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’. Australia is the most hydrologically variable continent on the planet, and so offers a unique sandbox within which to test ideas about how hydrology influences diversity within vegetation communities.

To this end, we collected data on species abundance, quantitative plant functional traits and hydrology from 15 sites distributed across south-eastern Australia. This study asked two questions: 1.) is functional diversity related to frequency and magnitude of flooding disturbance, and 2.) is functional diversity related to variability in seasonal water availability within the riparian zone?

We were able to confirm that metrics describing both flooding disturbance and patterns of water availability exhibit strong relationships with functional diversity within riparian vegetation communities of south-eastern Australia. The key finding of this study is functional heterogeneity in these systems tends to be 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 patterns of water availability as determinants of community composition in riparian vegetation. These ecohydrological relationships may have significant consequences for plant communities experiencing alterations to hydrology caused by anthropogenic flow modification and the changing climate.

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 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 the New World, this modification has taken place rapidly and has resulted in significant habitat degradation and biodiversity loss. Impoundment and flow regulation have 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, 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 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 (Aerts & Honnay 2011; Cadotte, Carscadden & Mirotchnick 2011; Montoya, Rogers & Memmott 2012). 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 challenging. 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 assessing 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 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 should be selected for analysing the community according to the chosen traits. Numerous metrics of functional diversity have been described in the literature; see for example Schleuter & Daufresne (2010). 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 also 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 univariate metrics of diversity to support its findings rather than a multivariate 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). 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 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).

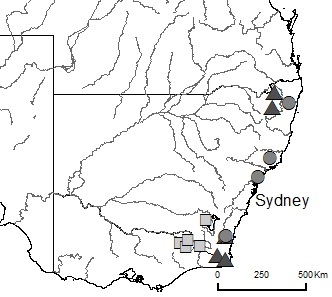
METHODS

*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 and Table 1). 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 following criteria were applied in the site selection process: 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), 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.

The resulting study area spanned latitude -29.467 to -37.371 and longitude 147.413 to 152.217. Sites spanned an altitudinal range of 23 – 732 m above sea level.

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***Figure 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. Note that the points representing the two southern-most unpredictable baseflow sites are overlapping.*

Table 1. Location and characteristics of field sites.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Site # | Gauge Name | Longitude | Latitude | Catchment area (km2) | Elevation (m asl) |
| 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 |

*Vegetation surveys*

Vegetation surveys were 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 gently sloping bank where possible), maximum 2m elevational difference between lower and upper edge of plot, 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.

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

*Rationale for trait selection*

Data for the following traits were collected: maximum canopy height, seed mass, specific leaf area (SLA), wood density, flowering period (proportion of the year spent in flower), leaf narrowness (the ratio of leaf width to length). These traits were chosen to encapsulate the key axes of variation relevant to ecological strategies employed by riparian plants. Variation throughout this suite of traits should provide a relevant indication of functional diversity for riparian communities. Below we detail the rationale for selection of each trait.

Specific leaf area, maximum canopy height and seed mass comprise the LHS (leaf, height, seed) triad of traits introduced by Westoby (1998) as a general scheme for comparing the properties of vegetation communities. These three traits are typically distributed orthogonally from each other and represent fundamental trade-offs that control plant ecological strategy.

Seed mass indicates maternal investment in offspring and is a fundamental determinant of seedling establishment success (Leishman *et al.* 2000); time to reproduction may offset this initial advantage, however (Moles & Westoby 2006). In the riparian environment, seed mass may therefore be constrained if repeated flooding disturbance excludes species with long generation times.

Maximum canopy height integrates the central trade-off between competition for light, and construction and maintenance of costly support structures such as woody stems (Westoby 1998). These costs are particularly accentuated where plants must defend stems from mechanical disturbance (Falster 2006).

Specific leaf area (the ratio of one-sided leaf area to oven dry mass) is a useful indicator of a species’ position along the leaf economics spectrum (ref). High SLA species invest considerable nutrients in their leaves, have high rates of photosynthesis and respiration, and short leaf longevity; these species typically exhibit high relative growth rates. Conversely, low SLA species receive slower return on investment on costly leaves, with lower rates of photosynthesis and respiration, but greater leaf longevity and ability to tolerate stressful conditions (Reich & Wright 2003; Wright *et al.* 2004).

Wood density, defined as oven dry mass divided by green volume, is an emergent property that integrates a number of anatomical traits of lignified tissues (Chave *et al.* 2009). Dense wood is costly to construct and has been linked with slower relative growth rates, but increased cohort survivorship (e.g. King, Davies, Tan, & Noor, 2006; Kraft, Metz, Condit, & Chave, 2010; Poorter et al., 2008; S. J. Wright et al., 2010). Wood density has also been associated with environmental stress tolerance (Preston, Cornwell & Denoyer 2006; Martínez-Cabrera *et al.* 2009) and enhanced resistance to disturbance (Telewski 1995; Curran *et al.* 2008)(+Lawson et al. 2014). These latter two associations are significant in riparian environments, where flooding disturbance and pulsed periods of water stress are commonplace.

Patterns of seasonality across south-eastern Australia are variable spatially as well as temporally, owing to complex interactions between geography and decadal-scale oscillations in climate, such as the Pacific Decadal Oscillation and El Nino Southern Oscillation (Nicholls 1989; Peel, Finlayson & McMahon 2007; Ward *et al.* 2010). The lack of a strong period of cold-induced dormancy in this region means plants may flower at any time of the year. Flowering period was used here as an indicator species’ ability to respond reproductively to favourable conditions.

Leaf narrowness provides two-fold information about plant ecological strategy. Firstly, narrow leaves are able to regulate temperature more efficiently and thus maintain photosynthesis in hot or highly insolated (i.e. consistent with disturbed) conditions (Cornelissen *et al.* 2003). Leaf narrowness is also strongly indicative of rheophyty – 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; see *Appendix 2* a detailed bibliography of references for data. If multiple values for field-measured data were found for a single site, values were excluded if they were measured from sites that were substantially different with respect to the environmental conditions of the field site they were found in. Remaining values were averaged. Single values for each trait were recorded, under the assumption that intraspecific variability is less than interspecific variability (Michaels, Benner & Hartgerink 1988; Westoby 1998). Leaf narrowness was not included for grasses, while seed mass and flowering period were not included for ferns.

Wood samples for wood density measurement were collected from dominant woody species present within each plot at >5% cover in shrub, sub canopy or canopy strata, and which had trunks robust enough to core (typically > 5 cm diameter at base). 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 in deionised water and 10 mm sections of mature wood were cut with a razor, using visual inspection of vessel occlusion as an indicator of maturity. Sections were measured to the nearest 0.01 mm (x, y and z dimensions) 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). Site-specific values were thus available for wood density (due to collection for a concurrent project focusing on woody tissues), but for the purposes of this study, an overall mean value was calculated for species which occurred at multiple sites. Species for which data could not be obtained in the field were assigned values from the Global Wood Density Database (Chave *et al.* 2009).

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

*Hydrological data*

Daily discharge data for each of the 15 sites were taken with permission from Lawson et al. (2014, in review). Hydrological analysis was identical to Lawson et al. (2014); the reader is referred to this publication for a full description of analysis methods. We generated 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 2for descriptions of individual metrics). Summary statistics for hydrological metrics are shown in Table 3. Metrics of flow magnitude which had units ML / day were standardised by mean daily flow to allow for comparison between different sizes of river. These metrics therefore represent ratios of flow magnitude to mean daily flow.

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 | | 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 return interval (ARI) floods are extreme flow events that have the potential to re-work 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\* | 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 | | Rise and fall rates represent flow ‘flashiness’. Fast rise rates are associated with flood waves and entrainment of debris into the flood channel. 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. |
| 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 | |
| *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 | |

Table 3. Summary statistics for hydrological and miscellaneous environmental variables.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| metric | min | max | mean | sd |
| 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 |
| Latitude (o) | -28.93 | -37.37 | -34.58 | -3.04 |
| Catchment area (km2) | 93 | 918 | 372.33 | 255.95 |
| Elevation (m asl) | 13 | 711 | 293.27 | 228.05 |

*Functional diversity 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/functional-diversity/tree/master/scripts. Statistical significance was interpreted at alpha = 0.05.

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 (see Table 4 for data density information). All trait values were transformed by log10 prior to analysis. Table 5 provides summary statistics for the trait dataset.

Table 4. 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.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| site # | coverage | wood density | max. height | seed mass | SLA | flowering period | leaf narrowness |
| 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 5. Summary statistics for trait dataset.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| trait | min | max | mean | sd |
| Max. height (m) | 0.2 | 50 | 10.47 | 13.18 |
| Seed mass (mg) | 0.04 | 323.99 | 16.55 | 45.06 |
| SLA (m2 / kg) | 1.41 | 63.27 | 17.93 | 14 |
| Flowering period (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 / cm3) | 0.33 | 0.95 | 0.61 | 0.13 |

Following Leps, Bello, Lavorel, & Berman, (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.

We used the *dbFD* function from the FD package for R (Laliberté & Legendre 2010) to calculate abundance-weighted functional dispersion (FDis). This package implements the method for distance-based tests for homogeneity of multivariate dispersions described by Anderson (2006). *dbFD* uses Gower's method (1971) to generate the 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 SYNCSA package (Debastiani & Pillar 2012).

*Regression models*

Ordinary least-squares (OLS) regression models were generated for 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, Krieger & Yekutieli 2006) for controlling the false discovery rate (*mt.rawp2adjp* function in multtest package for R) (Pollard, Ge & Dudoit 2008). This two step BH method has been shown to control the false discovery rate for positively dependent test statistics, and provides a better estimate of the false discovery rate than the original BH algorithm (Benjamini & Hochberg 1995) by adaptively controlling p value adjustment according to the number of true null hypotheses obtained from the first pass of the procedure.

The utility of functional diversity metrics depends on their ability to provide non-redundant information compared with measures of taxonomic diversity. To this end 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 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 which were individually determined to have non-significant relationships with FDis. PCA over the selected 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 R2 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 the second order of Akaike’s Information Criterion (AIC) (MuMIn package for R, Barton, 2012). Second order AIC is recommended in order to reduce bias when the ratio of sample size to number of predictor variables is small (Burnham & Anderson 2002).

RESULTS

Below we describe 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 (df = 2,12) provided a substantially better fit. Statistics for all univariate regression models are presented in the Supporting Information.

Table 5. 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.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| metric | p | p.adj | R2 | F(1,13) |
| CVAnnHSPeak | **0.0010** | **0.0152** | **0.5773** | **17.7500** |
| M\_MinM | **0.0094** | **0.0278** | **0.5404** | **\*7.0560** |
| MDFMDFSummer | **0.0031** | **0.0230** | **0.5032** | **13.1700** |
| CVMDFSummer | **0.0218** | **0.0325** | **0.4716** | **\*5.3560** |
| CVMDFWinter | **0.0096** | **0.0278** | **0.4143** | **9.1940** |
| CVAnnMRateRise | **0.0110** | **0.0278** | **0.4031** | **8.7810** |
| CVAnnMRateFall | **0.0129** | **0.0278** | **0.3896** | **8.2990** |
| MDFMDFSpring | **0.0134** | **0.0278** | **0.3862** | **8.1800** |
| AS20YrARI | **0.0148** | **0.0278** | **0.3774** | **7.8790** |
| M\_MDFM | **0.0209** | **0.0325** | **0.3470** | **6.9080** |
| M\_MaxM | **0.0258** | **0.0325** | **0.3275** | **6.3300** |
| CVMDFSpring | **0.0260** | **0.0325** | **0.3269** | **6.3130** |
| CVMDFAutumn | **0.0342** | **0.0386** | **0.3009** | **5.5950** |
| CVAnnHSNum | **0.0360** | **0.0386** | **0.2961** | **5.4680** |
| HSPeak | 0.0648 | 0.0648 | 0.2384 | 4.0690 |
| MDFMDFWinter | 0.0881 | 0.0780 | 0.2073 | 3.4010 |
| C\_MaxM | 0.0885 | 0.0780 | 0.2069 | 3.3920 |
| C\_MDFM | 0.1086 | 0.0861 | 0.1859 | 2.9680 |
| MDFMDFAutumn | 0.1091 | 0.0861 | 0.1854 | 2.9590 |
| C\_MinM | 0.1361 | 0.1021 | 0.1626 | 2.5240 |
| MRateRise | 0.1556 | 0.1072 | 0.1488 | 2.2720 |
| MRateFall | 0.1572 | 0.1072 | 0.1477 | 2.2530 |
| MDFAnnHSNum | 0.7270 | 0.4741 | 0.0097 | 0.1273 |

*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 explained by the magnitude of the 20 year average return interval flood (AS20YrARI, Fig 2a., adjusted p = 0.0278, R2 = 0.377). FDis was also significantly explained by interannual variability in high flow magnitude (CVAnnHSPeak, Fig. 2b, adjusted p = 0.0152, R2 = 0.577) and rates of flow rise (CVAnnMRateRise, Fig. 2c, adjusted p = 0.0278, R2 = 0.403) and fall (CVAnnMRateFall, Fig. 2d, adjusted p = 0.0278, R2 = 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. 2e, adjusted p = 0.0360 R2 = 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 patterns of flow which diverge strongly from “average” conditions.



Figure 2. 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.

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

Functional dispersion was positively associated with variability in seasonal flow patterns throughout the hydrological record. FDis was increased when seasonal patterns of minimum (M\_MinM, Fig. 3a, adjusted p = 0.0278, R2 = 0.540), maximum (M\_MaxM, Fig. 3b, adjusted p = 0.0325, R2 = 0.328) and average (M\_MDFM, Fig. 3c, 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 with was not consistent through the record. FDis was not significantly explained by inter-seasonal uniformity of minimum (Fig. 3d, C\_MinM, adjusted p = 0.1021, R2 = 0.166) or average (Fig. 3e, 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. 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. and e. depict non-significant relationships (note the strong influence over the regression fit of the two points at the lower bound of FDis).

This observation was corroborated by positive relationships between FDis and variability in mean daily flows for autumn (CVMDFAutumn, Fig. 4a, adjusted p = 0.0386, R2 = 0.301), winter (CVMDFWinter, Fig. 4b, adjusted p = 0.0278, R2 = 0.414) and spring (CVMDFSpring, Fig. 4c, adjusted p = 0.10325, R2 = 0.327). Summer flow variability (CVMDFSummer, Fig. 4d, adjusted p = 0.0325, R2 = 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. 4e, adjusted p = 0.0230, R2 = 0.503) and negative for spring (MDFMDFSpring, Fig. 4f, adjusted p = 0.0278, R2 = 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, since metrics describing discharge were standardised by mean daily flow. 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 4. 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 d. which is a quadratic fit. Shaded areas depict the smoothed 95% confidence interval around the regression model. All relationships shown are significant.

*Comparisons with measures of taxonomic diversity*

Across species used in the functional diversity analysis (i.e. present at above 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, R2 = 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 6.

Table 6. Multiple regression models with associated fitting parameters. \* in the model formula denotes both summation as well as interaction between variables. R2 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 | R2 | AICc | delta AIC |
| 1 | FDis ~ CVAnnHSNum | 0.2961 | -46.1414 | 12.78193 |
| 2 | FDis ~ CVAnnHSPeak | 0.5773 | -53.7899 | 5.13339 |
| 3 | FDis ~ MDFMDFSummer | 0.5032 | -51.3678 | 7.55549 |
| 4 | FDis ~ CVAnnHSNum + CVAnnHSPeak | 0.6359 | -54.5235 | 4.39977 |
| 5 | FDis ~ CVAnnHSNum + MDFMDFSummer | 0.6809 | -56.5027 | 2.4206 |
| 6 | FDis ~ CVAnnHSPeak + MDFMDFSummer | 0.5609 | -51.7131 | 7.21018 |
| 7 | FDis ~ CVAnnHSNum \* CVAnnHSPeak | 0.6545 | -51.9494 | 6.97387 |
| 8 | FDis ~ CVAnnHSNum\* MDFMDFSummer | 0.6647 | -52.3972 | 6.52611 |
| 9 | FDis ~ CVAnnHSPeak \* MDFMDFSummer | 0.5663 | -48.538 | 10.38533 |
| 10 | FDis ~ CVAnnHSNum + CVAnnHSPeak + MDFMDFSummer | 0.7036 | -54.2478 | 4.67554 |
| 11 | FDis ~ CVAnnHSNum \* CVAnnHSPeak + MDFMDFSummer | 0.7093 | -50.138 | 8.78527 |
| **12** | **FDis ~ CVAnnHSNum + CVAnnHSPeak \* MDFMDFSummer** | **0.8382** | **-58.9233** | **0** |
| 13 | FDis ~ CVAnnHSNum \* CVAnnHSPeak \* MDFMDFSummer | 0.9437 | -48.6223 | 10.30101 |

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 R2 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 description of the model is given in Table 7**.** 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 7. Regression summary for Model 12. Beta values are regression coefficents standardised by the standard deviation of the term.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | B | SE | beta | t | p |
| CVAnnHSNum | 0.240 | 0.054 | 0.540 | 4.414 | 0.0013 |
| CVAnnHSPeak | 0.071 | 0.026 | 0.498 | 2.773 | 0.0197 |
| MDFMDFSummer | 0.074 | 0.024 | 0.506 | 3.056 | 0.0121 |
| CVAnnHSPeak\*MDFMDFSummer | -0.190 | 0.060 | -0.459 | -3.186 | 0.0097 |

DISCUSSION

We surveyed vegetation communities along partially constrained 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 functional ecology of riparian vegetation communities using multiple quantitative functional traits. The overarching pattern across these relationships can be summarised as “heterogeneous flows breed hetereogenous communities”.

This pattern is consistent with existing understanding of the processes which 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 (Tabacchi *et al.* 1996; Naiman & Decamps 1997; Palmer & Poff 1997; Stromberg 2001; Corenblit *et al.* 2007; Bornette *et al.* 2008; Steiger & Corenblit 2012). Below we discuss significant relationships between functional diversity and hydrological conditions within this context. Because we surveyed geomorphically homogenous 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 sloping bank sections.

The sites surveyed in this study spanned a spectrum of flooding intensity: at the lower bound, the calculated 20 year average return interval (ARI) flood was just 18 times the mean daily flow; at the upper bound, flows 210 times greater than the mean daily flow occur approximately every 20 years. Higher magnitude flow events such as this are likely to be geomorphically effective across a greater extent of the fluvial landscape (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 2010a), 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. Flood rise and fall rates may determine entrainment of woody debris into the flood channel and subsequent bank deposition (Cadol & Wohl 2010). Debris entrainment in turn increases the erosive potential of floods, but its deposition provides structural heterogeneity, and resources for fungal and animal communities (Harmon *et al.* 1986). 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. 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 (Woolfrey & Ladd 2001; Robertson 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; this effect 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, Kaufman & Stevens 2003), and found no relationship between latitude and FDis.

It was notable that while FDis is statistically independent of species richness by construction, 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 almost all of the variation in FDis. We used traits in our analysis which 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. No contribution from other environmental variables such as latitude, altitude, catchment area etc. was necessary, and in any case, such contributions would likely reduce the parsimoniousness of the model. 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 which 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 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, although see Nepstad *et al.* 2007). These sites notwithstanding, we believe the relationships we have described form a strong case for our argument.

It was not possible with our dataset to dissect out which specific aspect of hydrology drove variation in functional diversity. Rather, it makes more sense to think about functional diversity as it relates to the correlated spectra of hydrological variability and disturbance intensity. 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, as it provides quantitative, real-world support for findings based on theoretical simulations (Schwilk & Ackerly 2005).

Our findings are also 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 peaks, alter seasonality and increase predictability of flows (Graf 2006). For example, flow regulation and diversion for irrigation and hydropower has resulted in a complete reversal of flow seasonality on the Sacramento River (California, United States) from heterogeneous winter dominated flows to a comparatively homogenous summer dominated regime (Singer 2007). Likewise, in south-eastern Australia, the River Murray’s hydrographs have been flattened by regulation, and its once highly variable flows are now stored for prescribed release during summer (Maheshwari, Walker & McMahon 1995). Dams also interrupt hydrochorous transport of propagules (Merritt *et al.* 2010a), such that flood flows below dams may cause net removal of seed 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. We urge managers to also consider simulating the natural variability in flow regime in their designed flows.

Reductions in mean summer precipitation have already occurred over large areas of Australia, coinciding with a warming of 0.4 – 0.7 oC since 1950 (Hennessy *et al.* 2007). Further changes of this nature are projected for Australia as well as other regions of the globe (Stocker *et al.* 2013). Lower average flows during hotter summers may stress riparian communities and constrain functional diversity. 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. Thus we should be careful not to promote high functional diversity as an ecological ‘good’ which must be maximised. Climate change induced increases in flow variability in systems which are not naturally highly variable may open up niche space to favour opportunistic species and promote invasion by exotic species.

CONCLUSION

Our study emphasises the importance of flooding disturbance and hydrological heterogeneity as drivers of functional composition in riparian plant communities. These findings should be general to river systems in other regions and biomes, 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 composition and functioning of riparian vegetation communities.

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