure 5: Univariate OLS regression statistics for exotic abundance.

Appendix 3c (Supplementary to Chapter 4)

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Hydrological conditions explain variation in wood density in riparian plants of south-eastern Australia

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Summary

1. Wood density is a key plant functional trait which integrates the trade-offs characteristic to riparian plant ecological strategies. Although high-density wood is costly to construct, it confers mechanical stiffness to stems, increasing a plant's capacity to withstand flooding, and also enables increased tolerance to water stress. For riparian plants, fluctuations in soil moisture driven by surface hydrology should therefore be an important driver of variation in wood density.
2. We asked the following questions in the study: (1) Does wood density increase with increasing frequency and magnitude of flood disturbance? (2) Does wood density increase with increasing unpredictability of water availability in the riparian zone? (3) Does dispersion of wood density peak at intermediate levels of hydrological disturbance?
3. We surveyed wood density of dominant species at 15 riparian sites along flow-gauged rivers across south-eastern Australia. Due to the broad range of hydrological variability associated with Australian river systems, this set of sites functions as a useful model for assessing the response of riparian plants to changing hydrological conditions.
4. We found wood density varied strongly along a single axis of hydrological variability. This axis integrates flood intensity and frequency with metrics of hydrological unpredictability and can be conceptualized as a gradient of environmental harshness, with higher wood density associated with harsher conditions.
5. *Synthesis.* Our study highlights the importance of hydrological conditions, particularly disturbance and environmental unpredictability, as determinants of ecological strategy in riparian plants. Large, rare flood events in particular appear to favour higher wood density strategies. This is likely to have significant ecological consequences for riparian plant communities in a south-east Australian context, as well as in other regions where increasing climatic variability and frequency of extreme events are hallmarks of climate change predictions.

Key-words: climate change, community assembly, determinants of plant community diversity and structure, disturbance, ecohydrology, ecological strategy, environmental unpredictability, functional traits, riparian

Introduction

Functional trait-oriented approaches to understanding community assembly (McGill *et al.* 2006) have become increasingly common over the last decade, particularly in the plant ecological literature (Kattge *et al.* 2011). These approaches attempt to understand community assembly processes by linking morphological or physiological attributes of species to organismal success under given environmental conditions. Suites of traits can be conceptualized as axes of variation in terms of 'ecological strategy', and the distribution of this variation across

environmental gradients can provide an insight into where these strategies are successful (Westoby *et al.* 2002).

Hydrology is widely considered to be the dominant abiotic force structuring riparian ecosystems (Poff, Allan & Bain 1997). Hydrological variability in turn drives variation in moisture and substrate availability and flooding disturbance, with cyclical resets to early successional conditions being characteristic of the riparian environment (Merritt *et al.* 2010). These are the conditions that determine the dominant selection pressures and environmental filters, which in turn dictate success of a particular plant ecological strategy in a riparian system (Naiman & Decamps 1997). Several authors have recently suggested functional trait biology as a means of

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understanding the response of riparian plant communities to hydrological gradients (Merritt *et al.* 2010; Catford *et al.* 2012). While ecohydrological classification is becoming established as a tool to explain plant community attributes such as species richness, stand structure and composition (Poff *et al.* 2010; Arthington *et al.* 2012), functional approaches to investigating the ecohydrology of riparian plant communities remain largely unexplored.

Woody plants determine the coarse physical structure of many riparian plant communities and are integral to the interplay of biological and physical elements that drive fluvial biogeomorphic processes (Corenblit *et al.* 2009). Consequently, an understanding of the mechanisms of riparian woody plant community assembly will provide important insights into the structure and function of fluvial landscapes. Wood density, defined as the ratio of kiln-dried mass to green volume of a wood sample (Cornelissen *et al.* 2003), is widely recognized as an important functional trait in plant ecology (Westoby & Wright 2006; Swenson & Enquist 2007) and has been proposed as one of just several key axes of variation within which all major plant ecological strategies can be described (Westoby *et al.* 2002). Wood density is in fact an emergent property of a combination of woody tissue traits, including vessel geometry and arrangement, and the density and proportion of surrounding lignified tissue (Chave *et al.* 2009). Combined variation in these traits corresponds to the wide range of wood density strategies among woody plants.

How might different wood density strategies confer advantages to woody plant species in riparian environments? There is little direct evidence from riparian species; however, general relationships between wood density and other ecological traits have been recognized in a variety of different systems and can provide some insight into the importance of variation in wood density in riparian systems. Dense wood confers mechanical stiffness, but requires more investment of biomass and is therefore more costly to construct per unit of stem height (Falster 2006; Niklas & Spatz 2010). Resources not invested in structural support may be used for purposes that contribute more directly to fitness, such as production of photosynthetic tissues or propagules, or rapid growth.

According to this trade-off, it follows that several relationships between wood density and life-history strategy are apparent. For example, wood density significantly explained variation in survival, fecundity and growth rate in a global data set of 222 species (Adler *et al.* 2014). Studies of tropical rain forest species have shown an inverse relationship between growth rate and wood density (King *et al.* 2006; Poorter *et al.* 2008, 2010; Kraft *et al.* 2010; Wright *et al.* 2010), although no such relationship was found in a study of New Zealand tree species (Russo *et al.* 2010). Cohort survival was positively correlated with wood density in the same tropical rain forest studies (King *et al.* 2006; Poorter *et al.* 2008, 2010; Kraft *et al.* 2010; Wright *et al.* 2010). In a study of 45 rain forest species in tropical Queensland, Falster & Westoby (2005) found that wood density increased with plant height along a successional gradient. Following mechanical disturbance caused by a large cyclone in northern Queensland,

Australia, wood density of rain forest trees was indicative of both damage sustained and subsequent recovery of biomass. Trees with dense wood were more likely to have experienced only minor damage. Of those trees that experienced major stem and branch damage, lower wood density trees were more likely to resprout and recover biomass faster post-disturbance (Curran *et al.* 2008). If the links observed in tropical rain forest communities between wood density, growth rate, successional status and recovery from mechanical disturbance hold true for riparian communities, the trade-off between rapid growth in response to high light and water availability, and construction of defences against flooding disturbance may be characteristic of woody plant ecological strategy in riparian zones.

In addition to influencing mean values of wood density, hydrological disturbance may also influence the dispersion of trait values within riparian communities. Niche diversity in riparian environments is promoted by fluvial geomorphic processes (Corenblit *et al.* 2007), and intermediate levels of disturbance have been theorized to promote divergence of disturbance-response strategies, resulting in a quadratic distribution of variance in associated trait values (Grime 2006; Sonnier, Shipley & Navas 2010).

While riparian plants potentially have the best access to water in a landscape, dramatic fluctuations in soil moisture are often characteristic of riparian environments (Nilsson & Svedmark 2002). Ecological strategies for coping with unpredictable water availability may therefore be adaptive under these conditions. The relationship between wood density and precipitation-driven patterns of soil moisture is unclear. Some studies (Weimann & Williamson 2002; Swenson & Enquist 2007) found little relationship between wood density and mean annual rainfall, while others found that wood density was correlated with mean annual rainfall across a transcontinental gradient (Martínez-Cabrera *et al.* 2009) and with soil moisture (Preston, Cornwell & Denoyer 2006). High wood density, along with low specific leaf area (SLA) and low maximum height, has been linked with environmental stress tolerance and conservative use of resources (Westoby 1998; Reich & Wright 2003; Swenson & Enquist 2007). Fluctuations in soil moisture driven primarily by hydrological conditions therefore should be an important driver of variation in wood density in riparian plant communities.

Given the extent to which flooding disturbance and fluctuations in water availability dominate riparian landscapes, woody tissue responses to these conditions are likely to be a primary indicator of riparian woody plant ecological strategy. Here, we consider variation in wood density of dominant woody riparian plant species over a broad range of hydrological conditions, across 15 riparian sites within south-eastern Australia. As the most hydrologically variable continent on the planet (Finlayson & McMahon 1988; Peel, McMahon & Finlayson 2004), Australia provides an ideal system to develop insight into the possible effects of increased hydrological variability in other regions under future climates. We sought to address the following questions: (i) Does wood density increase with increasing frequency and magnitude of

flood disturbance? (ii) Does wood density increase with increasing unpredictability of water availability in the riparian zone? (iii) Does dispersion of wood density peak at intermediate levels of hydrological disturbance?

Materials and methods

STUDY SITE SELECTION

Fifteen riparian sites were selected along gauged rivers within the south-east coast and south-eastern Murray Darling drainage basins of Australia (Fig. 1) (see Appendix S1 in Supporting Information for further detail). To differentiate rivers according to ecologically relevant components of hydrology, Olden & Poff (2003) described a statistical method for determining a minimally redundant set of hydrological descriptors. Kennard *et al.* (2010) followed this method to define a set of 120 hydrological metrics relevant to Australian rivers, which included metrics of central tendency and dispersion in all five dimensions of hydrological variation (magnitude, frequency, duration, timing and rate of change). These metrics were then used to classify Australian river systems into twelve distinct flow regime classes, providing a foundation for analysing the properties of ecosystems across hydrological gradients. In this study, sites were drawn from rivers corresponding to ‘stable winter baseflow’, ‘unpredictable baseflow’ and ‘unpredictable intermittent’ hydrological classes, as described by Kennard *et al.* (2010). These are the best represented hydrological classes in eastern New South Wales and Victoria and, combined, span clear gradients of flooding intensity and hydrological unpredictability. Five sites per hydrological class were selected based on the following criteria: gauged locations were selected that had >15 years of associated continuous hydrological data, and an absence of flow regulation, significant water extraction or catchment urbanization, following Kennard *et al.* (2010). To minimize signals associated with human land-use and river type, the following further criteria were used to shortlist possible study sites: all were partly confined valleys with discontinuous floodplain pocket River Styles, *c.f.* Brierley & Fryirs (2005), had an intact native riparian vegetation cover (a band of native riparian vegetation extending >15 m from the bankfull channel edge), were in good geomorphic condition (lack of significant human-induced erosional or depositional landforms), had minimal vegetation clearing (catchment predominantly covered by native vegetation) and occurred in a catchment smaller than 1000 km². These criteria were assessed using a combination of visual inspection of satellite photography (Google Earth, Microsoft Bing) and information from the NSW Riparian Vegetation Extent data set and the NSW Office of Water River Styles® geospatial data set (Healy *et al.* 2012). To select the 15 study sites from this shortlist, accessibility by road, permission from state or private landholders and proximity of accessible areas to continuous hydrological monitoring stations were taken into account.

SPECIES ABUNDANCE AND TRAIT DATA COLLECTION

Data collection was undertaken between December 2012 and May 2013. At each site, a 10-m-by-50-m plot was marked out, with the longest edge abutting the channel edge. Criteria for selection of plot locations were as follows: geomorphic homogeneity (the plot comprising only sloping bank where possible) and lack of anthropogenic disturbance such as built structures, roads or tracks, recent logging or clearing (in the last 20–30 years), herbicide spraying or animal

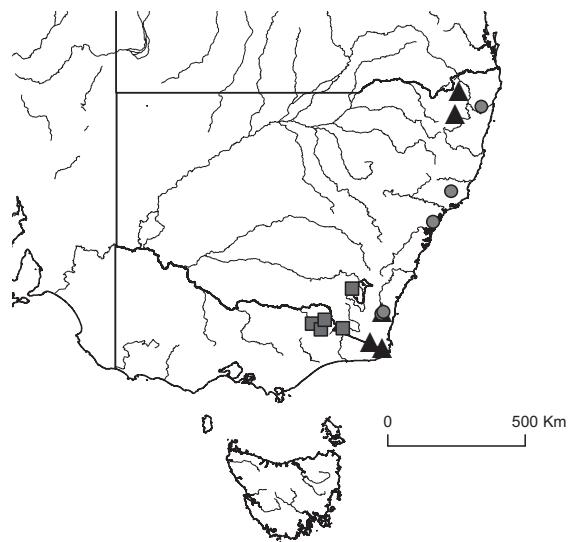


Fig. 1. Location of fifteen field study sites across south-eastern Australia chosen to represent the three major hydrological classes of south-east Australia. Hydrological class membership is denoted by: ■ stable winter baseflow, ▲ unpredictable baseflow, ● unpredictable intermittent.

grazing. Variation in the maximum height above the channel edge between plots was kept to within approximately 1.5 m.

Proportional cover of all woody species was assessed within three strata: shrub (1–4 m), subcanopy (4–8 m) and canopy (>8 m). Species were identified using appropriate field guides and were verified against herbarium specimens at the Macquarie University Herbarium. Some specimens were identified by staff at the Royal Botanic Gardens, Sydney.

Wood samples were collected from woody species present within the plot at >1% cover in shrub, subcanopy or canopy strata, which had trunks robust enough to core. A 100-mm wood sample from each of two individuals per species was extracted using a 5.15-mm-diameter, triple-threaded increment borer (Haglöf Sweden). Samples were extracted from the base of the main trunk, 10 cm above the leaf litter level, and air-dried at 20–45 °C. On return to the laboratory, samples were rehydrated to saturation in deionized water and 10-mm sections of mature heartwood were cut flush with a razor, using visual inspection of vessel occlusion as an indicator of maturity. Sections were measured (*x*, *y* and *z* dimensions) to the nearest 0.01 mm with callipers (Mitutoyo America Corporation, Aurora, IL, USA) to calculate wet volume, then oven-dried at 80 °C for 48 h and weighed using a microbalance (Mettler Toledo, Greifensee, Switzerland). Wood density was then calculated as the ratio of oven dry mass to wet volume (g cm⁻³).

Species that were present in plots but which could not be cored due to small size were assigned averaged values of wood density from the same species measured at other sites, where possible. Remaining species were assigned values from peer-reviewed literature sources. Appendix S1 contains further details about the data set, including data density information.

HYDROLOGICAL ANALYSIS

Daily discharge data pertaining to each field site were collated from the PINNENNA CW 10.1 data base (NSW Office of Water, Department of Primary Industries) and the NSW Office of Water

Continuous Water Monitoring network website (<http://realtimedata.water.nsw.gov.au/water.stm>) for NSW sites, and the Victoria State Government's Water Measurement Information System website (<http://data.water.vic.gov.au/monitoring.htm>) for Victorian sites. Where possible, 30-year time series were obtained, spanning years 1983–2012. Records were truncated for three sites, spanning 15, 19 and 28 years. Missing data were approximated using the Time Series Manager module in RIVER ANALYSIS Package (Marsh, Stewardson & Kennard 2003). Consistency of the resulting outputs was checked by visual inspection of hydrographs. For Mammy Johnson's River, Mann River, Sportsman's Creek and Wallagaraugh River, multiple linear regression was chosen as the most appropriate method for estimating missing data values. Linear interpolation was used for Jilliby Creek data. Daily discharge data for the remaining sites were complete.

A set of 24 hydrological metrics was pared from the full set described by Kennard *et al.* (2010). These metrics were chosen to be representative of variability in high flow magnitude and frequency as well as predictability and consistency of water availability in the riparian environment (see Table 1 for a description). We used the Time Series Analysis module in RIVER ANALYSIS Package to generate these metrics. Means and coefficients of variation were calculated for most metrics to indicate central tendency as well as spread within the data. Low and high spell metrics were thresholded at the 5th and 95th percentiles, respectively, with a flood independence criterion of 7 days between peak events. Twenty-year average return interval (ARI) flood magnitude was also calculated with a flood independence value of 7 days between peaks. Colwell's indices were calculated using mean flow values over monthly time periods and a class distribution of 11 flow classes. Metrics of flow magnitude which had units ml day^{-1} were normalized by mean daily flow to allow for comparison between different sizes of river. Some metrics were autocorrelated (see Appendix S1 for correlation analysis).

WOOD DENSITY ANALYSIS

All statistical analyses were performed using the R statistical programming environment (R Core Team 2013). The R code used for these analyses can be retrieved from <https://github.com/jamesrlawson/riparian-WD/tree/master/scripts>. Statistical significance was interpreted at $\alpha = 0.05$.

Characterizing community-level variation in wood density

To investigate variation in wood density across hydrological gradients at the community level, community-weighted means (CWMs) of wood density were generated for each site. Species relative abundance was compiled from records of percentage cover at the shrub (1–4 m), subcanopy (4–8 m) and canopy (>8 m) strata. Wood density values were then weighted according to species relative abundance and summed to produce the CWM. This method integrates particular trait values with their real-world abundance as a measure of 'performance', while providing a useful reduction in data dimensionality. Wood density varies only over one order of magnitude, while exhibiting relatively high intraspecies plasticity. As such, CWMs work well for environmental gradient studies of wood density because the focus is maintained on the functional characteristics of the community, rather than on species *per se*.

We also calculated community-weighted variance (CWV) in wood density for each site to characterize the dispersion of wood density values within communities. CWV describes divergence from the mean trait value of a community (Schleuter & Daufresne 2010).

When trait values of abundant species are clustered towards the mean, divergence is low. Conversely, divergence is high when abundant species are distributed towards the extremes of the trait range (Villéger, Mason & Mouillot 2008). Variance could not be calculated for Site 2 (Wallagaraugh River, unpredictable baseflow category) as only a single woody species was found at >1% cover at this site. This site was therefore omitted from subsequent analyses of CWV.

Testing relationships between wood density and hydrological conditions

Ordinary least squares regression models were generated for selected metrics to determine relationships between hydrological gradients and CWMs. Linear models were used except where nonlinear relationships were obvious. Wood density data were normally distributed and did not require transformation. To reduce the occurrence of Type 1 statistical error, we adjusted the resulting *P* values using the Benjamini–Hochberg (BH) procedure for controlling familywise error rate (STATS package; R Core Team 2013). Although ecological rationale supported inclusion of each subgroup of hydrological metrics, a number of these metrics were autocorrelated. The BH procedure has been shown to control the false discovery rate for positively dependent test statistics (Benjamini and Yekutieli, 2001).

We identified ecologically relevant axes of variation in hydrological conditions by running a principal components analysis (STATS package; R Core Team 2013) for hydrological metrics which had significant relationships with site mean wood density values. Having established the dominance of a single relevant axis of variation in hydrology (refer Fig. 5), we tested the fit of a quadratic model relating extent of hydrological disturbance (as characterized by site scores from the resulting first principal component) to CWV in wood density.

Spatial autocorrelation in CWM and CWV values was assessed using Moran's I (APE package; Paradis, Claude & Stimmer 2004).

Results

HOW DOES MEAN WOOD DENSITY CHANGE OVER HYDROLOGICAL GRADIENTS?

Below we describe patterns of community-weighted mean wood density in relation to the hydrological variables divided into two groups: those describing frequency and magnitude of flood disturbance and those describing predictability of water availability in the riparian zone. Regression statistics for all models are given in Table 2.

Community mean wood density varied by 50% between sites. The largest, most intense flood events throughout a river's hydrological record were found to show a strong positive relationship with mean wood density (Fig. 2a,b). Flooding frequency had no influence on wood density. Mean flood rise rate (Fig. 2c) as well as interannual variability in flood rise and fall rates (Fig. 2d,e) was positively related to wood density; this relationship was considerably stronger for interannual variability in flood rise rate than mean flood rise rate ($R^2 = 0.549$ vs. 0.360).

We found denser woody tissues were increasingly favoured as baseflow index decreased (Fig. 3a). Wood density increased as patterns of average flow conditions became (i)

Table 1. Hydrological parameters used as metrics of variability in high flow magnitude and frequency and predictability and consistency of water availability in the riparian environment

Parameter	Abbreviation	Units	Description
<i>Flood frequency and magnitude</i>			
Mean magnitude of high spells*	HSPeak	Dimensionless	High spells are periods of flow above the 95th percentile on the flow duration curve. We were interested in how frequently these conditions occurred over the time series as well as the mean magnitude of peak flows during these periods. Twenty-year average return interval (ARI) floods are extreme flow events that have the potential to rework the fluvial landscape. Together, these metrics indicate the intensity and frequency of mechanical stress experienced by plants in the riparian zone
CV of all years' mean high spell magnitude	CVAnnHSPeak	Dimensionless	
20-year ARI flood magnitude**	AS20YARI	Year ⁻¹	
Mean of all years' number of high spells	MDFAnnHSNum	Dimensionless	
CV of all years' number of high spells	CVAnnHSNum	Dimensionless	
<i>Rise and fall rates³</i>			
Mean rate of rise*	MRateRise	Day ⁻¹	Rise and fall rates represent flow 'flashiness'. Fast rise rates are associated with flood waves and intense mechanical stress to plant stems. Slow fall rates keep exposed substrate moist for longer periods, which may produce favourable conditions for germination. Historical discharge records are unfortunately limited to daily resolution, so are unable to fully capture flood discharge shapes. High variability between years indicates the occurrence of extreme events which may not have been captured by the mean value
Mean rate of fall*	MRateFall	Day ⁻¹	
CV of all years' mean rate of rise	CVAnnMRateRise	Dimensionless	
CV of all years' mean rate of fall	CVAnnMRateFall	Dimensionless	
<i>Baseflow index</i>			
Baseflow index	BFI	Dimensionless	Baseflow index is calculated using the ratio of flow during average conditions to total flow. It is a useful metric of consistency of water availability, in that it is maximized when average flow conditions dominate and minimized when total flow is dominated by above average flow events. Intra-annual variability in baseflow index measures how predictable baseflow index is between years
CV of all years' Baseflow Index	CVAnnBFI	Dimensionless	
<i>Low flow magnitude, frequency and duration</i>			
CV of all years' mean low spell magnitude	LSPeak	Dimensionless	Low spells are periods of flow below the 5th percentile on the flow duration curve. We were interested in how frequently these conditions occurred over the time series as well as the mean and interannual variability in magnitude and duration of low flows
Mean magnitude of low spells	CVAnnLSPeak	Dimensionless	
Mean of all years' number of low spells	MDFAnnLSNum	Year ⁻¹	
CV of all years' number of low spells	CVAnnLSNum	Dimensionless	
Mean duration of low spells	LSMeanDur	Days	
CV of all years' low spell mean duration	CVAnnLSMeanDur	Dimensionless	
Mean flow during driest week of the year**	MA_7daysMinMean	Dimensionless	
Mean days per year under 0.1 ml day ⁻¹ flow	MDFAnnUnder0.1	Days year ⁻¹	
CV of all years' days per year under 0.1 ml day ⁻¹ flow	CVAnnMDFAnnUnder0.1	Dimensionless	
<i>Colwell's indices</i>			
Constancy of monthly mean daily flow	C_MDFM	Dimensionless	Colwell's indices provide a measure of the seasonal predictability of flow events and, therefore, water availability within the riparian zone. Constancy (C) measures uniformity of flow across seasons and is maximized when flow conditions do not differ between seasons. Contingency (M) is a measure of interannual uniformity in seasonal flow patterns and is maximized when seasonal patterns of flow are consistent between years. We generated Colwell's indices for both average flow conditions and minimum flows conditions
Contingency of monthly mean daily flow	M_MDFM	Dimensionless	
Constancy based on monthly minimum daily flow	C_MinM	Dimensionless	
Contingency based on monthly minimum daily flow	M_MinM	Dimensionless	

* Normalized by mean daily flow (ml day⁻¹).

Table 2. Statistics for regression models comparing hydrological metrics with site mean wood density

Metric	P	P_{adj}	R^2
CVAnnBFI	0.008	0.031	0.549
CVAnnMRateRise	0.008	0.031	0.549
C_MinM	0.009	0.031	0.542
C_MDFM	0.012	0.031	0.522
HSPeak	0.004	0.031	0.485
AS20YrARI	0.005	0.031	0.467
LSPeak	0.006	0.031	0.447
CVAnnMRateFall	0.007	0.031	0.435
BFI	0.012	0.031	0.397
M_MDFM	0.013	0.031	0.388
MA.7daysMinMean	0.017	0.036	0.368
MRateRise	0.018	0.036	0.360
MDFAnnLSNum	0.030	0.055	0.314
MRateFall	0.053	0.091	0.258
M_MinM	0.062	0.100	0.242
CVAnnHSPeak	0.117	0.175	0.178
LSMeanDur	0.230	0.325	0.109
CVAnnLSPeak	0.390	0.493	0.057
CVAnnHSNum	0.390	0.493	0.057
CVAnnLSNum	0.454	0.545	0.044
MDFAnnUnder0.1	0.487	0.556	0.038
MDFAnnZer	0.553	0.603	0.028
CVAnnLSMeanDur	0.732	0.747	0.009
MDFAnnHSNum	0.747	0.747	0.008

P_{adj} denotes P-values adjusted by the Benjamini–Hochberg method. Significant results are shown in bold. Models used are either quadratic or linear, as shown in Figs 2 and 3. For non-significant relationships, statistics shown are for linear models.

less uniformly distributed across seasons (Fig. 3b) and (ii) less uniformly distributed year to year (Fig. 3c). Thus, mean wood density is maximized when average flow patterns are highly seasonal, but the season with which they are associated is not consistent throughout the record. A similar relationship was observed for interseasonal (Fig. 3d) but not interannual uniformity of minimum flows. In other words, wood density was highest where minimum flows were not associated with any particular season. Mean wood density also increased with increasing interannual variability in baseflow index (Fig. 3e), pointing to a strong effect from years in which baseflow deviated from the mean. Wood density also decreased with mean low spell flow (Fig. 3f) and with the mean 7-day minimum flow (Fig. 3g). For both metrics, higher values indicate wetter minimum flow conditions. Mean wood density also increased with low flow frequency (Fig. 3h). Metrics of low flow duration were not significantly associated with wood density.

No significant pattern of spatial autocorrelation was detected within values of CWM ($P = 0.228$).

WHAT ARE THE PRINCIPAL COMPONENTS OF VARIATION IN HYDROLOGICAL CONDITIONS THAT EXPLAIN VARIATION IN WOOD DENSITY?

Hydrological metrics that significantly explained site mean wood density were highly autocorrelated in our data set. Principal components analysis (PCA) identified one dominant axis

within these metrics, representing 80.3% of variation (Fig. 4). The remaining variation was split between several minor axes; PCA2 represented 6.3% of variation and the remaining axes each represented <3% of variation.

PC1 represents a gradient of environmental harshness that integrates baseflow characteristics, seasonality and flooding intensity. Metrics that are maximized under conditions of weak seasonality, high predictability and low variability of water availability were loaded towards the positive end of the PC1 axis, while metrics that are maximized under conditions of high interannual baseflow variability and high-intensity flooding were loaded towards the negative end. The results of the PCA analysis illustrated that variation in wood density is largely described by a single axis of variation from low to high variability in flow.

IS THERE A RELATIONSHIP BETWEEN HYDROLOGICAL DISTURBANCE AND WITHIN-COMMUNITY DISPERSION OF WOOD DENSITY?

No individual metrics describing hydrological disturbance showed significant relationships with CWV following P -value adjustment. The relationship between the PC1 axis and CWV in wood density could be significantly explained by a quadratic model, however ($R^2 = 0.450$, $P = 0.037$) (Fig. 5). The fitted curve shows a peak in CWV at intermediate values of PC1, which correspond to intermediate values of hydrological disturbance and variability. No significant pattern of spatial autocorrelation was detected within values of CWV ($P = 0.786$).

Discussion

We sought to understand how hydrology might influence wood density, a key plant functional trait. We asked whether mean wood density could be explained by the degree of flooding disturbance or hydrological unpredictability in the riparian zone and whether dispersion of wood density peaks in intermediately disturbed communities. To summarize, we found evidence that mean riparian wood density is positively related to flood magnitude and flow rise and fall rates, as well as to unpredictability in flow conditions over daily, seasonal and annual time-scales. We also found evidence for divergence in wood density strategy at intermediate levels of disturbance. While wood density is a complex trait that integrates trade-offs between multiple selection pressures, we believe the strong relationships between mean wood density and hydrology demonstrated here are evidence that hydrological conditions powerfully influence plant ecological strategy in the riparian environment.

Strong relationships with measures of interannual variability point to years in which the environment was extreme as favourable towards high wood density. Several relationships were described best by quadratic models, indicating a maximum above which variation in hydrology ceases to be associated with changes in mean wood density. Predictable hydrologies and weak flooding disturbance intensity were

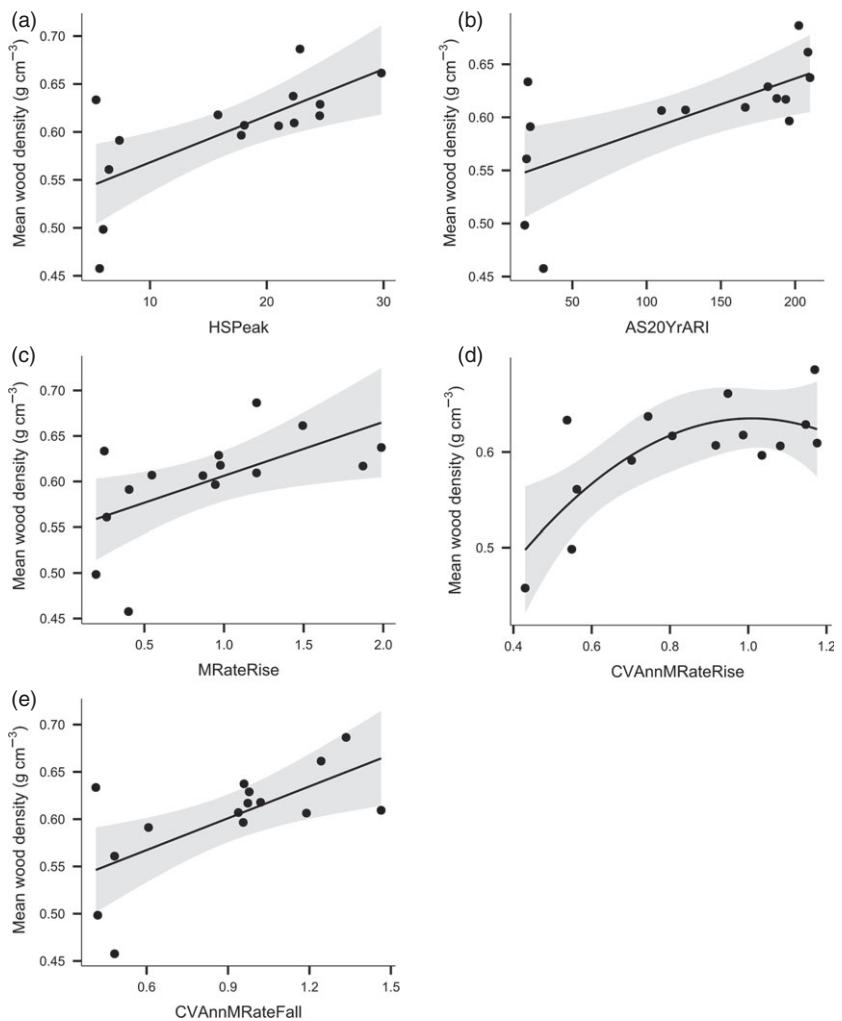


Fig. 2. Relationships between community-weighted mean wood density and hydrological metrics describing (a) mean high flow magnitude (HSPeak), (b) magnitude of the 20-year average return interval flood (AS20YrARI), (c) mean rate of flow rise (MRateRise), (d) interannual variability in flood rise rates (CVAnnMRateRise), (e) interannual variability in flood fall rates (CVAnnMRateFall). Fitted lines depict ordinary least squares regression models. (d) is a quadratic fit, all other models are linear fits. Shaded areas depict the smoothed 95% confidence interval around the regression model.

associated with a greater range of mean wood density values. This variability may be driven by other environmental factors, which become less influential as hydrological forcing increases. We also found that for *Casuarina cunninghamiana*, a common riparian species in SE Australia, intraspecific variation in wood density responded strongly to hydrology (see Fig. S1).

Specific aspects of high flow hydrology drove variation in wood density. Mean wood density was not correlated with the frequency of high flow spells, which individually may not correspond to significant disturbance events, depending on the hydrological characteristics of the given river. Rather, it was the actual magnitude of flow during high flow periods that was important. High rates of flow rise and fall, which may be associated with entrainment of large debris into the flood channel and subsequent bank deposition (Cadol & Wohl 2010), were also associated with high community wood density. Interannual variability in rate of flow rise was a substantially stronger predictor of wood density than the mean value, suggesting a greater influence of flow rise rates in extreme years than the general mean. A pattern is apparent then, in which mean wood density in riparian communities is driven by powerful but relatively rare flow events (e.g. 10- to 20-

year ARI flood). The abundance of high wood density strategies in these environments indicates that infrequent but high-stakes events may be a greater selective pressure in riparian plant communities than average conditions. For densely wooded species, persistence may be more influential on population dynamics than individual growth rates or fecundity (Adler *et al.* 2014). We therefore suggest that a ‘brick house’ ecological strategy is favoured in riparian environments that experience intense flooding. This suggestion concurs with findings that trees on windy slopes tend to overcompensate for mechanical stress, with investment in defences increasing cumulatively in response to rare, extreme events (Telewski 1995; Cohen & Mangel 1999).

We can extend the observation about the influence of intense ‘pulse’ flow events on wood density: plants living in environments where flow occurs unpredictably and largely within specific events, rather than being evenly distributed throughout time, are likely to experience more intense pulses of water stress (i.e. low soil moisture). High wood density may be symptomatic of wood anatomy strategies that allow plants to tolerate water stress (Hacke *et al.* 2001; Jacobsen & Ewers 2005; Jacobsen *et al.* 2007). Numerous studies have discussed the role of various anatomical components of

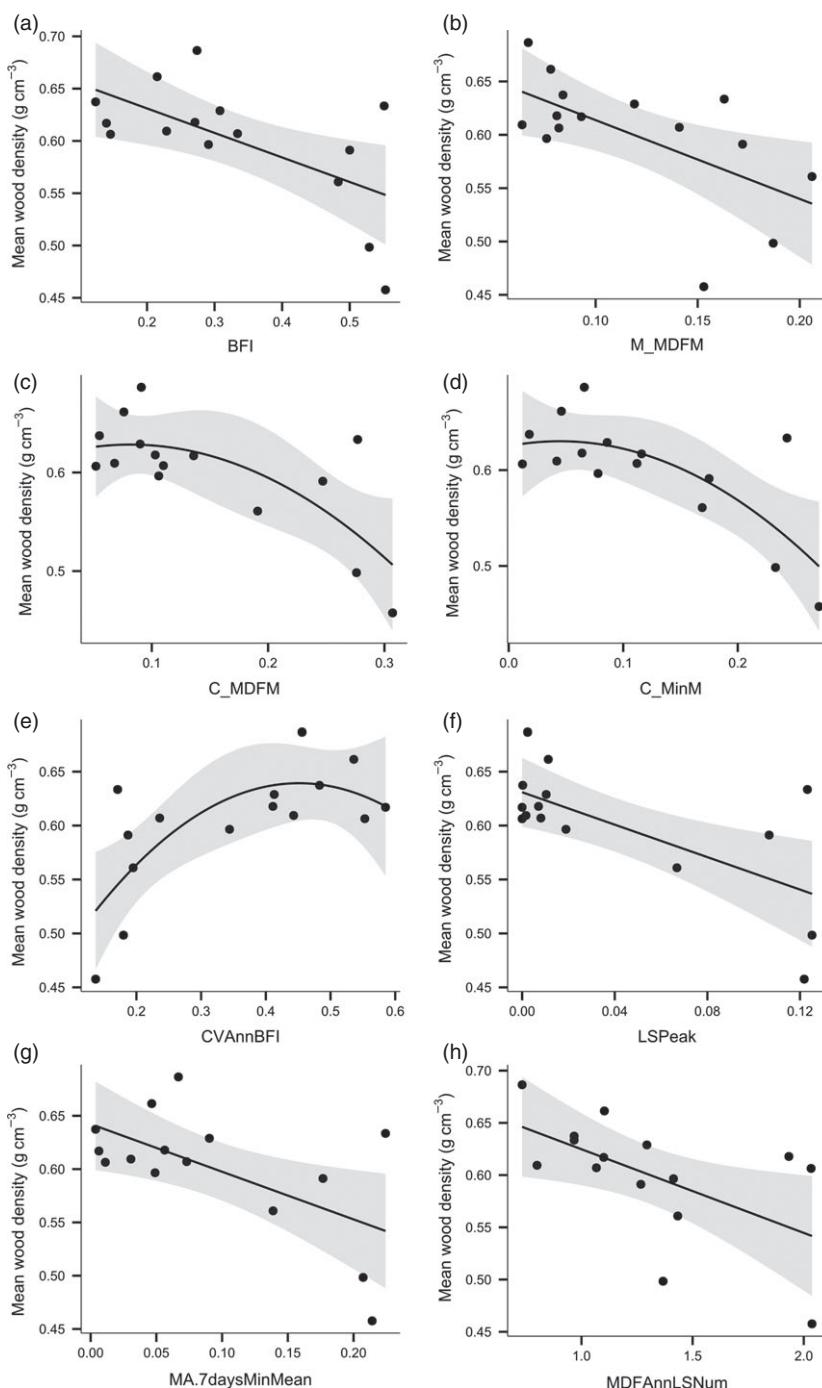


Fig. 3. Relationships between community-weighted mean wood density and hydrological metrics describing (a) baseflow index (BFI), (b) contingency of monthly mean daily flow (M_MDFM), (c) constancy of monthly mean daily flow (C_MDFM), (d) constancy of monthly minimum daily flow (C_MinM), (e) interannual variability in baseflow index (CVAnnBFI), (f) mean low flow magnitude (LSPeak), (g) mean flow during driest week of the year (MA.7daysMinMean), (h) annual frequency of low flows (MDFAnnLSNum). (c)–(e) are quadratic fits, and all other models are linear fits. Shaded areas depict the 95% confidence interval around the regression model.

woody tissue in stabilizing xylem against cavitation when plants are under severe water stress, but the exact role that woody fibres play in stabilizing xylem vessels appears to be inconsistent (Martínez-Cabrera *et al.* 2009). Overall, resistance against cavitation emerges from complex interactions between wood anatomical traits (Lens *et al.* 2011; Ziemska *et al.* 2013) and/or above-ground biomass production traits, both of which are tangentially related to wood density. With the exception of ephemeral dry land rivers, riparian environments tend not to be severely water limited, so specifically constructing woody tissue to deal with constant water stress may not be advantageous. For plants that are habituated to

plentiful soil moisture, however, having no backup strategy for surviving drought conditions may be risky.

A more compelling rationale for our findings is that riparian woody plants are again overcompensating for the possibility of rare, life-or-death stress events. In the absence of predictable cues about timing of watering flows, conservative resource-use phenotypes such as higher wood density would be favoured (Valladares, Gianoli & Gómez 2007). Environmental unpredictability may act as a modifier which shifts ecological strategy in favour of conservative resource use (for which wood density acts as a proxy, in this case). We can observe this effect in intraspecific variation (see Fig. S1) in wood den-

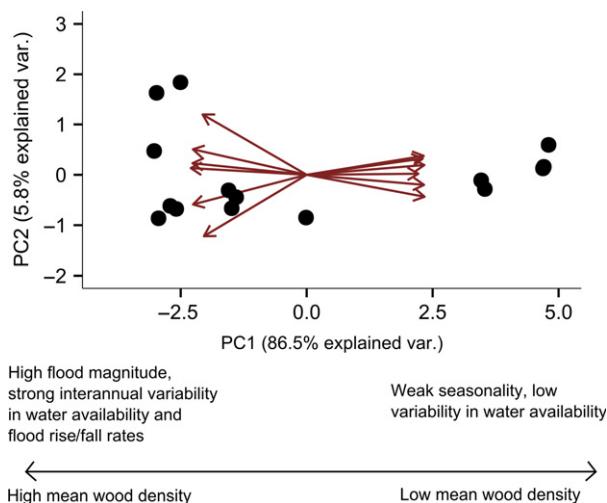


Fig. 4. Biplot of sites ordinated across the first two principal components as determined from principal components analysis of hydrological metrics displaying significant relationships with mean wood density across 15 sites in south-eastern Australia. Points represent individual sites. PC1 explains 80.3% of the variation in hydrology among the sites and represents a gradient of harshness of environmental conditions.

sity for the rheophytic (i.e. confined to frequently flooded substrates) species *C. cunninghamiana*: interannual variability in baseflow index, contingency of monthly minimum daily flow (M_MinM) and contingency of monthly mean daily flow (M_MDFM) describe interannual variability in water availability and all show strong relationships with intraspecific variation in *C. cunninghamiana* wood density. Traits associated with conservative resource use and better recovery following periods of extreme stress may actually confer as much or greater fitness than traits associated with coping with the stress itself (Gutschick & BassiriRad 2003).

Conservative resource use and heavy investment in structural strength fit within the ‘resister’ category of riparian plant strategies described by Naiman & Decamps’ (1997) classification of riparian plant life-history strategies. ‘Invader’ strategies with which species avoid harsh hydrological conditions by achieving sexual maturity as fast as possible are also common to the riparian environment (Naiman & Decamps 1997; Woolfrey & Ladd 2001). For pioneer species employing a fast relative growth rate, low wood density ecological strategy would be benefitted by repeated setbacks to early successional conditions (Westoby 1998). Coexistence at intermediate disturbance intensities of a broad spectrum of strategies between ‘invading’ and ‘resisting’ may be responsible for the observed peak in wood density CWV, but this suggestion is difficult to substantiate using our data set, as only a few sites were present in the middle range of the PC1 axis.

Under our argument, where hardy rheophytic species use high wood density ecological strategies to cope with powerful floods and unpredictable watering regimes, we would expect species such as *C. cunninghamiana* and *Tristaniopsis laurina* (two of the most common riparian species in our study region) to have the highest wood density in our data set.

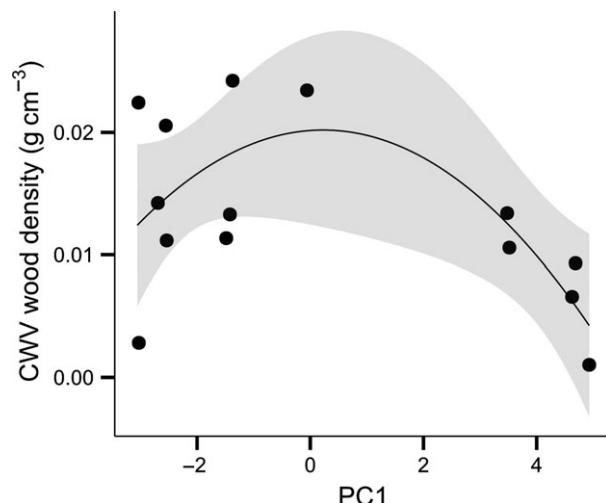


Fig. 5. Quadratic relationship between community-weighted variance in wood density and site scores for the first principal coordinate (PC1) of a principal components analysis of hydrological metrics displaying significant relationships with mean wood density (see Fig. 4), ($R^2 = 0.450$, $P = 0.037$). Variance peaks at intermediate values of hydrological disturbance, as described by the PC1 axis. Shaded areas depict the 95% confidence interval around the regression model.

However, both species exhibited highly variable trait values, ranging approximately between the median value and the 75th percentile. As with *C. cunninghamiana*, *T. laurina* is a light-demanding colonizer of within- and near-channel landforms (Webb, Erskine & Dragovich 2002). By establishing in close proximity to the channel, seedlings of these species must balance the risks of flooding with the advantages of growth unencumbered by competition for light or space. Maintaining a high relative growth rate, at least until the trees are physically large enough to endure flooding, allows these species to quickly fill space and build photosynthetic tissue (i.e. invading) (Melick 1990). If parallels with tropical rain forest species (King *et al.* 2006; Kraft, Valencia & Ackerly 2008; Poorter *et al.* 2008, 2010; Wright *et al.* 2010) hold, this strategy will not be conducive to setting down dense wood (i.e. resisting). In addition to morphological adaptations in *T. laurina* such as multi-stemmedness, narrow leaves and growth streamlined against the direction of flow (van Steenis 1981; Webb, Erskine & Dragovich 2002), the trade-off between flood resistance and rapid resource acquisition and growth during establishment serves to explain why the optimal wood density for rheophytic species might occupy a central position along the axis of wood density. Nonetheless, the wide plasticity in wood density shown by *C. cunninghamiana* and *T. laurina* suggests that intraspecific variation contributes to the species’ capacity to track hydrological gradients.

Notably, it is the tall, facultative riparian species from rain forest sites that had the highest wood density in our data set. Lacking the morphological adaptations required to thrive directly along the channel edge, these species may rely solely on generating mechanically strong stems to withstand flooding. High wood density species tended to occur further up the bank, so would be subject to only the more intense flooding

events. Since succession typically advances with elevation above the channel edge (Tabacchi, Correll & Hauer 1998), this observation agrees with previous work showing increasing wood density along a successional gradient (Falster & Westoby 2005). Further parallels in the existing wood density literature are also evident here, where high wood density individuals were much less likely to experience major wind damage following a cyclone (Curran *et al.* 2008).

The gradient identified by principal components analysis integrates predictability of water availability, seasonality and flood intensity into a single axis of hydrological variation. It is not possible to tease out individual drivers of variation in mean wood density, as the conditions associated with both environmental unpredictability and mechanical disturbance act in unison to drive community wood density towards higher mean values.

Community-weighted variance in wood density showed a quadratic distribution across this gradient of 'hydrological harshness'. Previous work has described a negative relationship between community-level variance in wood density and abiotic stress (using high latitude and elevation as proxies for stressful environments) (Swenson & Enquist 2007). Rather than constricting trait values, intermediate levels of pulsed fluvial disturbance may promote trait diversity by retarding competitive exclusion (Huston 1979; Naiman & Decamps 1997), while simultaneously generating structurally heterogeneous habitat (Corenblit *et al.* 2007). While the fit of our model is statistically significant, the paucity of values through the middle range of the PC1 axis gives rise to error around the peak of the fitted curve; interpretation of this result therefore necessitates some caution.

Damming and water extraction, and changing climatic conditions are altering hydrology globally (Nilsson & Berggren 2000; Stocker *et al.* 2014). Artificial flow modification by damming and water extraction reduces overall flow volume and the magnitude and frequency of high flow events, while increasing flow predictability, altering seasonality and limiting channel-floodplain connectivity (Maheshwari, Walker & McMahon 1995; Graf 2006). In these altered conditions, terrestrial species with softer wood and faster growth rates may encroach on what was once the province of rheophytic assemblages adapted to flooding and less predictable hydrological conditions. The converse of this situation is presented by predictions of future climatic conditions: in Australia, warming of 0.4–0.7 °C has occurred since 1950 (Hennessy *et al.* 2007), associated with a reduction in rainfall across southern and eastern regions of the continent (Smith 2004) and an increase in intensity and frequency of droughts (Hennessy *et al.* 2008). Extreme rainfall events are predicted to become more prevalent, even in areas where the trend is towards mean reductions in annual or seasonal rainfall (Chiew *et al.* 2009). River discharge in Australia is known to be particularly sensitive to the El Niño–Southern Oscillation (ENSO) phenomenon that is an integral driver of the continent's climate patterns (Nicholls 1989; Ward *et al.* 2010). Projected increases in climatic variability (Hennessy *et al.* 2008) may therefore overlay the already strong natural variability induced

by ENSO to produce significant alterations to streamflow. Under such conditions, near-channel abundance of opportunistic terrestrial species (with their broad diversity of wood density strategies) may decline in favour of rheophyte-dominated assemblages whose ecological strategies are optimized to harsh hydrological conditions. If changes in spatial extent of climate zones can be related to changes in runoff – a complicated but progressing area of research in hydroclimatology (Peel & Bloschl 2011) – functional approaches to ecohydrology can give insight into likely changes in riparian plant assemblages and associated changes in ecosystem function.

Conclusion

Our study emphasizes the importance of hydrological conditions, particularly disturbance and environmental unpredictability, as determinants of ecological strategy in riparian plant communities. These relationships may be generalizable to diverse biomes, given the strong constraints imposed by flooding and fluctuating water availability on woody plant ecological strategies in many riparian environments. The marked influence of rare, high-intensity floods on wood density is likely to have significant ecological consequences for riparian plant communities in a south-east Australian context and potentially in other regions where increasing climatic variability and frequency of extreme events are hallmarks of climate change predictions.

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Data accessibility

Data are available from the Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.72h45> (Lawson, Fryirs & Leishman 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Field site details, correlation between hydrological metrics, dataset characteristics, references for externally sourced wood density values.

Figure S1. Relationships between hydrological metrics and intraspecific variation in wood density for *Casuarina cunninghamiana*.



Heterogeneous flows foster heterogeneous assemblages: relationships between functional diversity and hydrological heterogeneity in riparian plant communities

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SUMMARY

1. Riparian ecosystems are biophysically complex and highly diverse taxonomically, structurally and functionally. While many environmental factors determine the structure and function of riparian vegetation communities, hydrology is thought to be the 'master variable'. Flooding and variability in water availability are known to be key drivers of taxonomic diversity, but their influence on the functional trait diversity of riparian vegetation communities remains largely unexplored.
2. We collected data on species abundance, quantitative plant functional traits and hydrology from 15 sites distributed across south-eastern Australia to address the following questions: (a) Is functional trait diversity related to the frequency and magnitude of flooding disturbance? (b) Is functional trait diversity related to variability in seasonal water availability within the riparian zone?
3. We confirm that metrics describing both flooding disturbance and patterns of water availability exhibit strong relationships with functional trait diversity in riparian vegetation communities of south-eastern Australia. Our key finding is that functional trait diversity in these systems tends to be positively associated with variability in hydrological conditions and the intensity of rare, high-magnitude flooding events, rather than average patterns of flow.
4. Our study highlights the importance of extreme flooding events and temporal patterns of water availability as determinants of diversity in riparian vegetation communities. These relationships may have significant consequences for plant communities experiencing alterations to hydrology caused by anthropogenic flow modification and the changing climate.

Keywords: disturbance, environmental heterogeneity, functional diversity, functional trait, riparian vegetation

Introduction

Riparian ecosystems are biophysically complex and highly diverse taxonomically, structurally and functionally (Naiman, Decamps & Pollock, 1993; Nilsson & Svedmark, 2002; Poff, 2002). Extensive flow regulation of river systems and changing patterns of run-off under future climates are likely to produce dramatically different future flow regimes, with significant consequences for the diversity and functioning of riparian assemblages. Riverine conservation and rehabilitation efforts must therefore be informed by general understanding of

the processes that generate patterns of diversity and drive ecosystem functioning in riparian ecosystems.

The prevailing paradigm in riparian ecology holds that heterogeneity in the riparian patch mosaic results from the sculpting action of hydrological processes across the biogeomorphic template (Tabacchi *et al.*, 1996; Palmer & Poff, 1997; Corenblit *et al.*, 2007; Bornette *et al.*, 2008). In riparian environments, it is this intrinsic environmental heterogeneity that fosters structural, taxonomic and functional heterogeneity within vegetation communities (Naiman *et al.*, 1993; Corenblit *et al.*, 2007; Bornette *et al.*, 2008). Local hydrology (river flow

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regime) is widely considered to be the most important determinant of community composition and functioning in riparian plant assemblages, as it dictates patterns of disturbance by flooding, as well as soil moisture availability (Poff, Allan & Bain, 1997; Arthington *et al.*, 2010).

Flooding may retard competitive exclusion by resetting the patch structure of parts of the landscape, thereby enhancing diversity (Huston, 1979; Naiman *et al.*, 1993), or constrain assemblages to species that have ecological strategies adapted to flooding, thereby decreasing diversity (Díaz, Cabido & Casanoves, 1998). General support has been found for the intermediate disturbance hypothesis (Connell, 1978) with respect to the relationship between flooding intensity and taxonomic diversity (e.g. Bendix, 1997; Bendix & Hupp, 2000; Lite, Bagstad & Stromberg, 2005; Corenblit *et al.*, 2007). This support is not equivocal, however (Nilsson *et al.*, 1989; Baker, 1990), and at within-reach scales, the geomorphic template is also a strong control on diversity (Bendix, 1997; O'Donnell *et al.* 2013).

In regions where riparian plants experience periodic water stress, soil moisture availability may be driven largely by hydrology (Castelli, Chambers & Tausch, 2000; Nilsson & Svedmark, 2002). Seasonal and interannual variability in patterns of disturbance and water availability are also known to influence species richness (Greet, Angus Webb & Cousens, 2011; Catford *et al.*, 2012, 2014), and this effect may be exacerbated for summer flows in hot or dry regions (Garsen, Verhoeven & Soons, 2014). A study investigating drivers of riparian vegetation community structure and composition in subtropical eastern Australia identified variability in dry season flows as the hydrological variable that was most strongly associated with variation in species richness (Arthington *et al.*, 2012).

Conservation and restoration activities increasingly aim to preserve the ecosystem functions associated with biological communities (Aerts & Honnay, 2011; Cadotte, Carscadden & Mirochnick, 2011; Montoya, Rogers & Memmott, 2012). Quantitative functional traits (such as specific leaf area, wood density and seed mass) can form the basis for mechanistic assessments of diversity that describe the range and distribution of ecological strategies in a community and their associated environmental effects. Such metrics of functional trait diversity (hereafter referred to as 'functional diversity') are substantially more powerful than taxonomic metrics as indicators of ecosystem functioning, ecosystem resilience and capacity to provide ecosystem services (Tilman *et al.*, 1997; Díaz & Cabido, 2001; Hooper, Chapin & Ewel, 2005). Reduced abundance of functionally unique

species may gradually undermine ecosystem resilience or functioning, and assessment of functional diversity can be useful to diagnose degradation before species loss occurs (Mouillot *et al.*, 2013). Assessments of ecosystem service production have also begun to give functional diversity priority over taxonomic metrics (Díaz & Lavorel, 2007).

Numerous metrics of functional diversity have been described in the literature (Schleuter & Daufresne, 2010; Mouillot *et al.*, 2013). These aim to quantify 'the distribution of species and their abundances in the functional space of a given community' (Mouillot *et al.*, 2013; p. 167) and typically process multidimensional trait data to output a single value describing various properties of these data. The framework described by Villéger, Mason & Mouillot (2008), consisting of functional richness (the volume of the convex hull circumscribing the range of trait values), functional divergence (divergence in the distribution of abundance within trait space) and functional evenness (the evenness of this distribution in trait space), has been commonly used to describe functional diversity (e.g. Biswas & Mallik, 2010; Pakeman, 2011; Clark *et al.*, 2012; Savage & Cavender-Bares, 2012). Functional dispersion (FDis), defined as the abundance-weighted mean distance in multivariate trait space of individual species to the centroid of all species in the community, represents an improvement on this framework (Laliberté & Legendre, 2010). FDis allows for consideration of species' abundances while integrating functional richness and functional divergence and is formulated to be independent of species richness, alleviating concerns that it merely tracks the patterns of species richness (as is possible with functional richness). FDis is also known to be more robust to bias due to missing trait data than metrics such as functional richness, evenness or divergence (Pakeman, 2014). In an empirical assessment of specific functional diversity metrics as indicators of ecosystem functioning in a Minnesota grassland, FDis was a useful predictor of three measures encompassing above- and belowground biomass production and light capture and compared favourably with other metrics (Clark *et al.*, 2012).

Considerably less is known about the drivers of functional diversity than of taxonomic diversity in riparian plant communities. Catford *et al.* (2011) analysed univariate functional trait distributions to show how flow impoundment along a large river system in south-eastern Australia was associated with greater cover of exotic species and reduced functional diversity in riparian wetlands. Support for the intermediate disturbance hypothesis with respect to functional diversity has been

described in communities along a gradient of disturbance associated with management for logging (Biswas & Mallik, 2010). Similarly in agricultural systems, land-use intensification has been linked with lower functional diversity across an international data set (Laliberté *et al.*, 2010) and the authors associated this effect with a reduced ability of communities to respond to disturbance. On the west coast of Scotland, increasing anthropogenic disturbance in arable fields, grazed grasslands, moorlands and woodlands was associated with reduced functional richness and increased functional evenness (Pakeman, 2011). A trend is apparent from these studies where functional diversity is inversely associated with human-induced environmental homogenisation.

Environmental heterogeneity is increasingly regarded as a key factor governing species richness gradients (Stein, Gerstner & Kreft, 2014). To date, however, advances in quantitative ecology based on functional traits have been sparsely applied to riparian systems. Describing the influence of hydrological heterogeneity on quantitatively derived measures of riparian functional diversity would represent a significant advance for riparian ecology and ecosystem-oriented riparian conservation.

We hypothesised that the environmental heterogeneity induced by repeated floods and fluctuating soil moisture levels should be reflected in the functional diversity of plant communities adapted to the riparian environment. We investigated the relationship between hydrologically driven environmental heterogeneity and functional diversity in riparian plant communities, using south-eastern Australia as a case study where a broad spectrum of hydrological heterogeneity is present within a relatively compact, contiguous landscape (Finlayson & McMahon, 1988; Peel, McMahon & Finlayson, 2004). Specifically, we asked the following questions: (i) Is functional trait diversity related to the frequency and magnitude of flooding disturbance? (ii) Is functional trait diversity related to variability in seasonal water availability within the riparian zone?

Methods

Study sites

Fifteen riparian sites were selected along gauged, partly confined rivers in the south-east coast and south-eastern Murray Darling drainage basins of Australia. These sites were distributed across clear gradients of ecologically relevant dimensions of hydrological variation: specifically, the magnitude, frequency, duration, timing and

rates of change of flow events and patterns. The study area spanned latitude -29.467 to -37.371 and longitude 147.413 – 152.217 . Sites spanned an altitudinal range of 23–732 m above sea level. Site-specific details can be found in the Data S1. Full description of site selection criteria and vegetation survey methods can be found in Lawson, Fryirs & Leishman (2015), as this study was undertaken simultaneously and at the same sites.

Rationale for trait selection

Data for the following traits were collected: specific leaf area, maximum canopy height, seed mass, wood density, flowering period length and leaf narrowness. These traits were chosen to encapsulate the key axes of variation and trade-offs relevant to ecological strategies employed by riparian plants (see Table 1 for justification and further description of functional traits).

Trait data set assembly

The data set for this study was assembled using measurements recorded in the field (specific leaf area, wood density), supplemented by data from the published literature, private and public trait databases and Australian flora texts; see Data S2 for a detailed bibliography of references for data. In the case that multiple values were found in the literature or online for a trait, values were excluded if they were measured from sites that were substantially different environmentally to the field site in which they were found in this study. Remaining values were averaged. Single values for each trait were recorded, under the assumption that for our chosen traits, interspecific variation is strong enough to allow differentiation between species despite noise due to intraspecific variation, and that species trait hierarchies are largely conserved across different spatial scales and data sets (Cordlandwehr *et al.*, 2013; Kazakou *et al.*, 2014). Leaf narrowness was not included for grasses, while seed mass and flowering period length were not included for ferns.

Specific leaf area was measured once for each species according to the procedure defined by Cornelissen *et al.*, (2003). A minimum of five new but fully mature leaves from well-lit areas were taken from each of five non-contiguous individual plants. Leaves were pressed in the field to maintain fresh area, allowed to air-dry at 20–45 °C and then scanned, and leaf area measurements were taken using image analysis software (ImageJ 1.48 for Windows). Leaves were then oven-dried at 70 °C for 72 h and weighed using a microbalance (Mettler Toledo,

Table 1 Justification for inclusion of traits in the functional diversity analysis

Trait	Definition	Ecological strategies and trade-offs captured by trait
Specific leaf area	Ratio of one-sided leaf area to oven-dry mass ($\text{cm}^2 \text{ g}^{-1}$)	Indicates species position along the leaf economics spectrum (Wright <i>et al.</i> , 2004) Associated with trade-off between rapid leaf construction and ability to tolerate stress (Reich & Wright, 2003)
Maximum canopy height	Height above ground of apical meristem (m)	Integrates trade-off between competition for light and cost of construction and maintenance of support structures (Falster, 2006)
Seed mass	Combined mass of the seed coat, endosperm and embryo (g). Does not include dispersal structures	Indicates maternal investment in individual offspring (Leishman <i>et al.</i> , 2000) Influences hydrochory (via seed buoyancy) (Carthey <i>et al.</i> , unpublished data) and ability to establish in different soil moisture conditions (Leishman <i>et al.</i> , 2000)
Wood density	Oven-dry mass divided by green volume (g cm^{-3})	Confers mechanical strength to stems but costly to construct Associated with slower relative growth rates (Chave <i>et al.</i> , 2009) but greater ability to tolerate water stress and disturbance (Telewski, 1995; Preston, Cornwell & Denoyer, 2006; Lawson <i>et al.</i> , 2015)
Flowering period length	Proportion of the year spent in flower (proportion, dimensionless)	Indicates species ability to respond reproductively to favourable conditions
Leaf narrowness	Ratio of average leaf width to average length (ratio, dimensionless)	Narrow leaves present less photosynthetically active tissue but can regulate temperature more efficiently and thus maintain photosynthesis in hot, dry or highly insolated (i.e. disturbed) conditions (Cornelissen <i>et al.</i> , 2003) Strongly indicative of rheophyt, the trait syndrome shared by plants adapted to growing near swift flowing, frequently flooded streams (Van Steenis, 1981)

Greifensee, Switzerland). Specific leaf area was calculated as one-sided fresh area divided by oven-dry mass.

Wood density data were collected according to the procedure outlined in Lawson *et al.* (2015). Site-specific values were available for wood density, but for this study, an overall mean value was calculated for species that occurred at multiple sites. Wood density values for species for which data were not available from the field were obtained from the Global Wood Density Database (Chave *et al.*, 2009).

Hydrological analysis

Daily discharge data for each site were obtained from the PINNENA CW 10.1 database (New South Wales Office of Water, Department of Primary Industries) and the New South Wales Office of Water Continuous Water Monitoring network website (<http://realtimedata.water.nsw.gov.au/water.stm>) for New South Wales sites, and the Victoria State Government's Water Measurement Information System website (<http://data.water.vic.gov.au/monitoring.htm>) for Victorian sites. Thirty-year time series spanning 1983–2012 were obtained where possible, although three sites had truncated the records of 15, 19 and 28 years. Missing data were approximated by multiple linear regression (four sites) and linear interpolation (one site) using the Time Series Manager module in the River Analysis Package (Marsh, Stewardson & Kennard, 2003). We used the Time Series Analysis module in the River Analysis Pack-

age to generate a set of 23 hydrological metrics for each site, based on a reduction of the minimally redundant set of ecologically relevant metrics for Australian rivers described by Kennard *et al.* (2010). These metrics were chosen as descriptors of the frequency and magnitude of flooding disturbance, as well as variability in water availability across seasons and between years (see Table 2 for descriptions and rationale for inclusion of individual metrics). Collinearity between these metrics was analysed using principal components analysis (PCA); the results of this PCA as well as summary statistics for hydrological metrics are given in the Data S1. Parameters used to generate hydrological metrics were identical to Lawson *et al.* (2015). Metrics of flow magnitude, which had units mL day^{-1} , were standardised by mean daily flow to allow for comparison between different river channel sizes. These metrics therefore represent ratios of flow magnitude to mean daily flow.

Functional trait diversity analysis

Functional dispersion characterises the distribution of species traits at a site in multivariate trait space. We used the *dbFD* function from the FD package for R (Laliberté & Legendre, 2010) to calculate abundance-weighted functional dispersion (FDis) from species trait values and relative abundances for each site. This package implements the method for distance-based tests for homogeneity of multivariate dispersions described by Anderson (2006).

Table 2 Hydrological parameters used as metrics of frequency and magnitude of flooding disturbance and variability in seasonal water availability in the riparian zone

Parameter	Abbreviation	Units	Description
Flood frequency and magnitude			
Mean magnitude of high spells*	HSPeak	Dimensionless	
CV of all years' mean high-spell magnitude	CVAnnHSPeak	Dimensionless	Together, these metrics characterise the patterns of flooding intensity and frequency. High spells are periods of flow above the 95th percentile on the flow duration curve. HSPeak describes the mean magnitude of peak flows during high spells throughout the record. MDFAnnHSNum describes the mean annual frequency of high-spell periods. The coefficients of variation of these metrics between years characterise hydrological variability as it pertains to patterns of high flows. 20-year average return interval (ARI) floods are larger flow events with the potential to be geomorphically effective and rework the fluvial landscape.
20-year ARI flood magnitude*	AS20YrARI	Dimensionless	
Mean of all years' number of high spells	MDFAnnHSNum	Year ⁻¹	
CV of all years' number of high spells	CVAnnHSNum	Dimensionless	
Rise and fall rates			
Mean rate of rise *	MRateRise	Day ⁻¹	
Mean rate of fall *	MRateFall	Day ⁻¹	Flow rise and fall rates describe the shape of high-flow curves. Interannual variability within these metrics captures the diversity of peak flow shapes within a system. Unfortunately, these metrics are constrained to daily resolution by the limitations of historical discharge records.
CV of all years' mean rate of rise	CVAnnMRateRise	Dimensionless	
CV of all years' mean rate of fall	CVAnnMRateFall	Dimensionless	
Colwell's indices			
Constancy of monthly mean daily flow	C_MDFM	Dimensionless	Colwell's indices provide a measure of the seasonal predictability of flow events and therefore water availability within the riparian zone. Constancy (C) measures uniformity of flow across seasons and is maximised when flow conditions do not differ between seasons. Contingency (M) is a measure of interannual uniformity in seasonal flow patterns and is maximised when seasonal patterns of flow are consistent between years. We generated Colwell's indices for both average flow conditions and minimum flow conditions.
Contingency of monthly mean daily flow	M_MDFM	Dimensionless	
Constancy based on monthly minimum daily flow	C_MinM	Dimensionless	
Contingency based on monthly minimum daily flow	M_MinM	Dimensionless	
Flow seasonality			
Average mean daily flow for Spring *	MDFMDFSpring	Dimensionless	These metrics describe the average magnitude and variability within mean daily flows for each season. Averages and coefficients of variation are calculated across yearly means. Seasonal average mean daily flows were standardised by overall mean daily flow, so actually represent the ratio of mean daily flow in a given season to the total mean daily flow.
Average mean daily flow for Summer *	MDFMDFSummer	Dimensionless	
Average mean daily flow for Autumn *	MDFMDFAutumn	Dimensionless	
Average mean daily flow for Winter *	MDFMDFWinter	Dimensionless	
CV of mean daily flow for Spring	CVMDFSpring	Dimensionless	
CV of mean daily flow for Summer	CVMDFSummer	Dimensionless	
CV of mean daily flow for Autumn	CVMDFAutumn	Dimensionless	
CV of mean daily flow for Winter	CVMDFWinter	Dimensionless	

*metrics were standardised by mean daily flow.

dbFD uses Gower's method (1971) to generate the trait dissimilarity matrix, which can account for missing values, and automatically standardises traits by their ranges; Cailliez's correction was applied to the matrix (Cailliez, 1983). Simpson's diversity was calculated using the SYNCSEA package (Debastiani & Pillar, 2012).

Only species present at >1% cover in plots were included in the analysis ($n = 126$, from 327 species). Data-deficient species lacking values for more than four traits could not be included in the analysis as they produced gaps in the distance matrix used to calculate

functional diversity. Thus, a final total of 107 species were included in the analysis. Data density exceeded 90% for all sites and averaged 97%; full data density information including trait-specific values is shown in the Data S3. All trait values were transformed by \log_{10} prior to analysis. Summary statistics for the trait data set are also available in the Data S3.

Following Leps *et al.* (2006), we performed principal components analysis (PCA) (stats package, R Core Team 2013) on trait data to check for redundancy. Although not completely orthogonal, traits were well distributed across

multiple principal components. Therefore, we believe there is both ecological (as previously discussed) and statistical rationale to retain all six traits in the analysis.

All statistical analyses were performed using the R statistical programming environment (R Core Team 2013). Statistical significance was interpreted at alpha = 0.05.

Relationships between FDis, hydrological metrics and taxonomic diversity

Ordinary least-squares (OLS) regression models were generated for the selected metrics to determine the relationships between hydrological gradients and FDis. To reduce the occurrence of type 1 statistical error, we adjusted the resulting P values using the two-step Benjamini–Hochberg (BH) procedure (Benjamini, Krieger & Yekutieli, 2006) for controlling the false discovery rate (*mt.rawp2adjp* function in *multtest* package for R) (Polland, Ge & Dudoit, 2008).

The utility of functional diversity metrics depends on their ability to provide non-redundant information compared with measures of taxonomic diversity. We further tested relationships (using OLS regression) between FDis and species richness and Simpson's diversity (for species used in the analysis, present at >1% cover), and species richness for the full set of 327 species was identified in the study.

We selected a minimal multiple regression model designed to incorporate the descriptors of disturbance frequency and magnitude and variability in seasonal flow. The full set of hydrological metrics was initially screened to remove metrics that were individually determined to have non-significant relationships with FDis. PCA over the remaining metrics identified one major and two minor axes of variation (PC1 – 71.4%, PC2 – 9.0% and PC3 – 8.3% of variance explained). For PC1, there was no clear differentiation in eigenvalues; the metric with highest individual R^2 value (interannual variability in high flows) was selected. PC2 identified mean daily flow in summer and PC3 identified interannual variability in flood frequency as further sources of variability. Models were then built pertaining to all possible permutations of summation and interaction for these three metrics. Values for each metric were centred by subtracting the mean value (after Robinson & Schumacker, 2009). Multicollinearity was tested for according to the variance inflation factor (VIF) score (HH package, Heiberger & Holland, 2004), and models were compared according to the second order of Akaike's information criterion (AIC) (MuMIn package for R, Barton, 2012; Burnham & Anderson, 2002).

Assessing the influence of other environmental variables

Climatic and edaphic conditions are known to be important abiotic drivers of plant diversity at landscape scales (Laliberté *et al.*, 2013; Vázquez-Rivera & Currie, 2015) and may exhibit strong interdependence with hydrological flow regime. We used a variance-partitioning approach to assess the individual contributions of hydrology, climatic and edaphic conditions to modelling variation in FDis. Climate data were taken from eMast/TERN at a resolution of 0.01 degrees (Hutchinson, Kesteven & Tingbao, 2014). Bioclimatic variables representing annual trends, seasonality and extremes were then calculated following the BIOCLIM concept (Busby, 1991). Edaphic data were obtained from the CSIRO Soil and Landscape Grid of Australia at a resolution of 3 arc seconds (~3 m) (Rossel *et al.*, 2014a, 2014b, 2014c, 2014d, 2014e, 2014f, 2014g, 2014h, 2014i, 2014j, 2014k; Wilford *et al.*, 2014). Further details on these climate and edaphic data sets are given in the Data S1. Optimal models explaining variation in FDis according to climatic and edaphic variables were then generated using the same process as for hydrological metrics. Variance explained by these models was partitioned by partial regression following Legendre (2007), using the function *varpart* in R (vegan package, Oksanen *et al.*, 2013). Adjusted R^2 , which controls for sample size and number of predictors (Peres-Neto *et al.*, 2006), was used to estimate the proportion of variation jointly and independently explained by each model.

Results

Below, we describe the patterns of variation in functional dispersion (FDis) as they relate to the hydrological metrics described in Table 2. All models are linear apart from M_MinM and CVMDFSummer, for which a quadratic model (d.f. = 2,12) provided a substantially better fit. Statistics for all univariate regression models are presented in the Supporting Information (S4).

Is functional diversity related to the frequency and magnitude of flooding disturbance?

Functional dispersion was positively associated with metrics describing intense but rare episodes of flooding disturbance. FDis was significantly associated with the magnitude of the 20-year average return interval flood (AS20YrARI, Fig. 1a, adjusted P = 0.0278, R^2 = 0.377). FDis was also significantly associated with interannual variability in high-flow magnitude (CVAnnHSPeak,

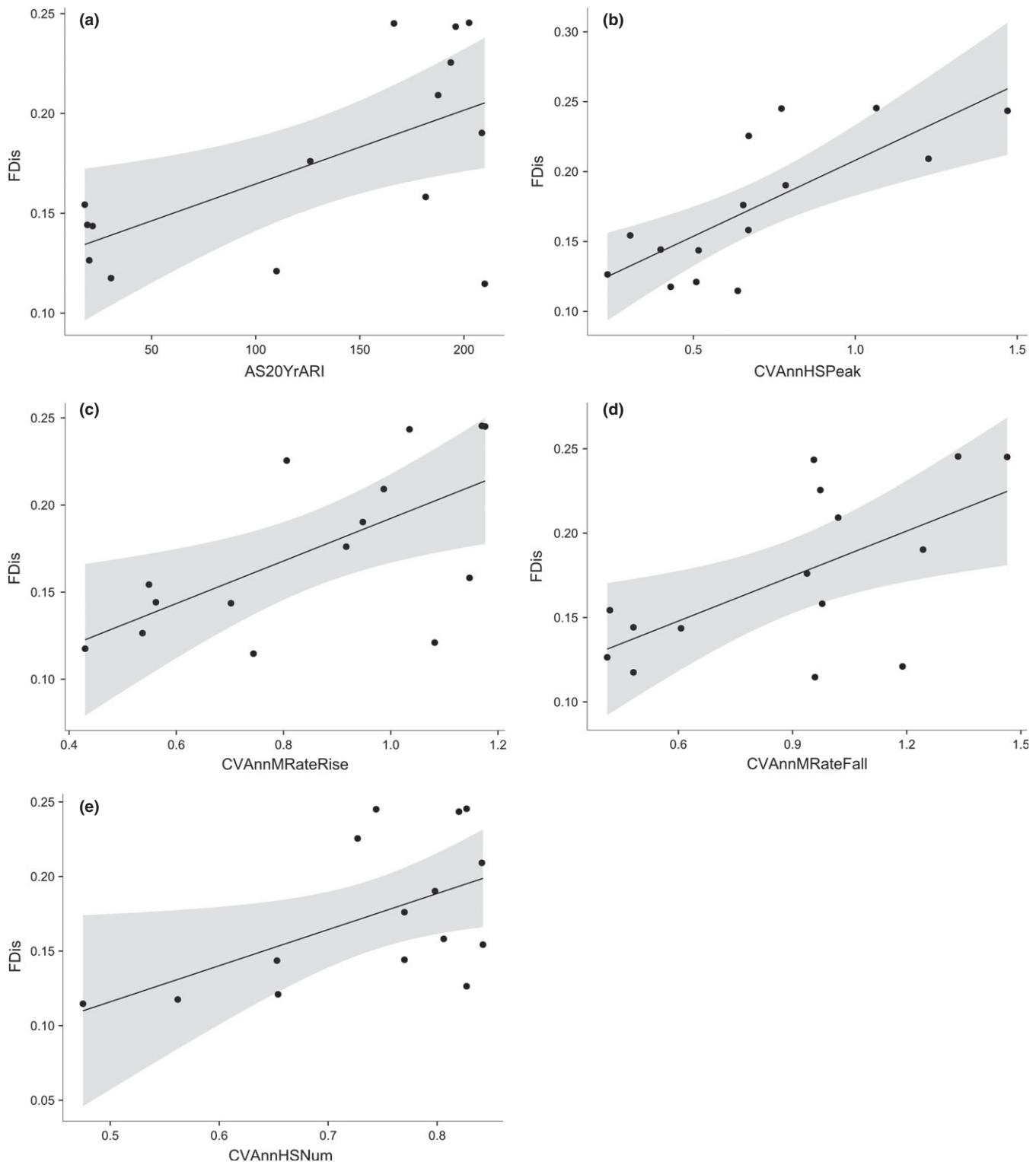


Fig. 1 Relationships between FDis and hydrological metrics describing (a) magnitude of the 20-year average return interval flood (AS20YrARI), (b) interannual variability in high-flow magnitude (CVAnnHSPeak), (c) interannual variability in flood rise rate (CVAnnMRateRise), (d) interannual variability in flood fall rate (CVAnnMRateFall), (e) interannual variability in high-flow frequency. Fitted lines depict ordinary least-squares regression models. All models are linear fits. Shaded areas depict the smoothed 95% confidence interval around the regression model. All relationships shown are significant. Units are shown in Table 2.

Fig. 1b, adjusted $P = 0.0152$, $R^2 = 0.577$) and rates of flow rise (CVAnnMRateRise, Fig. 1c, adjusted $P = 0.0278$, $R^2 = 0.403$) and fall (CVAnnMRateFall, Fig. 1d, adjusted $P = 0.0278$, $R^2 = 0.390$), whereas relationships with metrics describing average conditions were not significant (mean high-flow magnitude, HSPeak, adjusted $P = 0.065$; mean flood rise rate, MRateRise, adjusted $P = 0.156$; mean flood fall rate, MRateFall, adjusted $P = 0.157$). Likewise, while interannual variability in flood frequency (CVAnnHSNum, Fig. 1e, adjusted $P = 0.0360$, $R^2 = 0.296$) was significantly associated with FDis, mean annual flood frequency was not (MDFAnnHSNum, adjusted $P = 0.727$). These results indicate that functional diversity is higher at sites that experience extreme flooding events and heterogeneous patterns of flow.

Is functional diversity related to variability in seasonal water availability in the riparian zone?

Functional dispersion was positively associated with variability in flow seasonality. FDis was increased when seasonal patterns of minimum (M_MinM, Fig. 2a, adjusted $P = 0.0278$, $R^2 = 0.540$), maximum (M_MaxM, Fig. 2b, adjusted $P = 0.0325$, $R^2 = 0.328$) and average (M_MDFM, Fig. 2c, adjusted $P = 0.0325$, $R^2 = 0.347$) flows became less uniform (smaller values of M) between years. In other words, at high FDis the season with which these flows were associated was not consistent through the record. FDis was not significantly explained by interseasonal uniformity of minimum (Fig. 2d, C_MinM, adjusted $P = 0.1021$, $R^2 = 0.166$) or average (Fig. 2e, C_MDFM, adjusted $P = 0.0861$, $R^2 = 0.186$) flows, although visual inspection of the scatterplots for these relationships indicates two sites at the lower bound of the x-axis (i.e. strongly seasonal patterns of flow), with substantially lower FDis than predicted by the regression model. If we consider these trends, we can infer that functional dispersion was increased when discharge patterns differed strongly between seasons, but the season with which those patterns were associated was not consistent between years.

This observation was corroborated by positive relationships between FDis and variability in mean daily flows for autumn (CVMDFAutumn, Fig. 3a, adjusted $P = 0.0386$, $R^2 = 0.301$), winter (CVMDFWinter, Fig. 3b, adjusted $P = 0.0278$, $R^2 = 0.414$) and spring (CVMDFSpring, Fig. 3c, adjusted $P = 0.10325$, $R^2 = 0.327$). Summer flow variability (CVMDFSummer, Fig. 3d, adjusted $P = 0.0325$, $R^2 = 0.472$) exhibited a humped relationship with FDis. Mean daily flows for both summer and spring were associated

with FDis, however. This association was positive for summer (MDFMDFSummer, Fig. 3e, adjusted $P = 0.0230$, $R^2 = 0.503$) and negative for spring (MDFMDFSpring, Fig. 3f, adjusted $P = 0.0278$, $R^2 = 0.3862$). Note that this metric actually represents the ratio of seasonal mean daily flow to the general mean of daily flow for a given river. Even though FDis was highest at sites where average flow is not associated with any particular season (low M_MDFM), these sites still had high values for mean daily flow in summer. Pearson correlation confirms a significant negative relationship between M_MDFM and MDFMDFSummer (Pearson's $r = -0.657$, $P = 0.008$) but not C_MDFM and MDFMDFSummer (Pearson's $r = -0.423$, $P = 0.1164$). Summer mean daily flow may have been inflated by exceptional periods where very high average flows occurred during summer. Mean daily flow in spring, conversely, was strongly positively correlated with M_MDFM (Pearson's $r = 0.8357$, $P = 0.0001$) and C_MDFM (Pearson's $r = 0.7839$, $P = 0.0005$), indicating that where mean daily flows in spring are high, this pattern is stable and consistent between years.

Comparisons with measures of taxonomic diversity

Across the species used in the functional diversity analysis (i.e. present at >1% plot cover), FDis was independent of species richness ($P = 0.274$, $F_{1,13} = 1.302$) and Simpson's diversity ($P = 0.513$, $F_{1,13} = 0.454$) for species included in the functional diversity analysis, but significantly associated with species richness for the full set of 327 species ($P = 0.030$, $F_{1,13} = 5.957$, $R^2 = 0.314$).

A minimal multiple regression model to explain functional diversity according to hydrology

We used an information theoretic procedure to select the best fitting, most parsimonious multiple regression model from the factorial set of possible models which included FDis as the dependent variable and the following independent variables: interannual variability in high-flow frequency (CVAnnHSNum), interannual variability in high-flow magnitude (CVAnnHSPeak) and mean daily flow during summer (MDFMDFSummer). This set of models is described in Table 3.

Model 12 was determined to be the optimal model according to AICc. Models 4, 5 and 10 were close to optimal but offered lower explanatory power according to the adjusted R^2 of the model. Although Model 13 offered higher explanatory power, it was less parsimonious according to AICc and exhibited multicollinearity. Multicollinearity was determined not to be of importance for

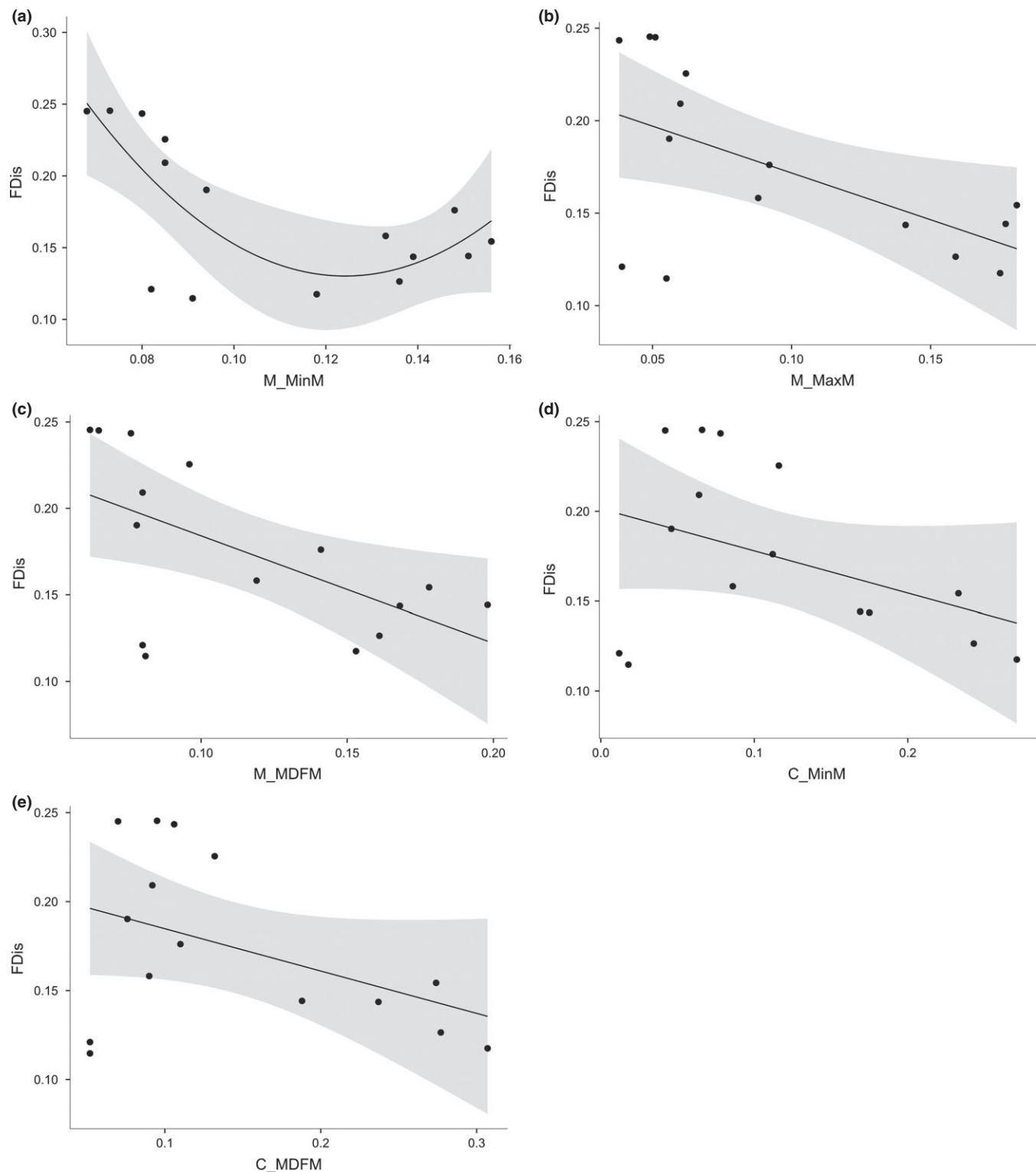


Fig. 2 Relationships between FDis and hydrological metrics describing (a) contingency of monthly minimum daily flow (M_MinM), (b) contingency of monthly maximum daily flow (M_MaxM), (c) contingency of monthly mean daily flow (M_MDFM), (d) constancy of monthly minimum daily flow (C_MinM), (e) constancy of monthly mean daily flow (C_MDFM). Fitted lines depict ordinary least-squares regression models. (a–c) depict significant relationships. (d–e) depict non-significant relationships (note the strong influence over the regression fit of the two points at the lower bound of FDis). Units are shown in Tables 1 and 2.

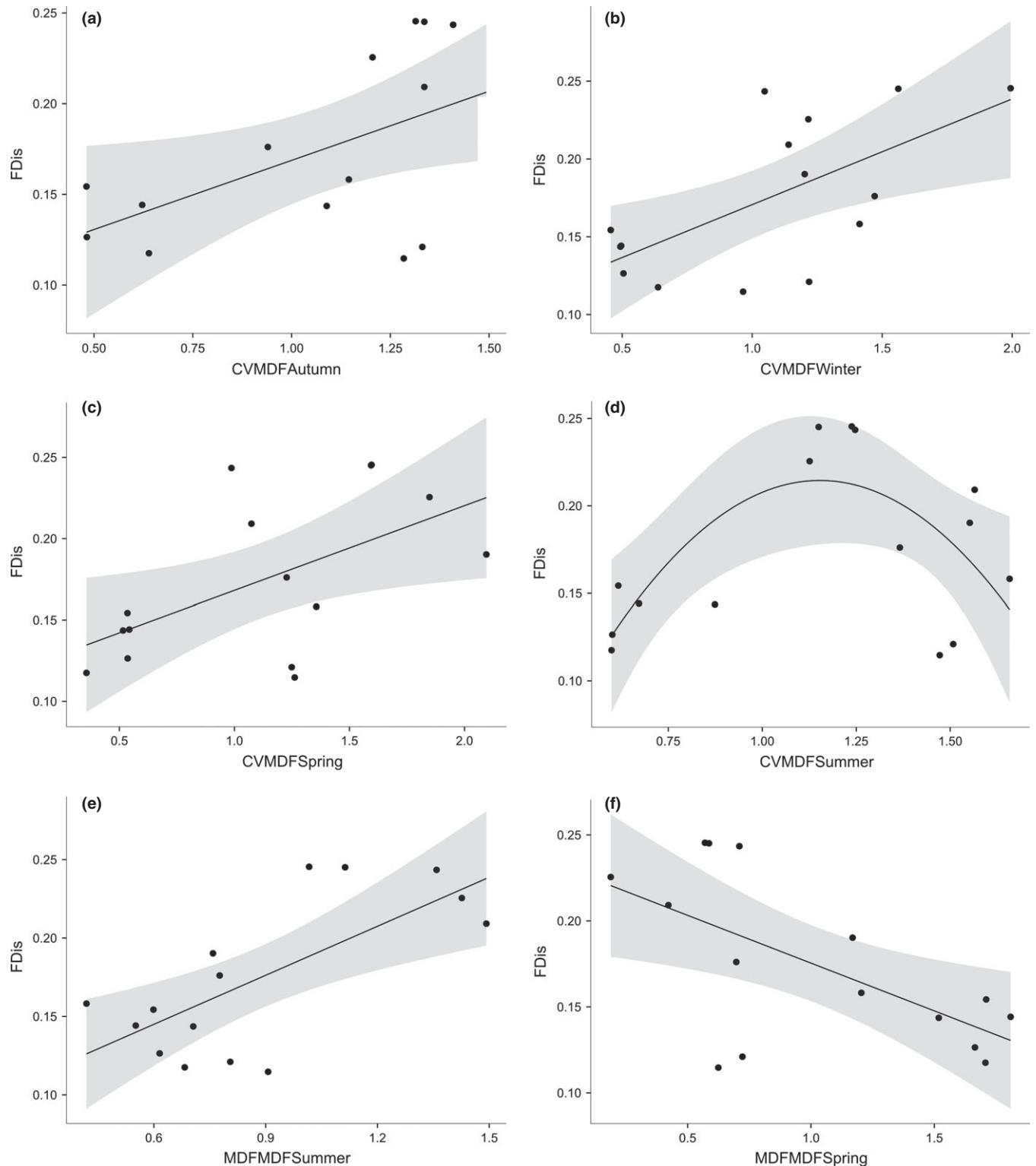


Fig. 3 Relationships between FDis and hydrological metrics describing (a) variability in autumn mean daily flow, (b) variability in winter mean daily flow, (c) variability in spring mean daily flow, (d) variability in summer mean daily flow, (e) mean daily flow in summer, (f) mean daily flow in spring. Fitted lines depict ordinary least-squares regression models. All models are linear fits except in (d), which is a quadratic fit. Shaded areas depict the smoothed 95% confidence interval around the regression model. All relationships shown are significant. Units are shown in Tables 1 and 2.

Table 3 Multiple regression models with associated fitting parameters. * in the model formula denotes both summation and interaction between variables. R^2 values have been adjusted for multiple regression for models using more than one variable. The optimal model according to AICc is indicated by bold typeface

#	Model	Adj. R^2	AICc	Delta AIC
1	FDis ~ CVAnnHSNum	0.296	-46.14	12.78
2	FDis ~ CVAnnHSPeak	0.577	-53.79	5.13
3	FDis ~ MDFMDFSummer	0.503	-51.37	7.56
4	FDis ~ CVAnnHSNum + CVAnnHSPeak	0.636	-54.52	4.40
5	FDis ~ CVAnnHSNum + MDFMDFSummer	0.681	-56.50	2.42
6	FDis ~ CVAnnHSPeak + MDFMDFSummer	0.561	-51.71	7.21
7	FDis ~ CVAnnHSNum*CVAnnHSPeak	0.655	-51.95	6.97
8	FDis ~ CVAnnHSNum* MDFMDFSummer	0.665	-52.40	6.53
9	FDis ~ CVAnnHSPeak*MDFMDFSummer	0.566	-48.54	10.39
10	FDis ~ CVAnnHSNum + CVAnnHSPeak + MDFMDFSummer	0.704	-54.25	4.68
11	FDis ~ CVAnnHSNum*CVAnnHSPeak + MDFMDFSummer	0.709	-50.14	8.79
12	FDis ~ CVAnnHSNum + CVAnnHSPeak*MDFMDFSummer	0.838	-58.92	0
13	FDis ~ CVAnnHSNum*CVAnnHSPeak*MDFMDFSummer	0.944	-48.62	10.30

Model 12 according to variance inflation factor scores (all <3 on centred variables). All terms in Model 12 were individually significant; a full summary of the model is given in Table 4. Notably, the coefficient of the interaction term was negative, indicating a diminishing influence on FDis when values of CVAnnHSPeak and MDFMDFSummer are both high.

Do climatic or edaphic conditions explain variation in FDis that is unaccounted for by hydrological metrics?

Of the 19 climatic variables examined, a number exhibited statistically significant univariate relationships with FDis; the quadratic function of isothermality was determined by AICc to be the optimal regression model. Of the 12 edaphic variables examined, no significant univariate relationships with FDis were found. Variance partitioning showed that while the dominant fraction of variation explained by the two models was shared (0.612), the climatic model explained a minimal amount of non-redundant information (0.016) compared with the hydrological model (0.226), indicating a dominant influence of hydrological flow regime on functional disper-

sion in this study. Table 5 shows the partition table generated from this analysis.

Discussion

We surveyed vegetation communities along partly confined river systems across south-eastern Australia and found that functional diversity, as characterised by functional dispersion, exhibited strong relationships with local patterns of hydrology. To our knowledge, this is the first study to examine the relationships between hydrological conditions and the diversity of ecological strategies within riparian vegetation communities using multiple quantitative functional traits. The overarching pattern across these relationships can be summarised as 'heterogeneous flows foster heterogeneous communities'.

This pattern is consistent with existing understanding of the processes that generate and maintain biological diversity in the riparian environment. Briefly stated, this paradigm holds that riparian biodiversity is a function

Table 4 Regression summary for Model 12. Beta values are regression coefficients (B) standardised by the standard deviation of the term

	B	SE	Beta	t	P
CVAnnHSNum	0.240	0.054	0.540	4.414	0.001
CVAnnHSPeak	0.071	0.026	0.498	2.773	0.020
MDFMDFSummer	0.074	0.024	0.506	3.056	0.012
CVAnnHSPeak*	-0.190	0.060	-0.459	-3.186	0.001
MDFMDFSummer					

Table 5 Partitioning of variance in FDis as explained by optimal hydrological and climatic models. The 'l' symbol denotes 'controlled for'; that is, variation explained non-redundantly by a fraction

Combined fractions	d.f.	Adjusted R^2
a + b (hydrology)	4	0.838
b + c (climate)	2	0.629
a + b + c (hydrology + climate)	6	0.854
Individual fractions		
a (hydrology l climate)	4	0.226
b (shared variation)	0	0.612
c (climate l hydrology)	2	0.016
d (unexplained variation)		0.146

of landscape complexity generated by hydrogeomorphic processes, overlain by feedback interactions between these processes and biotic components of the riparian environment (Tabacchi *et al.*, 1996; Palmer & Poff, 1997; Corenblit *et al.*, 2007; Bornette *et al.*, 2008). Because we surveyed geomorphically homogeneous sections of sloping bank, our argument is presented under the assumption that functional diversity is a property of riparian communities at the reach scale. Influx of species from more physically complex adjacent patches, then, is responsible for the diversity we observed on these geomorphologically homogeneous sloping bank sections.

The sites surveyed in this study spanned a spectrum of flooding intensity: the 20-year average return interval (ARI) flood ranged from 18 times the mean daily flow to 210 times the mean daily flow. Higher-magnitude flow events are more likely to be geomorphically effective in partly confined river systems (Huang & Niemann, 2006). The strong positive relationship between functional diversity and 20-year ARI flood magnitude supports the supposition that disturbance retards competitive exclusion as a diversity-limiting process (*sensu* Huston, 1979). Notably, no significant relationships were found between functional diversity and metrics describing mean high flow conditions, whereas metrics describing variability had high explanatory power. Interannual variability in high-flow magnitude showed the strongest relationship with functional diversity in this study. If a causal relationship exists, it could be because the average high-flow magnitude determines what proportion (in terms of elevation above the main channel) of the riparian zone experiences flooding in a given year. Variability in high-flow magnitude, combined with geomorphic heterogeneity, will produce variability in the time since last inundation (without significant disturbance), or combined inundation and disturbance, for a given patch of vegetation. Since flood flows also function as an important dispersal pathway for propagules (Merritt, Nilsson & Jansson, 2010), variability in high-flow magnitude should influence recruitment processes in a similar manner. Likewise, variability in the frequency of flood flows also results in variable time since last inundation or disturbance. Interannual variability in flood rise and fall rates was also positively associated with functional diversity. Overall, the combination of occasional high-intensity flooding disturbance with year-to-year variability in patterning of high-flow events results in a heterogeneous patch mosaic. This environmental heterogeneity provides a broad range of niches, facilitating the success of a diversity of ecological strategies (Bornette *et al.*, 2008).

We can extend this framework to account for the observed relationships between functional diversity and variability in seasonal water availability. Our sites spanned a gradient of flow seasonality: at one end, rivers exhibited weak but stable patterns of seasonality; at the other, rivers were characterised by high interannual variability and modal, seasonally inconsistent distributions of flow. Once again, communities with higher functional diversity tended to be located towards the 'variable' end of the spectrum. South-eastern Australian plants do exhibit characteristic species-level responses to seasonality, although there is no general coordination of growth and reproduction phenologies as in the Northern Hemisphere (Ford, Paton & Forde, 1979). Flowering times within the Myrtaceae (a dominant family in riparian plant communities of south-eastern Australia) are often staggered where species are sympatric (Beardsell, Obrien & Williams, 1993), and growth and reproduction of riparian plants are commonly associated with the arrival of favourable conditions (Robertson, 2001; Woolfrey & Ladd, 2001; Siebentritt, Ganf & Walker, 2004). High coefficients of variation in seasonal mean daily flows may therefore act to temporarily provide species with favourable conditions according to their seasonal biology.

Exceptions to these patterns included the quadratic fit for variability in summer mean daily flows, with high values being associated with a reduction in functional diversity, and mean daily flow for summer, which was positively associated with functional diversity and broke the trend of associations with seasonal means being either non-significant or negative. A meta-analysis of the effect of drought on riparian vegetation showed reduced species richness and a shift towards drought-tolerant species following climate-induced increases in the intensity and duration of drought, an effect that was exacerbated by high temperatures (Garsen *et al.*, 2014). Higher temperatures in the absence of drought were associated with higher rates of primary production. Higher mean daily flows in summer, then, potentially alleviate the water stress induced by hot weather while stimulating plant growth. We did investigate whether sites at subtropical latitudes simply had higher functional diversity than temperate sites, according to well-known latitudinal patterns of species richness (Willig, Kaufman & Stevens, 2003), and found no relationship between latitude and FDis (data not presented).

It was notable that while FDis is statistically independent of species richness, in this study functional dispersion was significantly associated with total species richness (as opposed to richness of the set of species used in the FDis analysis that were present at >1% abun-

dance). A broad species pool therefore appears to facilitate higher functional dispersion within the dominant flora of a community, even though the richness of the dominant group of species does not necessarily determine functional diversity. It is difficult to interpret this finding, however, as adding data for rare species to the analysis would necessarily render the new value of FDis independent of total species richness.

The multiple regression model selected according to AICc explained a high proportion of variation in FDis. This model described functional diversity as a function of variability in flood frequency and magnitude, and in summer mean daily flow. The combination of flow heterogeneity with extra watering during summer appears to provide optimal conditions for functionally diverse communities. The coefficient of the interaction term between variability in flood magnitude and summer mean daily flow was significant but negative, indicating that the additive effect is subject to diminishing returns at high values of both terms. The key finding here is that these three metrics of hydrological conditions are able to account for most of the variation in FDis; data on climatic conditions and edaphic properties add very little non-redundant information to our model. We used traits in our analysis that capture a broad spectrum of ecological strategies, rather than solely traits associated with riparian specialist strategies, which might be expected to bias results towards flow response. We caveat, however, that this model does not account for the effect of plot-scale geomorphic variability on diversity, as this was controlled for in the site selection process.

Two sites had anomalous values for FDis that do not fit within this conceptual model of disturbance and flow variability providing high niche heterogeneity. These sites experience highly variable flows but had low functional diversity. We experimentally adjusted the abundances of dominant species at these sites and found that the low values for FDis appear to result from dominance of a single species at each site (the medium-sized tree *Acmena smithii* at Mammy Johnson's Creek and the liana *Ripogonum album* at Jilliby Creek). These sites may represent cases in which species with 'variability' specialist strategies have become dominant. *Acmena smithii* has a relatively large seed and is shade tolerant (Melick, 1990) but, once established, develops a lignotuber and is highly resistant to drought and disturbance (Ashton & Frankenberg, 1976). With respect to *Ripogonum album*, there is evidence to suggest that abundance of lianas may be associated with disturbance (Laurance & Pérez-Salicrup, 2001) and that lianas have a competitive advantage over trees in dry conditions ((Swaine &

Grace, 2007; Cai, Schnitzer & Bongers, 2009), but see Nepstad *et al.*, 2007).

Our survey covered approximately half of the range of hydrological variability present within the Australian continent; much of the lower range and middle range was captured, but highly variable dryland systems were not included (Peel *et al.*, 2004). Our results mostly show monotonic relationships between FDis and hydrological heterogeneity, and as such, they do not support intermediate disturbance associated patterns found in other studies of taxonomic diversity (Bendix, 1997; Bendix & Hupp, 2000; Lite *et al.*, 2005; Corenblit *et al.*, 2007) and functional diversity (Biswas & Mallik, 2010) of riparian plant communities. This finding is consistent with the assertion of Mouillot *et al.* (2013) that metrics of functional diversity should show monotonic rather than unimodal relationships with disturbance intensity. It is difficult to be conclusive on this point, however, as it is possible that we have found only the ascending half of a unimodal curve. To this end, it would be useful to survey communities that experience more extreme hydrologies, such as those in Australia's arid regions or the monsoon tropics. Disturbance intensity and hydrological heterogeneity may not necessarily be connected in such systems. Arid zone rivers characterised by 'all or nothing' flow regimes may not experience the moderate flood events that generate and maintain diversity at the patch scale; for monsoonal rivers, disturbance may be similarly intense, but seasonal and interannual patterns of flow are relatively predictable (Kennard *et al.*, 2010). In large tropical riverscapes, hydrological rhythmicity (i.e. the opposite of hydrological heterogeneity) has in fact been associated with greater richness of fish and bird taxa, and greater production in riparian forests (Jardine *et al.*, 2015).

Unlike anthropogenic disturbances associated with agricultural land use, which have been shown to be associated with lower functional richness (Pakeman, 2011) and lower functional redundancy (Laliberté *et al.*, 2010), recurring hydrological disturbance appears to promote riparian plant functional diversity in this study. A similar response to natural fire regimes in the Patagonian steppe has also been observed (Sottile *et al.*, 2015). It seems reasonable to assume that the generative effect of natural disturbance on niche heterogeneity is not reproduced by typical anthropogenic disturbances.

Our findings are important from an applied river management and conservation perspective. Widespread anthropogenic river modification has altered the hydrology of river systems throughout the world, and the changing climate has the potential to exacerbate the

impacts of flow modification as well as affecting unaltered river systems. A key issue with river modification is that it reduces flow heterogeneity. Dams flatten flood hydrographs (and peaks), alter seasonality and increase predictability of flows (Graf, 2006; Singer, 2007). These alterations to flow have 'terrestrialised' riparian areas and wetlands, reducing functional diversity and facilitating invasion by exotic terrestrial weed species (Catford *et al.*, 2011). Dams also interrupt hydrochorous transport of propagules (Merritt *et al.*, 2010), such that flood flows below dams may cause net removal of propagule material from fluvial substrates, rather than deposition. When designing environmental flows (e.g. Howell & Benson, 2000), river managers typically consider magnitude, frequency and seasonality of flows. The findings in this study agree with recent suggestions (Naiman *et al.*, 2008) that managers should also attempt to simulate flow regime variability in their designed flows.

Future run-off predictions are regionally specific but similarly include changes to total discharge, flow seasonality and flow variability. In regions with projected increases in climatic variability, changes to the prevalence, intensity and timing of extreme flooding or drought events can be expected (Hennessy *et al.*, 2008). Reductions in mean summer precipitation have already occurred over large areas of Australia, coinciding with a warming of 0.4–0.7 °C since 1950 (Hennessy *et al.*, 2007). Lower average flows during hotter summers may stress riparian communities and constrain functional dispersion. Alternatively, greater climatic variability associated with future climates (Hennessy *et al.*, 2008) may promote hydrological heterogeneity in regions that were previously associated with more stable flow conditions. This may result in opening of niche space to favour opportunistic ecological strategies and promote invasion by exotic species.

Restoring functional diversity to pre-degradation levels may be a useful goal for riparian rehabilitation efforts along regulated or otherwise degraded river reaches. High functional diversity communities encompass a broad range of ecological strategies and should have a greater capacity to adapt to environmental change (Tilman *et al.*, 1997; Standish *et al.*, 2014). By working to restore functional diversity along impacted river systems, managers may increase the likelihood that riparian communities will be able to maintain critical ecosystem functions under future climates.

The identification of such a strong relationship between environmental variability and functional diversity has significance for lotic ecology (Palmer & Poff, 1997), as well as ecology in general. Our study emphasises the importance of flooding disturbance and hydro-

logical heterogeneity as drivers of functional diversity in riparian plant communities. These findings should be applicable to river systems in other regions and biomes characterised by moderate hydrological variability, given the profound influence of hydrology in shaping the structure of fluvial landscapes and determining the ecological strategies of plants that are able to persist and thrive in the riparian environment. Comparisons with data sets from regions with harsh but highly predictable seasonal patterns of hydrology, for example monsoonal or nival regimes, are needed to confirm this assertion. In the south-eastern Australian context, at least, alterations to flow variability and disturbance regimes by dams and the changing climate may have significant consequences for the diversity and functioning of riparian vegetation communities.

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Data availability

Trait data for all species are available in the Data S2.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1 Characteristics of field sites and associated environmental data.

Data S2 Trait data and bibliography.

Data S3 Trait dataset attributes.

Data S4 Univariate regression model statistics.

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