

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); ?.

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 indigenous 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 et al. (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 et al. (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 et al. (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 (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 ask 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 extends 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, are 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 describe 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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