INTRODUCTION

Riparian ecosystems are biophysically complex and highly diverse taxonomically, structurally and functionally (Naiman, Decamps & Pollock 1993; Poff 2002; Nilsson & Svedmark 2002). They provide a disproportionate amount of ecosystem goods and services compared with the fraction of the landscape which 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 the New World, this modification has taken place rapidly and has resulted in significant habitat degradation and biodiversity loss. Impoundment and flow regulation has altered the hydrology of river systems globally, resulting in reductions to total discharge, reduced flow variability, dampening of flood peaks and changes to seasonality of flows (Nilsson & 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 (Stocker *et al.* 2013). 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 and intensity of extreme flooding or drought events can be expected (Hennessy *et al.* 2008). The combination of flow regulation and alterations to baseline discharges may well produce dramatically different future hydrologies, with significant consequences for the diversity and functional composition of riparian assemblages. An understanding of the processes that generate patterns of diversity and drive ecosystem functioning in riparian ecosystems must therefore inform future riverine conservation and rehabilitation efforts.

Conservation and ecological restoration activities increasingly aim to preserve the ecosystem functions associated with biodiversity (Cadotte 2011, Aerts &Honnay 2011, Montoya et al 2012 – emerging perspectives in the restoration of biodiversity based ecosystem services). Conservation management approaches oriented around patterns of taxonomic diversity may be problematic, however, as relationships between environmental conditions and community species composition can be difficult to generalise across landscapes. Where sites harbour dissimilar species assemblages, comparison becomes problematic. Compressed taxonomic descriptors of communities such as species richness or species-oriented metrics of 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 (Tilman *et al.* 1997; Dı́az & Cabido 2001; Díaz & Lavorel 2007).Describing communities in terms of functional traits - any morphological, physiological or phonological 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. This allows for direct comparisons between communities that do not necessarily contain matching assemblages. In such a manner, communities can be compared in terms of how their component species both respond to and have an effect on their environment (Lavorel & Garnier 2002). A functional trait oriented approach, then, allows us to search for generalities in the influence of hydrology on ecosystem processes and patterns of diversity across disparate riparian plant communities. 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). To date, however, functional approaches remain a novel tool in ecohydrology.

Functional traits can form the basis for mechanistic assessments of diversity that describe the range and distribution of ecological strategies within a community. While species richness (Whitaker 1972) has to date been the most commonly used metric of biodiversity for investigating the relationships between biodiversity and ecosystem functioning (Duffy 2009), functional diversity and composition are able to reveal the mechanisms underlying these relationships (Dı́az & Cabido 2001; Hooper, Iii & Ewel 2005) Loss of functionally unique species may gradually undermine ecosystems, and may be useful in diagnosing degradation before species loss occurs (Mouillot et al. 2013). Assessments of ecosystem service production have also begun to give functional diversity privilege over simple taxonomic metrics of diversity (Díaz & Lavorel 2007).

Two requirements must be satisfied to achieve a functionally informed mechanistic understanding of biodiversity-ecosystem function relationships. Firstly, traits should be selected carefully so as to capture the spectrum of ecological strategies within a community, with specific ecological relevance to the study system (Petchey & Gaston 2006; Gallagher, Hughes & Leishman 2013). Secondly, an appropriate metric of functional diversity must be selected for analysing the community according to the chosen traits. Numerous metrics of functional diversity have been described in the literature; we direct the reader to Schleuter & Daufresne (2010) for an introduction to the subject. These metrics typically take multidimensional trait data as an input and output a single value describing various properties of this data. The framework described by Villéger, Mason & Mouillot (2008) consisting of functional richness (the volume of the convex hull circumscribing range of trait values), functional divergence (divergence in the distribution of abundance within traitspace) and functional evenness (the evenness of this distribution in traitspace) has been commonly used to describe functional diversity (e.g. Biswas & Mallik 2010; Pakeman 2011; Savage & Cavender-Bares 2012; Clark *et al.* 2012). Functional dispersion, defined as the mean distance of individual species to the centroid of all species in the community, represents an improvement on this framework (Laliberte & Legendre 2010). This metric is useful as it allows for consideration of species abundances while integrating functional richness and functional divergence, and is independent of species richness by construction.

A common goal of community ecologists and conservationists has been to find general rules that explain patterns of ecological diversity. Heterogeneity in the riparian patch mosaic results from the sculpting action of hydrological processes across the biogeomorphic template. In riparian environments, it is this intrinsic environmental heterogeneity which fosters structural, taxonomic and functional heterogeneity within vegetation communities (Naiman *et al.* 1993; Corenblit *et al.* 2007; Bornette *et al.* 2008).

Local hydrology is widely considered to be the master 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) (more REFs). 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 which 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 richness in riparian plant communities (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); 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). Resource availability hypotheses predict that diversity should be lowest at either very low or very high levels of water availability (Grime 1973). This pattern has been demonstrated in taxonomic diversity across spatial gradients of water availability in dryland river systems of South Western North America (Lite *et al.* 2005) and Egypt (Ali, Dickinson & Murphy 2000), where water availability is especially limiting. Seasonal and interannual variability in patterns of disturbance and water availability are known 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 (Garssen, Verhoeven & Soons 2014). A study investigating drivers of riparian vegetation community structure and composition in subtropical eastern Australia identified variability in dry season (summer) flows as the hydrological variable which was most strongly associated with variation in species richness (Arthington *et al.* 2012).

Understanding of drivers of plant functional diversity in riparian communities is nascent. Catford *et al.* (2011) showed 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. Their study used multiple unidimensional metrics of diversity to support its findings rather than a multidimensional index, however. Another study looked at functional diversity in riparian vegetation communities along gradients of disturbance associated with management for logging, and found support for the intermediate disturbance hypothesis (Biswas & Mallik 2010). Some further insights into the impact of disturbance on functional diversity in general come from work on gradients of land use intensity. Land use intensification has been linked with lower functional diversity across an international dataset (Laliberté *et al.* 2010), and the authors associated this effect with a reduced ability to 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 environmental homogeneity. At a meeting of the North American Benthological Society in 1995, the attendees of a symposium on ecological heterogeneity urged stream researchers to “examine heterogeneity from a functional perspective” (Palmer & Poff 1997). Progress on this front has been sparse, and confirmation of an opposite trend – i.e. where functional diversity increases with environmental heterogeneity – would be a significant development for riparian ecology and conservation.

We hypothesised that the environmental heterogeneity induced by repeated floods and fluctuating soil moisture levels should be reflected in the functional composition of plant communities adapted to the riparian environment. To this end, we investigated the relationship between hydrologically driven environmental heterogeneity and functional diversity in riparian plant communities. Specifically, we asked the following questions:

1. Is functional diversity related to the frequency and magnitude of flooding disturbance?
2. Is functional diversity related to variability in seasonal water availability in the riparian zone?

South-eastern Australia was used as a sandbox, as a broad spectrum of hydrological heterogeneity is present within a relatively compact, contiguous landscape (Finlayson & McMahon 1988; Peel, McMahon & Finlayson 2004).