METHODS

The current study is an extension of a previous larger study (Arthington *et al.* 2012) conducted to test the ELoHA framework (Poff *et al.* 2010), and to determine hydro-ecological relationships to inform environmental flow management in south-east Queensland. Field data was collected between 2008 – 2010; the trait dataset was assembled and analyses described here were performed in 2015. The report describing the original study provides extensive detail not included here (Arthington *et al.* 2012). Except where specified, all statistical analyses were performed using the R statistical programming environment (R Core Team 2013)

*Study area*

The study was conducted across seven catchments within coastal south-east Queensland, Australia. Sites were located between -25.82 and -28.23 degrees latitude and 152.35 and 153.42 degrees longitude. The dominant land-use in the region is agriculture, with approximately 40 % of the area under grazing, and 4 % used for cropping. Urbanisation is also extensive, particularly along the coast. Native vegetation within conservation estate or state forest comprises 20 % of the study area, and additional native vegetation remnants are common in steep terrain. This study area has a subtropical climate, and is influenced by both tropical and temperate weather patterns. Little variation in temperature is present throughout the region, although mean annual rainfall varies considerably, from 800 mm in the west to 1400 mm in the eastern coastal catchments. The majority of rainfall is associated with summer thunderstorms between January and March, although southerly weather systems during autumn and winter are also responsible for a substantial amount of precipitation. Precipitation patterns are associated with high year-on-year variability, and river discharge regimes in the region are typically unpredictable, with high coefficients of variation in mean daily flow. This said, substantial hydrological variability is represented across coastal south-east Queensland. Four of the twelve hydrological classes identified on the Australian continent by Kennard et al. (2010) are present in the area: perennial, stable baseflow; perennial, unpredictable baseflow; intermittent, unpredictable; and highly intermittent, unpredictable summer dominated.

River flow regimes throughout the study region are modified by dams, weirs, intra- and inter-basin water transfer, and unsupplemented water extraction. The majority of the dams were constructed by the mid 1970s and have a maximum capacity of less than 50,000 ML. Two substantially larger dams (Wivenhoe Dam – 1,150,000 ML and Hinze Dam – 165,000 ML) in the area were constructed during the 1980s. Mackay *et al.* (2014) compared historic daily discharge data with modelled predevelopment discharge data and found that flow modification by structures and diversions in south-east Queensland is diverse and system specific. Reduced flow variability is prevalent, and while increased perenniality in drier systems and altered low spell duration are also common, few other generalisations can be made about the effects of regulation on streamflows in the region (Mackay *et al.* 2014).

*Site selection and vegetation sampling*

Riparian vegetation was surveyed between August and October in 2008, 2009 and 2010 at 42 sites. Twenty river reaches were selected to sample the range of flow regime classes determined by a regional classification of flow regimes (see Mackay et al., 2014). Proximity to flow monitoring gauges with an associated recording history of >25 years was of primary importance. Duplicate surveys were made along each river reach as close as possible to the flow monitoring station, but separated by at least 2 km to ensure independence. Sampling sites required 100 continuous metres of relatively intact riparian vegetation, which was not subjected to regular burning and had not been cleared in at least 20 – 30 years. Ideally sites were not currently grazed, although this restriction was relaxed somewhat given the extensive pastoral land use throughout the region.

Three transects were randomly placed at each site, running perpendicular to the river. Additional transects were conducted at three sites (27, 31, 44), where low vegetation densities occurred. Transects extended from the water’s edge to the macrochannel bank, or a maximum of 50 m from the water’s edge. A standard sampling area was not used due to variability in vegetation structure, channel landforms and adjacent land uses. Site sampling areas were typically greater than 400 m2 but ranged from 260 – 1013 m2. All trees, shrubs, ferns rushes, and sedges within a 5 m band centred on the transect line were identified and counted. Species identifications were confirmed by the Queensland Herbarium.

*Describing stream hydrology and quantifying flow regulation*

Daily discharge data for each reach were obtained from Queensland DERM (). Thirty five year time series spanning 1975 – 2009 were obtained where possible. Missing data were infilled using the Timer Series Manager module in River Analysis Package (Marsh, Stewardson & Kennard 2003), using linear interpolation for periods less than 15 days, or multiple regression using data from adjacent stream gauges. One site (Reynolds Creek) had substantial periods of missing data which could not be infilled by multiple regression, as the flow at this gauge is altered by Moogerah Dam. The record for this site was truncated to exclude the periods where data was missing. The shortest remaining period (34 days) was infilled by linear interpolation. Flow data for one site (Obi Obi Creek at Kidaman) was obtained from Water Quality Accounting (Queensland DERM) as modelled gauge data derived from a calibration model for the Mary River catchment.

River Analysis Package was used to generate a set of 18 ecologically relevant hydrological metrics for each site, describing mean and interannual variability in the frequency, magnitude and duration and seasonal timing of high and low flows conditions. Table 1 provides definitions of these metrics and describes their ecological importance and contribution to environmental heterogeneity. As a number of these metrics exhibited collinearity, we have included a principal components analysis of this data in the Supporting Information S1. Metrics of flow magnitude which had units ML / day were standardised by mean daily flow to allow for comparison between different river cha­­nnel sizes. These metrics therefore represent ratios of flow magnitude to mean daily flow.

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

Table 1. Hydrological variables used as metrics of fluvially induced environmental heterogeneity in the riparian zone (adapted from Lawson et al. 2015b).

|  |  |  |  |
| --- | --- | --- | --- |
| **Parameter** | **Abbreviation** | **Units** | **Description** |
| *Frequency, magnitude and duration of floods and dry spells* | | | |
| Mean magnitude of high spells\*  Mean magnitude of low spells\* | HSPeak  LSPeak | dimensionless  dimensionless | Together, these metrics characterise the frequency, magnitude and duration of floods and dry spells. High flow spells are periods of flow above the 95th percentile; low flow spells are periods of flow below the 5th percentile. HSPeak and LSPeak describes the mean magnitude of highest and lowest flows during high and low spells throughout the record, respectively. MDFAnnHSNum and MDFAnnLSNum describe the mean annual frequency of high and low spells. HSMeanDur and LSMeanDur describe how long the flow event lasted. Coefficients of variation (CV) of these metrics between years characterise temporal heterogeneity in flow patterns. |
| CV of all years’ mean high spell magnitude  CV of all years’ mean low spell magnitude | CVAnnHSPeak  CVAnnLSPeak | dimensionless  dimensionless |
| Mean of all years’ number of high spells  Mean of all years’ number of low spells | MDFAnnHSNum  MDFAnnLSNum | year-1  year-1 |
| CV of all years’ number of high spells  CV of all years’ number of low spells | CVAnnHSNum  CVAnnLSNum | dimensionless  dimensionless |
| High spell mean duration  Low spell mean duration | HSMeanDur  LSMeanDur | days  days |
| CV of all years’ high spell mean duration  CV of all years’ low spell mean duration | HSMeanDur  LSMeanDur | dimensionless  dimensionless |
| *Baseflow index* | | | |
| Baseflow index  CV of all year’s baseflow index | BFI  CVAnnBFI | dimensionless  dimensionless | Baseflow index is calculated using the ratio of flow during average conditions to total flow. It is a useful metric of perenniality of water availability, in that it is maximised when average flow conditions dominate, and minimised when total flow is dominated by above average flow events. |
| *Colwell’s indices* | | | |
| Constancy of monthly minimum daily flow | C\_MinM | dimensionless | Colwell’s indices provide a measure of the seasonal predictability of flow events, and as such are a direct measure of heterogeneity in flow seasonality. 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 minimum and maximum flows conditions. |
| Contingency of monthly minimum daily flow | M\_MinM | dimensionless |
| Constancy based on monthly maximum daily flow | C\_MaxM | dimensionless |
| Contingency based on monthly maximum daily flow | M\_MaxM | dimensionless |
| *Flow seasonality* | | | |
|  |  |  | These metrics describe the average magnitude and variability within mean daily flows for each season (dry = May to October, wet = November to April). Averages and coefficients of variation are calculated across yearly means. Seasonal average mean daily flows were standardised by overall mean daily flow, so actually represent the ratio of mean daily flow in a given season to the total mean daily flow. |
| Average mean daily dry season flow \*  Average mean daily wet season flow \* | MDFMDFDry  MDFMDFWet | dimensionless  dimensionless |
| CV of mean daily dry season flow  CV of mean daily dry season flow | CVMDFDry  CVMDFWet | dimensionless  dimensionless |

*Other environmental variables*

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

Climate data were obtained from eMast/TERN, at a resolution of 0.01 degrees (Hutchinson, Kesteven & Tingbao 2014). Bioclimatic variables representing annual trends, seasonality and extremes were calculated following the BIOCLIM framework (Busby 1991). The resulting set of 19 climate variables were strongly collinear, PCA was used to identify a subset of 6 variables which represented over 90 % of the variation in the data. Soil data were taken from the CSIRO Soil and Landscape Grid of Australia, at a resolution of 3 arc seconds (~ 3 m) (Rossel *et al.* 2014 a b c d e f g h i j k; Wilford *et al.* 2014).

*Trait selection and dataset asssembly*

We assembled a dataset of 7 continuous (specific leaf area, leaf area, maximum canopy height, seed mass, wood density and flowering duration) and 1 categorical (growth form) functional traits with which to calculate functional diversity. These traits collectively describe central trade-offs associated with ecological strategies of riparian plants (functional responses), as well as flow-on effects of species on ecosystem functioning (functional effects). Table 2 provides further description of the utility of each of these traits in describing the functional ecology of riparian vegetation communities.   
Data was taken from published literature, private and published trait datasets, and Australian flora texts. Where multiple records for a trait were found, values were removed if they were measured at sites with an environment substantially different from south east Queensland. With the exception of maximum height, for which the highest value was used, the remaining values were averaged to provide a single value for each species-trait combination. Not all species-trait combinations could be assigned data, so to reduce biases associated with analyses of incomplete trait datasets (Penone *et al.* 2014), only species with fewer than 3 missing trait values (174 / 260) were retained for the analysis. 7The remaining missing values were imputed using a non-parametric random forests approach (*missForest* package for R, Stekhoven & Buhlmann, 2012). Dataset density information can be found in the Supporting Information S1.

Table 1. Rationale for selection of functional response and effect traits as descriptors of riparian plant community functional diversity.

|  |  |  |  |
| --- | --- | --- | --- |
| **Trait** | **Definition** | **Functional responses & inherent trade-offs** | **Functional effects** |
| *Growth form* | Categorical description of morphology: tree, shrub, woody climber, herbaceous climber, graminoid, herb | Differential responses to mechanical and biochemical stresses associated caused by flooding; different strategies for coping with drought and heat stress. | Differential biogeomorphic effects on fluvial landform cohesion and sediment deposition. |
| *Specific leaf area (SLA)* | Ratio of one-sided leaf area to oven dry mass (cm2 / g). | SLA is associated with leaf construction cost, photosynthetic rate and carbon : nitrogen economics. Indicator of ecological strategy under favourable vs. stressful conditions(Wright *et al.* 2004). | Affects ecosystem productivity and nutrient recycling (Wright *et al.* 2004). |
| *Leaf area* | One-sided leaf area (cm2) | Shade tolerance (larger leaves) vs. enhanced thermal regulation ability in hot, dry conditions (smaller leaves) (Cornelissen *et al.* 2003). | May influence flow resistance of vegetation (and therefore fluvial erosion / deposition) when inundated. |
| *Maximum canopy height* | Height above ground of apical meristem (m). | Affects ability to tolerate mechanical disturbances such as flooding and maintain xylem integrity in dry conditions (Westoby & Wright 2006). | Determines coarse physical structure of plant community. Surrogate for competitive ability: taller plants receive more light but must construct and maintain support structures (Falster 2006). |
| *Seed mass* | Combined mass of the seed coat, endosperm and embryo (g). Excludes dispersal structures. | Larger seed mass confers ability to establish in unfavourable conditions (Leishman *et al.* 2000). Also related to seed buoyancy (Carthey 2014, *unpublished data*). | Seeds may be an important food source for animals. |
| *Wood density* | Oven dry mass divided by green volume (g/cm3) | Dense wood tissue confers mechanical strength, but is energetically expensive to construct. Wood density influences ability to tolerate drought stress and disturbance (Telewski 1995; Preston, Cornwell & Denoyer 2006; Lawson *et al*. 2015). | Regulates decomposition rate; this affects nutrient cycling and determines the residency time of woody debris in the fluvial system (Mackensen, Bauhus & Webber 2003). |
| *Flowering period length* | Proportion of the year spent in flower (proportion, dimensionless). | Indicates species’ ability to respond reproductively to favourable conditions. | Flowers may be an important food source for animals. |

*Calculating functional diversity, species richness and proportional abundance of exotics*

Functional richness (FRic) and functional divergence (FDiv) are complementary metrics of functional trait diversity, which together, describe the range and distribution of trait values in a community (Villéger, Mason & Mouillot 2008). FRic represents the volume of the convex hull of trait values in a given community while FDiv provides information about the abundance distribution of trait values across this range.

We calculated functional richness and abundance-weighted functional dispersion (FDis) of vegetation communities at each site, using the *FD* package for R (Laliberté & Legendre 2010). Gower’s method, which scales traits by their range, was used to generate the required dissimilarity matrix, and Cailliez’s correction was applied to render the matrix euclidean. We transformed FRic and FDis into standardised effect sizes (SES): SES = (obs – nullExp) / sd(nullExp), where obs is the observed functional diversity value and nullExp and sd(nullExp) are the mean and standard deviation of the expected functional diversity in 999 randomized communities (Gotelli & Rohde 2002). The null model for comparison with FRic was generated using the trial-swap algorithm (Miklós & Podani 2004) in the *picante* package (Kembel *et al.* 2010) to remove dependence on species richness. The null model for comparison with FDis was generated by randomizing abundances among species but within plots (using the resamp.2s function in *spacodiR*) (Eastman, Paine & Hardy 2011), to generate a metric of pure functional divergence. The resulting indices, FRic.SES and FDis.SES, have greater power to detect community assembly processes than their unstandardized counterparts (Mason *et al.* 2013).

We calculated the standardized effect size (SES) of FRic and FDis according to Gotelli & Rohde (2002) as the ratio between observed to expected values of trait diversity: SES = (Obs − Exp)/sd(Exp), where Obs is the observed trait diversity value and Exp and sd(Exp) are the mean and the standard deviation of the expected trait diversity in the 999 random communities.

Where required, trait values were normalised by either log10 (SLA, seed mass) or square root (leaf area, maximum height, flowering duration) transformation prior to analysis. Wood density was not transformed. Summary statistics for the trait dataset are shown in the Supporting Information S1.

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

*Constructing variance partitioning models*

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

The following process was used to derive an optimal set of environment-diversity models for variance partitioning analysis (Legendre 2007):

* We first generated minimal ordinary least-squares regression models for each set of environmental variables (i.e. descriptors of flow regime, flow modification, land use etc.).
* For each dependent variable, the full set of explanatory variables was reduced to the subset which had statistically significant (p < 0.05) linear or quadratic relationships. Second order AIC was used to determine whether the linear or quadratic term better explained variation in the dependent variable (*MuMIn* package for R, Barton, 2012; Burnham & Anderson 2002).
* For each set of environmental variables, variance explained by these univariate models was partitioned by partial regression using the varpart function in R (*vegan* package, Oksanen *et al.* 2013). Multiple regression models were derived from the combinations of variables with the highest adjusted R2 values (Peres-Neto *et al.* 2006). These multiple regression models optimally combine the variation explained by all significant univariate models.
* The four best multiple regression models were fed into a second variance partitioning analysis, and adjusted R2 was used to estimate the proportion of variation jointly and independently explained by each environmental model.

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