INTRODUCTION

Riparian ecosystems are highly biodiverse, provide important ecosystem services, and receive substantial management effort worldwide (Naiman, Decamps & Pollock 1993; Palmer *et al.* 2009). Rapid development of catchments has changed fundamental processes which create and maintain biodiversity within riparian landscapes (Nilsson & Svedmark 2002). 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 (Nilsson & Berggren 2000; Stromberg *et al.* 2007; Cooper *et al.* 2013). Maintaining indigenous plant assemblages and their associated ecosystem functions, and controlling invasive species are central goals in river rehabilitation and riparian conservation.

Environmental heterogeneity is one of the major factors influencing spatial patterns of species diversity (Costanza, Moody & Peet 2011; Stein, Gerstner & Kreft 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 traitspace: 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. Metrics of functional diversity derived from community functional trait data provide a useful complement to taxonomic diversity metrics in conservation, as they allow a mechanistic characterisation of biodiversity-ecosystem functioning relationships (Hillebrand & Matthiessen 2009).

Much of the riparian ecology literature identifies fluvial hydrology as the dominant abiotic force structuring riparian ecosystems (Poff, Allan & Bain 1997). The spatial and temporal heterogeneity inherent in fluvial processes is considered largely responsible for the complex biogeomorphology of riparian environments (Naiman *et al.* 2005; Corenblit *et al.* 2007). Sediments are scoured and deposited, some plants are washed away while others are watered; woody debris moves through the system and propagules are dispersed. The spatial distribution of this process within the fluvial landscape is contingent on the characteristics of fluvial landforms present and the magnitude of the flow event (Hughes 1997). Temporal variability in flooding then 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 not so 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 & Svedmark 2002). Intermediate disturbance-type unimodal relationships between fluvial disturbance and species richness are commonly described (e.g. Bendix 1997; Bendix & Hupp 2000; Lite, Bagstad & Stromberg 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 links between functional trait diversity and flow heterogeneity (Lawson et al. *in press*): 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 & Berggren 2000; Nilsson *et al.* 2005). While the effects of individual dams tend to be idiosyncratic (Mackay, Arthington & James 2014), flow regulation typically homogenises hydrographs by reducing flood peaks, altering seasonality and increasing predictability of flows (Graf 2006; Singer 2007). According to the magnitude and character of the change, 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 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 (Stokes 2008; Merritt & Poff 2010; Catford *et al.* 2011).

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 (Vitousek *et al.* 1997; Gerstner *et al.* 2014). This effect is often exacerbated by the entourage of exotic species brought by humans into the landscapes we occupy (Vitousek *et al.* 1996), local extirpation of indigenous species (Davis 2003) and stifling of successional processes (Catford *et al.* 2012) being common outcomes of plant invasion. A recent international meta-analysis linked land-use intensification to diminished functional redundancy and ability to respond to disturbance (Laliberté *et al.* 2010).

Environmental homogenisation of riparian landscapes ecosystems 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 the indigenous ecology (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 extend a previous study of vegetation responses to hydrological alteration in a modified landscape in south-east Queensland, Australia (Arthington *et al.* 2012). 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.

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flow modification and land use intensification (homogenising disturbances) reduce species richness and functional diversity, while increasing the abundance of exotic species. 2a.) more heterogeneous flow regimes are monotonically associated with greater species richness and functional diversity, and reduced exotic abundance; 2b.) more heterogeneous flow regimes are unimodally associated with species richness and functional diversity, and exotic abundance.