

1 Environmental drivers of taxonomic and functional diversity of riparian plant communities in a modified landscape

Abstract

Human populations have a profound impact on the biodiversity of riparian plant communities, and understanding the nature and mechanisms of these impacts is central to river conservation and rehabilitation. Reduction of the inherent environmental heterogeneity in riverscapes by flow modification and land-use intensification is thought to cause degradation of riparian communities.

We sampled vegetation and assembled environmental data for 20 river reaches in south-east Queensland, Australia. Plant functional trait data collated from on-line databases and the ecological literature were used to characterise diversity in terms of ecological strategy and functional effects. Our aim was to tease apart the environmental factors associated with taxonomic and functional trait diversity in riparian plant communities. We specifically tested the hypotheses that environmental heterogeneity is the dominant control on taxonomic and functional trait diversity, and that flow modification and land use intensification is associated with reduced plant diversity.

Contrary to our expectations, hydrological metrics of environmental heterogeneity had limited power to explain patterns of species richness. Rivers which experienced seasonal, but temporally consistent flow regimes supported the most species rich communities, and modification of flow regime towards temporal consistency was also associated with greater species richness. Functional diversity metrics showed unimodal relationships with some metrics of hydrological heterogeneity, but were only weakly predicted by flow modification and showed no relationship with catchment land-use intensity.

The absence of strong linkages between the extent flow modification and metrics of functional diversity suggests that use of environmental flows may not be effective as a tool for riparian rehabilitation in modified subtropical landscapes such as south-eastern Queensland.

Keywords

Riparian, functional diversity, flow regime, environmental heterogeneity, land use, flow modification, dams

1.1 Introduction

Riparian ecosystems are highly biodiverse, provide important ecosystem services and are the focus of substantial management effort worldwide (Naiman et al., 1993; Palmer et al., 2009). Rapid development of catchments has changed fundamental processes which create and maintain biodiversity within riparian landscapes (Nilsson and Svedmark, 2002), and as such, riparian management often takes place within this context of catchment modification. Wholesale vegetation clearing notwithstanding, regulation of river flow regimes, catchment land-use change are considered key drivers of ecological change (Cooper et al., 2013; Nilsson and Berggren, 2000). Maintaining indigenous plant assemblages and their associated ecosystem functions, and controlling invasive species are central goals in river rehabilitation and riparian conservation (Richardson et al., 2007).

Environmental heterogeneity is one of the major factors influencing spatial patterns of species diversity (Costanza et al., 2011; Stein et al., 2014). According to classical niche-based theories of species co-existence e.g. Chesson (2000), where each niche is associated with an optimal ecological strategy, structural complexity and steep resource and energy gradients between patches promote diversity by extending niche space and reducing niche overlap. More recently, niches have been characterised in trait-space: niches and their interrelationships are described by patterns of clustering of functional traits (any morphological, physiological or phenological feature measurable at the individual level (Violle et al., 2007)), the values of which are optimised to a given set of environmental conditions (Adler et al., 2013). Thus the distribution of functional traits within a community can be expected to be patterned by the degree of heterogeneity in environmental conditions present. Describing communities in traitspace dissolves species distinctions and emphasises ecological strategies: what species do within their community and how they do it. In turn, metrics of diversity derived from functional traits provide a useful complement to taxonomic diversity metrics, as they allow a mechanistic characterisation of biodiversity-ecosystem functioning relationships (Hillebrand and Matthiessen, 2009).

Much of the riparian ecology literature identifies hydrology and geomorphology as the dominant abiotic force structuring riparian ecosystems (Bendix and Hupp, 2000; Poff et al., 1997). The spatial and temporal heterogeneity inherent in fluvial processes is considered largely responsible for the complex biogeomorphology of riparian environments (Corenblit et al., 2007; Naiman et al., 2005). Sediments are scoured and deposited, some plants are washed away while others are watered; organic matter and woody debris moves through the system and propagules are dispersed; large flood events have been shown to produce substantial 'heterogeneous imprints' on the fluvial landscape (Parsons et al., 2005). The spatial distribution of these processes within the fluvial landscape is contingent on the magnitude and frequency of the flow events that drive erosion and deposition processes, and the resultant morphology and sedimentology of fluvial landforms produced (Fryirs and Brierley, 2012). This subsequently determines the extent to which different surfaces/landforms are inundated under a range of different flow

conditions (Hughes, 1997). Temporal variability in flooding patterns adds a further layer of complexity by influencing the success of plant ecological strategies for a given patch. More frequently flooded patches are likely to support graminoids and rheophytes, while succession is likely to proceed further on patches which are less frequently disturbed (Corenblit et al., 2009). Soil moisture conditions are also strongly driven by hydrology in riparian environments, with further implications for plant community assembly (Nilsson and Svedmark, 2002).

Intermediate disturbance-type unimodal relationships between fluvial disturbance and species richness are commonly described, e.g. Bendix (1997), Bendix and Hupp (2000), Lite et al. (2005), Corenblit et al. (2007), Pollock et al. (1998). Unimodal relationships between environmental heterogeneity and diversity are also hypothesised to occur as a result of microfragmentation at high levels of heterogeneity (Tamme et al., 2010). Previous work on riparian plant communities has shown strong positive links between functional trait diversity and flow heterogeneity (Lawson et al., 2015b): relationships between functional dispersion and metrics of flow variability were mostly monotonic, with the exception of interannual variability in summertime flows, which showed a unimodal relationship.

Over half the worlds large river systems and countless smaller watercourses are affected by dams, weirs and diversions (Nilsson and Berggren, 2000; Nilsson et al., 2005). While the effects of individual dams tend to be idiosyncratic (Mackay et al., 2014), flow regulation typically homogenises hydrographs by removing small-moderate flows, reducing flood peaks, altering seasonality and increasing predictability of flows (Graf, 2006; Poff et al., 2007; Singer, 2007). Depending on the magnitude and form of change to the flow regime, flow modification may result in reduced niche complexity in downstream riparian zones (Lloyd et al., 2004). In a recent comprehensive review of ecological responses to flow modification, Poff and Zimmerman (2010) found that 152 out of 165 studies reported decreased values for recorded ecological metrics. Invasion by exotic plants in response to flood reduction often results in extensive shifts in riparian plant assemblages and reduction of both taxonomic and functional diversity (Catford et al., 2011; Merritt and Poff, 2010; Stokes, 2008). Terrestrialisation of riparian plant communities has also been described as a response to flood reduction (Poff and Zimmerman, 2010).

Human land use also has a profound effect on diversity and functioning in natural ecosystems. Land transformation for agricultural and silvicultural production, urbanisation and resulting habitat fragmentation have resulted in extensive losses of both alpha and beta diversity (Gerstner et al., 2014; Vitousek et al., 1997). A recent multi-biome meta-analysis found that land-use intensification was associated with diminished functional redundancy and ability to respond to disturbance (Laliberté and Legendre, 2010).

Environmental homogenisation of riparian landscapes by this combination of flow modification and land-use change therefore has profound implications for riparian biodiversity. The environmental flows concept posits that given a solid understanding of the hydroecology of a given riparian assemblage, restoration of riparian ecosystems on regulated rivers can be facilitated by releasing engineered flows which support indigenous plant assemblages (Poff et al., 2010). The success of such endeavours in modified landscapes, however, is likely to be contingent

on the relative contribution of flow modification and other pressures on riparian ecosystems.

To this end, we used a functional trait diversity approach to examine vegetation responses to hydrological alteration in a modified landscape in south-east Queensland, Australia. Our aim was to tease apart the environmental factors associated with taxonomic and functional diversity in riparian plant communities. A set of hypotheses about environmental heterogeneity diversity relationships guided our approach: 1.) species richness and functional diversity increase monotonically as a function of hydrological heterogeneity; 2.) species richness, functional diversity and abundance of exotic species show unimodal relationships with hydrological heterogeneity, due to microfragmentation and intermediate disturbance-type effects; 3.) species richness and functional diversity decrease along gradients of increasing flow modification and catchment land-use intensity, as an outcome of environmental homogenisation.

1.2 Regional setting and hydrology

The study was conducted across seven catchments in coastal south-east Queensland, Australia (25.82 to 28.23 °S, and 152.35 to 153.42 °E, see Fig. 1.1). The dominant land-use in the region is agriculture, with approximately 40 % of the area under livestock 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 (Bureau of Meteorology 2009). 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 (Kennard et al., 2010; Rustomji et al., 2009). 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).

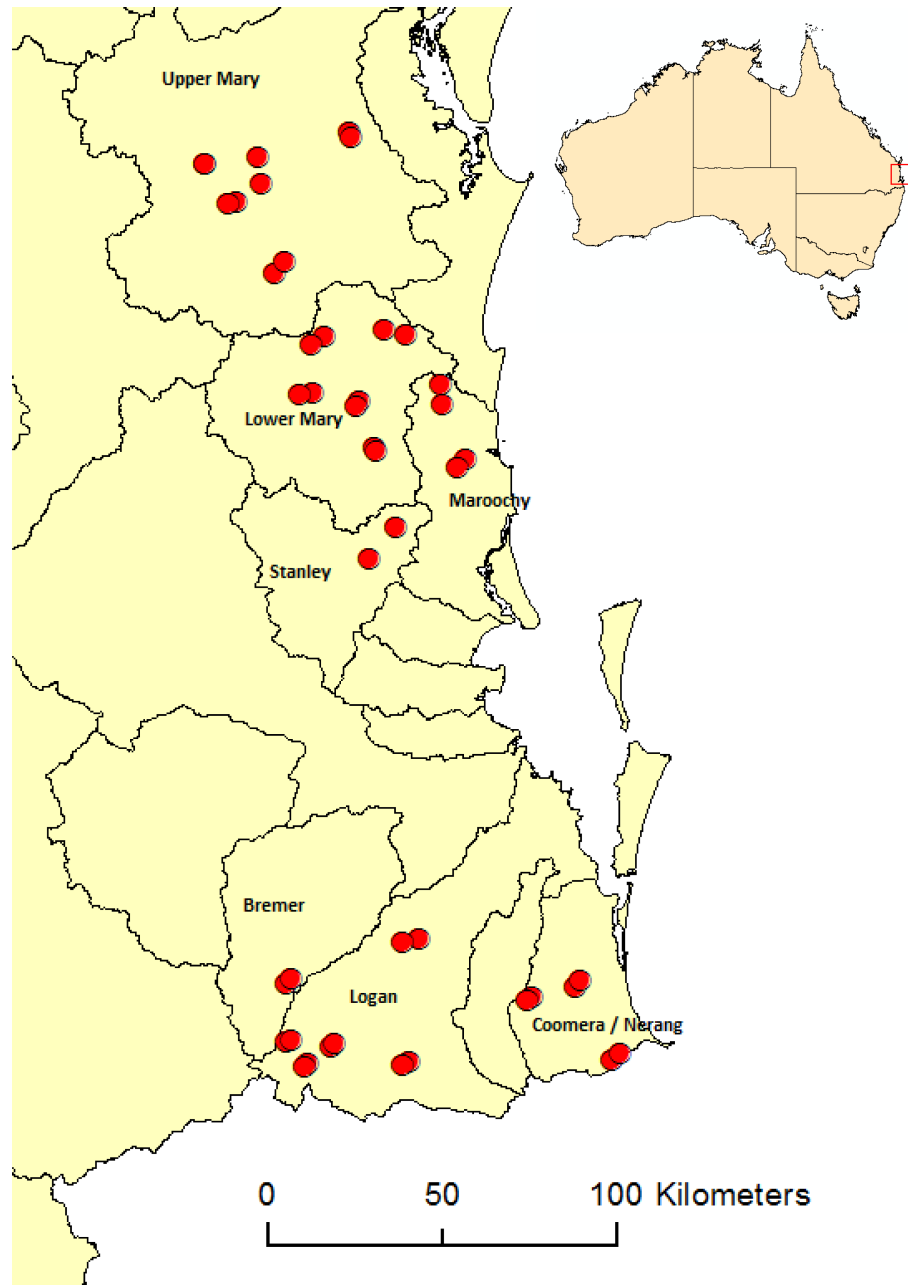


Figure 1.1: Study area (inset), study catchments and locations of field sites in south-eastern Queensland.

1.3 Methods

The current study is an extension of a previous larger study (Arthington et al., 2012); the report describing the original study provides extensive detail not included here. Except where specified, all statistical analyses were performed using the R statistical programming environment (R Core Team, 2015), and statistical significance was thresholded at $\alpha = 0.05$.

Site selection and vegetation sampling

Riparian vegetation was surveyed between August and October in 2008, 2009 and 2010. 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 (to give a total of 40 sites), but separated by at least 2 km. 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, where low vegetation densities occurred. Transects extended from the waters edge to the macrochannel bank, or to a maximum of 50 m from the waters edge. A standard sampling area was not used due to variability in vegetation structure, channel landforms and adjacent land uses; sampling area was controlled for in subsequent analyses. Site sampling areas were typically greater than 400 m² but ranged from 260 - 1013 m². All vascular plants 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 Government Department of Natural Resources and Mines (DNRM) Water Monitoring Data Portal (<https://www.dnrm.qld.gov.au/water/water-monitoring-and-data/portal>). 35 year time series spanning 1975 - 2009 were obtained where possible. Missing data were infilled using the Time Series Manager module in River Analysis Package (Marsh et al., 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 DNRM) as modelled gauge data derived

from a calibration model for the Mary River catchment. See Mackay et al. (2014) for further information on interpolation of hydrological data.

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 flow conditions. Table 1.1 provides definitions of these flow regime characteristics 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 Supplementary 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 from a generic integrated water quantity and quality simulation model (IQQM) developed for the region (Simons et al., 1996). IQQM data were available only for the period up to 1999, so data from the timeframe 1975-1999 were used for comparison.

Table 1.1: Hydrological variables used as metrics of fluvially induced environmental heterogeneity in the riparian zone (adapted from (Lawson et al., 2015b))

<i>Variable</i>	<i>Abbreviation</i>	<i>Units</i>	<i>Description</i>
Frequency, magnitude and duration of floods and dry spells			
Mean magnitude of high spells *	HSPeak	dimensionless	Together, these metrics characterise the frequency, magnitude and duration of floods and dry spells. Extreme low or high flows contribute to spatial environmental heterogeneity, in that their effects (flooding disturbance, soil moisture stress) are spatially variable throughout the riparian landscape. 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 flow events last. Coefficients of variation (CV) of these metrics between years characterise temporal heterogeneity in flow patterns.
Mean magnitude of low spells *	LSPeak	dimensionless	
CV of all years' mean high spell magnitude	CVAnnHSPeak	dimensionless	
CV of all years' mean low spell magnitude	CVAnnLSPeak	dimensionless	
Mean of all years' number of high spells	MDFAnnHSNum	year ⁻¹	
Mean of all years' number of low spells	MDFAnnLSNum	year ⁻¹	
CV of all years' number of high spells	CVAnnHSNum	dimensionless	
CV of all years' number of low spells	CVAnnLSNum	dimensionless	
High spell mean duration	HSMeanDur	days	
Low spell mean duration	LSMeanDur	days	
CV of all years' high spell mean duration	HSMeanDur	dimensionless	
CV of all years' low spell mean duration	LSMeanDur	dimensionless	

<i>Variable</i>	<i>Abbreviation</i>	<i>Units</i>	<i>Description</i>
Baseflow index			
Baseflow index	BFI	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. Thus higher baseflow systems experience more homogeneous flows.
CV of all year’s baseflow index	CVAnnBFI	dimensionless	
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 temporal heterogeneity of flow patterns. 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			
Average mean daily dry season flow *	MDFMDFDry	dimensionless	These metrics describe the average magnitude and temporal variability in 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 wet season flow *	MDFMDFWet	dimensionless	
CV of mean daily dry season flow	CVMDFDry	dimensionless	
CV of mean daily dry season flow	CVMDFWet	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). These data were 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 et al., 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, consequently PCA was used to identify a subset of six variables which represented over 90 % of the variation in the data. Soil data were obtained from the CSIRO Soil and Landscape Grid of Australia, at a resolution of 3 arc seconds (~ 3 m) (Rossel et al., 2014a,b,c,d,e,f,g,h,i,j,k; Wilford et al., 2014).

Trait selection and dataset assembly

We assembled a dataset of six continuous (specific leaf area, leaf area, maximum canopy height, seed mass, wood density and flowering duration) and one 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 1.2 provides further description of the utility of each of these traits in characterising the functional ecology of riparian vegetation communities.

Data was taken from published literature, private and published trait datasets, and Australian flora texts. Substantial contributions were taken from the following sources: (Fonseca et al., 2000; Gallagher and Leishman, 2012; Gardens and Trust, 2015; Gleason et al., 2012; Kew, 2015; Kooyman et al., 2013; Wright et al., 2000; Zanne et al., 2009) as well as from Ian Wright (pers. comm.) and Cassandra James (pers. comm.). 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. The remaining missing values were imputed using a non-parametric random forests approach (missForest package for R) (Stekhoven and Bühlmann, 2012). Dataset density information and imputation error estimates can be found in the Supplementary Information S1.

Table 1.2: Rationale for selection of functional response and effect traits as descriptors of riparian plant community functional diversity.

<i>Trait</i>	<i>Definition</i>	<i>Functional responses & inherent trade-offs</i>	<i>Functional effects</i>
Growth form	Categorical description of morphology: tree, shrub, woody climber, herbaceous climber, graminoid, herb.	Differential responses to mechanical and biochemical stresses associated with flooding; different strategies for coping with drought and heat stress.	Differential biogeomorphic effects on surface roughness, sediment deposition and fluvial landform cohesion.
Specific leaf area (SLA)	Ratio of one-sided leaf area to oven dry mass (cm^2 / 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 (cm^2).	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 and 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 et al., 2015).	Seeds may be an important food source for animals.
Wood density	Oven dry mass divided by green volume (g / cm^3)	Dense wood tissue confers mechanical strength, but is energetically expensive to construct. Wood density influences ability to tolerate drought stress and disturbance (Lawson et al., 2015a; Preston et al., 2006; Telewski, 1995).	Regulates decomposition rate; this affects nutrient cycling and determines the residency time of woody debris in the fluvial system Mackensen et al. (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 and species richness

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 (Vill  ger et al., 2008). Functional evenness is also included in the framework introduced by Vill  ger et al. (2008) but has since shown limited ability to describe change in functional composition across environmental gradients (Mason et al., 2012; Pavoine and Bonsall, 2011). 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 (Lalibert   and Legendre, 2010). Gowers method, which scales traits by their range, was used to generate the required dissimilarity matrix, and Cailliez’s correction was applied to allow for PCoA axes corresponding to negative eigenvalues and render the matrix Euclidean (Cailliez, 1983). 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 and Rohde, 2002). The null model for comparison with FRic was generated using the trial-swap algorithm (Mikl  s and 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 et al., 2011), to generate a metric of pure functional divergence (FDiv). The resulting indices, FRic.SES and FDis.SES, have greater power to detect community assembly processes than their unstandardised counterparts or the metric of functional divergence defined by Vill  ger et al. (2008) (Mason et al., 2013).

To more closely comply with the assumptions of statistical tests, trait values were normalised by either \log_{10} (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 Supplementary Information S1.

True species richness values were estimated by rarefaction according to species accumulation across the three replicate transects taken at each site. We used the "chao1" function in the fossil package in R (Vavrek, 2011) to calculate abundance-based Chao’s Species Estimator (Chao, 1987).

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 soil properties to modelling variation in riparian plant species richness, functional diversity. We also investigated exotic proportional abundance as an explanatory variable for species richness and functional diversity metrics. Proportional abundance of exotic species

was calculated as the number of exotic individuals divided by the total number of individuals counted at each site.

The following process was used to derive an optimal set of environment-diversity models for variance partitioning analysis (Legendre, 2007): We first generated minimal multiple regression models for each set of environmental variables (i.e. descriptors of flow regime, flow modification, land use etc.): for each individual dependent variable, the full set of explanatory variables was reduced to the subset which showed 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 and Anderson, 2002). For each set of environmental variables, variance explained by significant 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 R^2 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 R^2 was used to estimate the proportion of variation jointly and independently explained by each environmental model.

1.4 Results

Below we describe the patterns of variation in species richness, functional richness and functional dispersion of riparian plant communities, as they relate to metrics describing river hydrology, flow modification, land use, climate and soil properties. Due to considerable collinearity in the environmental dataset, description of univariate relationships is generally limited here to variables selected by variance partitioning for inclusion in the final multiple regression models. Statistics for the all statistically significant univariate regression models can be found in the Supplementary Information S2. The adj. R^2 value shown in variance partitioning Venn diagrams (Figs 1.2-??b) may not correspond directly to the sum of its fractions as represented in Figs 1.2-??a, as negative R^2 values (not shown in Figs 1.2-??a) can result from the adjustment algorithm. All R^2 values given in the text are adjusted R^2 .

Environmental drivers of variation in species richness

The majority of variation in species richness across the study area (0.635) could be explained by a combination of models describing flow modification, climate and soil conditions (Fig. 1.2a,b). The hydrological model explained no variation in species richness independently. There was no significant relationship between total species richness per hectare and exotic species richness per hectare, and although species richness did decrease with exotic proportional abundance ($R^2 = 0.152$) (see

Supplementary Information S2), exotic abundance did not independently explain variation in species richness.

A weak but significant model associated richer plant communities with sites which experienced unevenly distributed patterns of minimum flows (C_MinM, $R^2 = 0.098$, Fig. 1.2c), and where those patterns tended to be consistent between years (M_MinM, $R^2 = 0.130$, Fig. 1.2d). Greater interannual consistency in patterns of maximum flows was also associated with richer communities (M_MaxM, $R^2 = 0.207$, Fig. 1.2e), although a pair of sites caused the quadratic model to dip at the upper bounds of consistency. Variation in species richness was well explained by modification of seasonal consistency of minimum flow patterns (M_MinM.mod, $R^2 = 0.342$, Fig. 1.2f), despite the relatively weak relationship between species richness and M_MinM. A significant quadratic relationship was found between species richness and modification of seasonal consistency of maximum flow conditions (M_MaxM.mod, $R^2 = 0.243$, Fig. 1.2g); in this case the relationship was corroborated by a similar distribution over M_MaxM. Species richness declined with increasing interannual variability in baseflow index (CVAnnBFI.mod, $R^2 = 0.108$, Fig. 1.2h). With respect to climate, species richness was greater at sites which experienced higher rainfall in both dry (clim_pdry, $R^2 = 0.417$, Fig. 1.2i) and wet seasons (clim_pwet, $R^2 = 0.465$, Fig. 1.2j), and declined as temperature seasonality increased (clim_tsea, $R^2 = 0.349$, Fig. 1.2k). Lower soil cation exchange capacity (soil_ece, $R^2 = 0.373$, Fig. 1.2l) and soil organic carbon content (soil_soc, $R^2 = 0.252$, Fig. 1.2l) also were associated with richer communities.

The data did not support hypothesis 1, that rivers with more heterogeneous flow regimes support communities with higher species richness. In fact, greater species richness at sites which experienced less variability in timing of minimum flow patterns (Fig. 1.2d) supports the counter-argument - species richness here is associated with less flow heterogeneity. Hypothesis 2, that there is a unimodal relationship between species richness and flow heterogeneity, was supported by a single relationship (M_MaxM, Fig. 1.2e), although the effect of modification of M_MaxM towards less flow heterogeneity was also strongly unimodal (M_MaxM.mod, Fig. 1.2g). These results also contradict hypothesis 3 (that species richness and functional diversity should decrease along gradients of increasing flow modification and catchment land-use intensity), given that rivers with artificially increased consistency of minimum flow patterns (M_MinM.mod, Fig. 1.2f) and lower interannual variability in baseflow index (CVAnnBFI.mod, Fig. 1.2h) hosted richer plant communities.

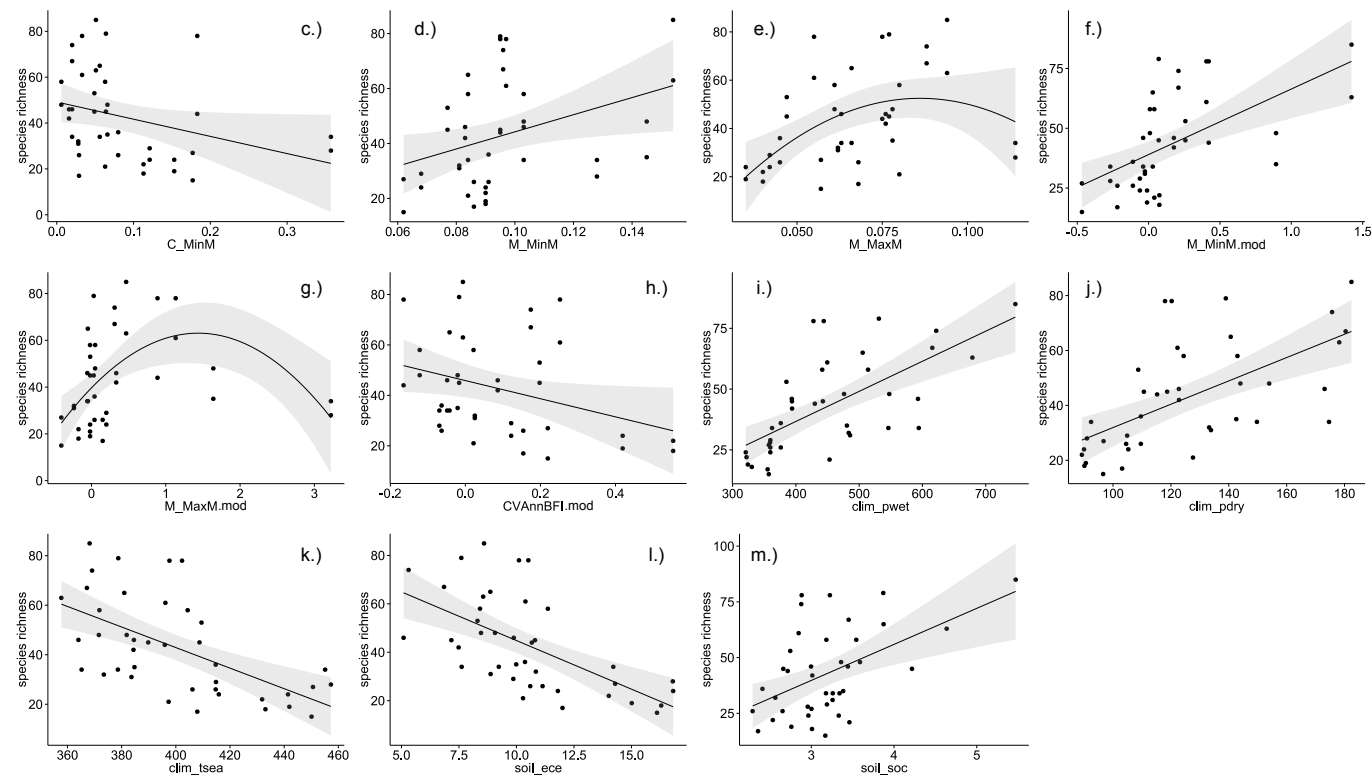
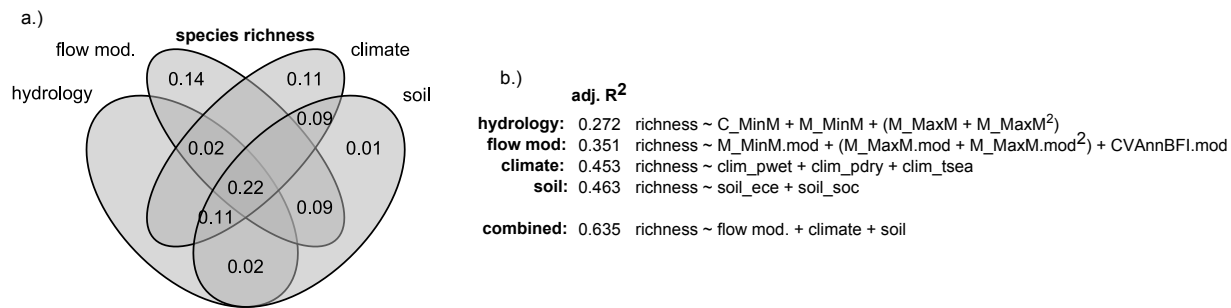


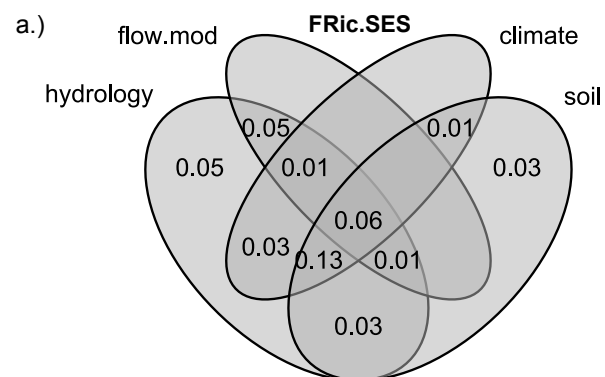
Figure 1.2: Environmental drivers of area-standardised species richness (units = species per m²) in riparian plant communities. a.) variance partitioning Venn diagram. Numbers within the diagram represent adjusted R² (adj. R²) values associated with each fraction of variation; b.) multiple regression models representing each set of environmental conditions, and their optimal combination. Quadratic terms are enclosed in parentheses. Selected univariate relationships between species richness and environmental variables describing c.) constancy of monthly minimum daily flows (C_MinM); d.) contingency of monthly minimum daily flows (M_MinM); e.) contingency of monthly maximum daily flows (M_MaxM); f.) modification of contingency of monthly minimum daily flows (M_MinM.mod, % change); g.) modification of contingency of monthly maximum daily flows (M_MaxM.mod, % change); h.) modification of interannual variability in baseflow (CVAnnBFI); i.) precipitation in the wettest quarter of the year (clim_pwet, mm); j.) precipitation in the driest quarter of the year (clim_pdry, mm); k.) temperature seasonality (clim_tsea) l.) soil effective cation exchange capacity (soil_ece, meq per 100 g); m.) soil organic carbon content (soil_soc, %). Species richness is presented as the abundanced-based Chao's Species Estimator. Fitted lines depict ordinary least-squares regression models. Shaded areas depict the smoothed 95 % confidence interval around the regression model.

Environmental drivers of functional richness (FRic.SES)

Variation in FRic.SES was best explained by a combination of hydrological and soil models (variation explained by the combined model = 0.405) (Fig. 1.3a,b), of which the hydrological model gave the most explanatory power. Soil variables independently explained a small fraction of variation, and while flow modification and climatic variables were also associated with FRic.SES, neither model explained any variation independently.

FRic.SES was distributed unimodally across gradients of interannual variability in baseflow index (CVAnnBFI, $R^2 = 0.170$, Fig. 1.3c); the modelled slope increased steeply at the lower end of the gradient but was only somewhat reduced from the peak by the top of the gradient. Greater frequency of high flow periods was associated with lower functional richness (MDFAnnHSNum, $R^2 = 0.142$, Fig. 1.3d). FRic.SES also declined as rainfall (clim_pwet, $R^2 = 0.246$, Fig. 1.3e), soil total nitrogen (soil_nto, $R^2 = 0.144$, Fig. 1.3f) and soil organic carbon (soil_soc, $R^2 = 0.257$, Fig. 1.3g) increased.

Hypothesis 1 was not supported, given that reduced functional richness was associated with increasing frequency of high flows. Hypothesis 2 was supported by a significant unimodal relationship interannual variability in baseflow (Fig. 1.3c) and functional richness (delta AICc between linear and quadratic models = 3.70). Although not selected for the final hydrological model, mean and interannual variability in duration of high flow periods (HSMeanDur, CVAnnHSMeanDur) also showed significant unimodal relationships with FRic.SES ($R^2 = 0.213$, 0.182 , respectively; Supplementary Information S2). Hypothesis 3 was not supported: we found no effect of either land use or flow modification on functional richness, except a weak relationship with modification of dry season mean daily flow (Supplementary Information S2).



b.)

adj. R^2

hydrology: 0.364 FRic.SES ~ (CVAnnBFI + CVAnnBFI²) + MDFAnnHNum

flow mod: 0.119 FRic.SES ~ MDFAnnHNum.mod

climate: 0.226 FRic.SES ~ clim_pwet

soil: 0.268 FRic.SES ~ soil_nto + soil_soc

combined: 0.405 FRic.SES ~ hydrology + soil

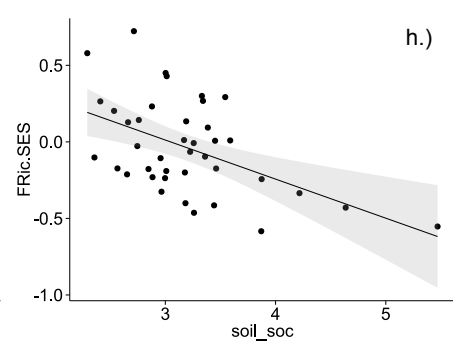
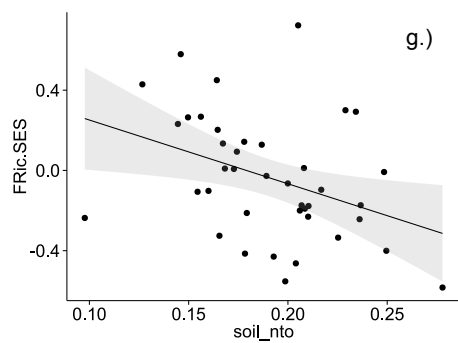
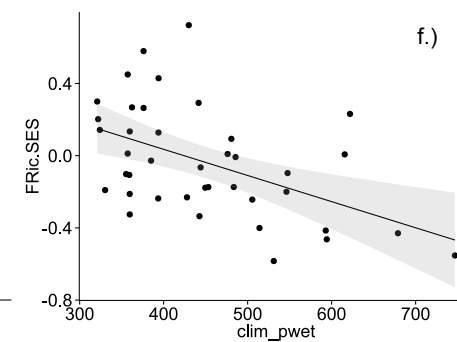
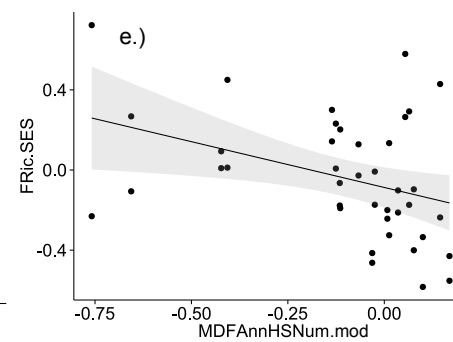
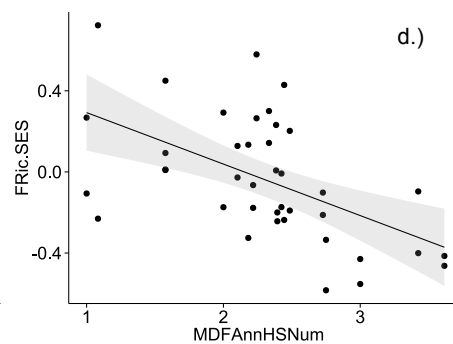
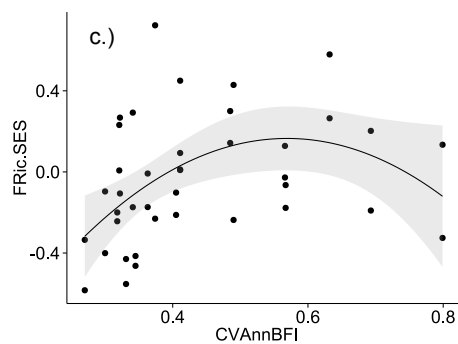


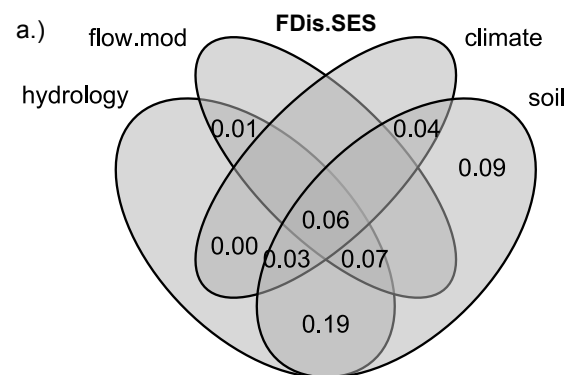
Figure 1.3: Environmental drivers of standardised effect size functional richness (FRic.SES) in riparian plant communities. a.) variance partitioning Venn diagram. Numbers within the diagram represent adjusted R^2 (adj. R^2) values associated with each fraction of variation; b.) multiple regression models representing each set of environmental conditions, and their optimal combination. Quadratic terms are enclosed in parentheses. Selected relationships between FRic.SES and environmental variables describing c.) interannual variability in baseflow (CVAnnBFI); d.) mean annual frequency of high flow periods (MDFAnnHSNum); e.) modification of mean annual frequency of high flow periods (MDFAnnHSNum.mod, % change); f.) precipitation in the wettest quarter (clim_pwet, mm); g.) soil total nitrogen (soil_nto, %); h.) soil organic carbon (soil_soc, %). Fitted lines depict ordinary least-squares regression models. Shaded areas depict the smoothed 95 % confidence interval around the regression model.

Environmental drivers of functional divergence (FDis.SES)

FDis.SES varied substantially across the study area (3.96 standard deviations of the null distribution), and was associated with gradients of hydrology, flow modification, climatic and soil conditions. The soil model explained 0.483 of the variation in FDis.SES; hydrology, flow modification and climatic models did not independently explain further variation (Fig. 1.4a,b).

Rivers with moderate seasonality of maximum flows tended to support communities with high functional divergence (C_MaxM, $R^2 = 0.321$, Fig. 1.4c). The entire range of FDis.SES was represented by rivers associated with highly seasonal patterns of maximum flows (C_MaxM), however. As with functional richness, FDis.SES declined with increasing frequency of high flows (MDFAnnHSNum, $R^2 = 0.112$, Fig. 1.4d). Functional divergence also varied with flow modification affecting high flow frequency (MDFAnnHSNum.mod, $R^2 = 0.144$, Fig. 1.4e): lower flooding frequency tended to be associated with higher functional divergence. Also tracking trends observed for FRic.SES, FDis.SES declined with increasing rainfall (clim_pwet, $R^2 = 0.141$, Fig. 1.4f), soil total nitrogen (soil_nto, $R^2 = 0.111$, Fig. 1.4g) and soil organic carbon (soil_soc, $R^2 = 0.344$, Fig. 1.4h).

Environmental heterogeneity (as indicated by high flow frequency) was associated with lower functional divergence (Fig. 1.4d,e), opposing the prediction made in hypothesis 1, while the unimodal relationship with constancy of maximum flows (Fig. 1.4c) provided some support for hypothesis 2 (delta AICc between linear and quadratic models = 10.08). Scant evidence to support hypothesis 3 was found: as with FRic.SES, a weak but significant relationship was present between FDis.SES and modification of flood frequency (Fig. 1.4d).



b.)

adj. R^2

hydrology: 0.321 FDis.SES ~ (C_MaxM + C_MaxM²) + MDFAnnHNum
flow mod: 0.141 FDis.SES ~ (MDFAnnHNum.mod²)
climate: 0.118 FDis.SES ~ clim_pwet
soil: 0.483 FDis.SES ~ (soil_nto + soil_nto²) + (soil_soc + soil_soc²)

combined: 0.483 FDis.SES ~ soil

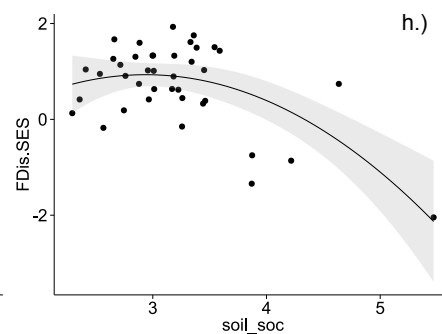
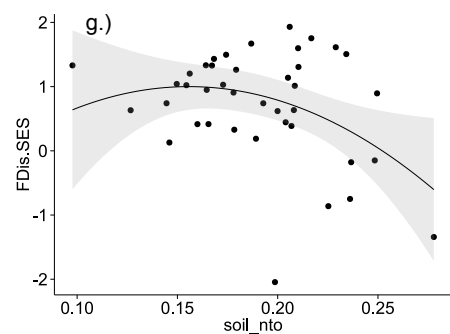
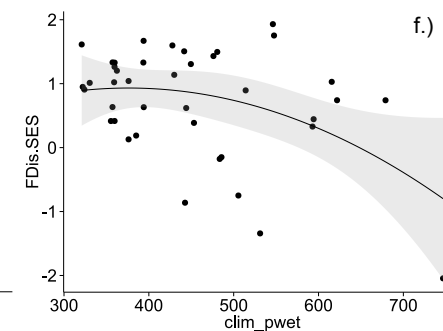
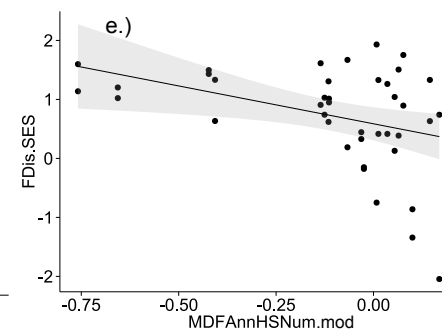
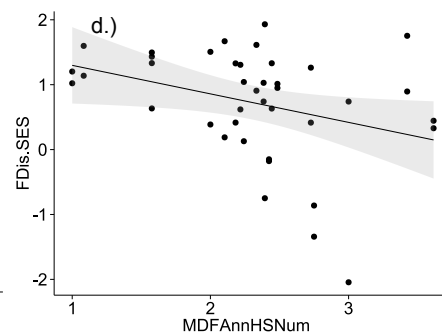
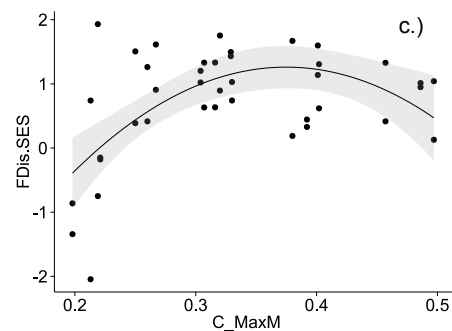


Figure 1.4: Environmental drivers of standardised effect size functional dispersion (FDis.SES) in riparian plant communities. a.) variance partitioning Venn diagram. Numbers within the diagram represent adjusted R^2 (adj. R^2) values associated with each fraction of variation; b.) multiple regression models representing each set of environmental conditions, and their optimal combination. Quadratic terms are enclosed in parentheses. Selected relationships between FDis.SES and environmental variables describing c.) constancy of monthly maximum daily flows (C_MaxM); d.) mean annual frequency of high flow periods (MDFAnnHSNum); e.) modification of mean annual frequency of high flow periods (MDFAnnHSNum.mod, % change); f.) precipitation in wettest quarter (clim_pwet, mm); g.) soil total nitrogen (soil_nto, %); h.) soil organic carbon (soil_soc, %). Fitted lines depict ordinary least-squares regression models. Shaded areas depict the smoothed 95 % confidence interval around the regression model.

1.5 Discussion

We proposed that generation of niche complexity by spatially and temporally heterogeneous environmental conditions is the dominant control on diversity in riparian plant communities. Under this framework, suppression of natural environmental heterogeneity by human modification of river flow regimes and catchment landscapes would result in lower diversity (Poff et al., 1997; Poff and Zimmerman, 2010). This niche-oriented model of riparian plant diversity received mixed support in our study: by some metrics, species richness in fact decreased as hydrological conditions became more heterogeneous, and anthropogenic flow homogenisation was associated with greater species richness. Although abundance of exotic species did increase with the proportion of surrounding land used for agricultural or silvicultural production, there was no relationship between exotic abundance and flow modification, and negative relationships were found with metrics of hydrological heterogeneity. The proportion of variation in functional diversity explained by environmental variables was comparatively lower than species richness. Functional diversity metrics showed unimodal relationships with some metrics of hydrological heterogeneity, and declined with others. Flow modification was a weak predictor of functional diversity, and we found no effect of land use.

Flow heterogeneity was not an important driver of riparian vegetation composition

Given that a large proportion of variation in diversity metrics explained by flow regime was co-explained by soil and climatic variables, is it possible to attribute flow regime as the dominant control on diversity? Taken individually, metrics of flow regime were the single best predictors of vegetation descriptors for FRic.SES (flood frequency, Fig. 1.3d). Species richness was best predicted by precipitation in the wet season (Fig. 1.2i), while FDis.SES was best predicted by soil organic carbon content (Fig. 1.4h). Variance partitioning showed that optimal models derived from flow regime metrics independently explained only a small proportion of variation in FRic.SES (Fig. 1.3a), and no independent variation in species richness (Fig. 1.2a) or FDis.SES (Fig. 1.4a). Extent of flow modification independently explained variation only in species richness, and changes to only a fraction hydrological metrics were important (Fig. 1.2). As such it was not possible to give a conclusive affirmative response to this question; it is possible that relatively shallow extent of flow modification in the region over a relatively short timeframe (~30 years) (Mackay et al., 2014) did not provide the contrast required to find a consistent effect. The inherent dependency between between climate and hydrology mean that manipulative experiments are required to confidently determine the influence of flow regime on riparian plant communities.

Despite these limitations, we can make some interesting observations about the role of environmental heterogeneity as a driver of species richness in riparian plant communities. Contrary to expectation, sites with lower species richness were found where temporal patterns of minimum (Fig. 1.3d) and maximum flows (Fig. 1.3e)

were less consistent between years, where interannual variability in baseflow was higher (Fig. 1.3h), and also where temperature seasonality was greater (Fig. 1.3k). A global meta-analysis of the ecology of tropical riverscapes showed that consistent, seasonal flow regimes support communities with higher net primary productivity and higher species richness in bird and fish assemblages than rivers with arrhythmic flow regimes (Jardine et al., 2015). Lundholm found in a meta-analysis of studies describing relationships between species richness, spatial environmental heterogeneity and energy availability, that energy availability was a better predictor of species richness than environmental heterogeneity (Lundholm, 2009). Temporal consistency in patterns of resource and energy availability may compete with environmental heterogeneity as a control on riparian plant diversity in this system.

Further insight into the processes controlling riparian plant community assembly can be derived from patterns of functional diversity assembly across environmental gradients. FRic.SES represents the volume of the convex hull of trait values in a given community, as a fraction of the expected convex hull volume generated from randomized communities (Mason et al., 2013). FRic.SES is not weighted by species abundance and describes only the range of trait values present. FDis.SES, a pure measure of functional divergence (Mason et al., 2013), provides information about the abundance distribution of trait values across this range: functional divergence is maximised when highly abundant species are distant from the community centre of gravity in traitspace (Mouchet et al., 2010). Functional richness was unimodally related to temporal variability in baseflow index. The mechanism behind this is unclear, although following the line of reasoning developed for species richness, the effect of increased niche complexity may be offset by irregular resource availability and habitat microfragmentation as environmental heterogeneity increases (Laanisto et al., 2013).

Most communities had higher functional dispersion than predicted by the abundance-swapped null model, and a similar set of hydrological variables as FRic.SES had significant relationships with FDis.SES. FDis.SES showed a skewed, unimodal distribution across a gradient of constancy of maximum flows (C_MaxM). Strongly negative values for several communities at the lower bound of C_MaxM indicates functional underdispersion (i.e. environmental filtering), although the full range of variation in FDis.SES was present at low C_MaxM (Mason et al., 2013). Variation in FDis.SES constricts as constancy increases, however, so with the exception of communities at this lower bound, communities along rivers with similar C_MaxM tend to have similar species abundance distributions in traitspace. Interestingly, temporal variability in minimum flows (C_MinM, M_MinM) predicted species richness but temporal variability in maximum flows (C_MaxM) predicted functional divergence. Compared with species richness, both FRic.SES and FDis.SES showed opposite relationships with climate and soil variables (clim_pwet, clim_tsea and soil_soc, among others), indicating that trait range is not reduced in concert with species richness. The traits which do remain are clustered towards the edges of the range, producing hollowed-out community trait distributions.

Environmental models explain a limited proportion of variation in vegetation composition

Environmental conditions may also have interactive effects on riparian plant diversity. We originally intended to model a set of competing hypotheses about the effects of interactions between environmental conditions on diversity, but the analyses described here were performed post-hoc, and the scope of possible models proved too wide to winnow down based on our limited prior understanding of the system. Future studies which explicitly accommodate tests for interactions into experimental design may provide more insight into environmental controls on diversity.

Environmental models in this study accounted for only part of the total variation in functional diversity (40.5 % for FRic.SES and 48.3 % for FDis.SES). In a previous study of relatively unmodified riparian plant communities in south-eastern Australia, 80 % of variation in functional dispersion was explained by a combination of variability in flood frequency, variability in flood magnitude, and mean daily summer flow (Lawson et al., 2015b). A fraction of this variation was independently explained by climate, and none was independently explained by soil variables. In contrast, much of the variance in functional diversity metrics in the current study was jointly explained by hydrological, climate and soil models. The weak link observed between functional diversity and flow modification (Fig. 1.3e, Fig. 1.4e) suggests that local land management practices and land use histories, which could not be accounted for in this study, may have had a strong influence on diversity (Foster et al., 2003). Additionally, our environmental gradient analyses are based on a niche optimisation paradigm of community assembly, and do not account for neutral processes or biotic interactions (Kraft et al., 2015). Competitive interactions may play a more important role in assembly of diverse subtropical plant communities than in more austere environments dominated by abiotic forces (Callaway, 1995). Indeed, as is characteristic of subtropical forests, many of the species identified in this study were not obligate riparian species (James et al., in review) and could not necessarily be expected to display traits associated with adaptation to the riparian environment.

Implications for management of riparian communities in modified south-east Queensland

Despite previous findings that ecosystem multifunctionality scales linearly with functional divergence (Mouillot et al., 2011), we caution that communities which are functionally diverse but species poor may have low functional redundancy (i.e. the number of species performing similar ecological roles), which has been associated with diminished resilience to environmental change (Laliberté and Legendre, 2010). Riparian plant communities supported by rivers with highly variable flow regimes may therefore be inherently sensitive to environmental change and exotic invasion.

Our findings also suggest that greater runoff variability predicted to characterise future climates in south-east Queensland (Hennessy et al., 2008) could have dele-

terious consequences for riparian plant communities. Less defined patterns of seasonality and greater variability in monthly flow patterns between years may shift assemblages towards species more tolerant of environmental variability and promote exotic invasion. Environmental flows designed to alter interannual variability in flow seasonality have the potential to significantly influence species richness in riparian communities, although their potential effects on functional diversity remain unclear. Although evidence for strong links between flow conditions and riparian plant functional diversity has been found in natural catchments of south-eastern Australia (Lawson et al., 2015b), local land use histories are likely to confound the influence of environmental flows on functional diversity in modified landscapes.

Conclusion

This study was motivated by a desire to provide corroboration to previous work showing strong associations between flow heterogeneity and riparian plant functional diversity (Lawson et al., 2015b), and to extend these findings into more modified landscapes. The current study demonstrates that flow regime may not necessarily be the dominant force shaping riparian plant assemblages in modified landscapes of subtropical south-east Queensland, and provides little evidence that environmental heterogeneity *per se* is an important control on species richness or functional diversity. Rather, generation and maintenance of diversity by rhythmic influx of energy and resources may be key (Jardine et al., 2015; Lundholm, 2009). The two processes are likely active together, but it remains unclear how or why one process might become dominant over the other in a given system. Species richness was associated with the extent of modification of several flow metrics, although not linearly. The absence of strong linkages between the extent flow modification and metrics of functional diversity suggests that use of environmental flows may not be effective as a tool for riparian rehabilitation in modified subtropical landscapes such as south-eastern Queensland.

Acknowledgements

The original study upon which the present analysis is based was funded by the National Water Commission (NWC) under the Raising National Water Standards (RNWS) programme, hosted and managed by the International Water Centre (IWC) and Griffith University, Brisbane. We particularly thank Anna Barnes and Stephen Mackay for all their efforts in the field, and to Angela Arthington who, as the leader of the NWC project, was instrumental in getting the field survey section of this project off the ground and completed. This research was supported by Macquarie University and an Australian Postgraduate Award scholarship to James Lawson. Thanks to Stuart Allen for his help in sourcing climate and soil data.

Authors' contributions

Cassandra James designed and carried out the field component of the original study. Rachael Gallagher provided the majority of the trait data and contributed to the study design and analysis. Kirstie Fryirs and Michelle Leishman advised on the study design and analysis. James Lawson initiated and led the current project, curated the trait dataset, performed the analysis and wrote the manuscript. All authors contributed comments on the manuscript.

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2 Supplementary Information S1 (Information about hydrological and trait datasets)

Table 2.1: Importance of components, from Principal Components Analysis of the set of 18 hydrological metrics used as explanatory variables in this study.

	<i>PC1</i>	<i>PC2</i>	<i>PC3</i>	<i>PC4</i>	<i>PC5</i>
Standard deviation	2.787	1.995	1.273	1.079	0.996
Proportion of variance	0.431	0.221	0.090	0.065	0.042
Cumulative proportion	0.431	0.653	0.743	0.807	0.862

Table 2.2: Loadings across principal components for the set of 18 hydrological metrics used as explanatory variables in this study.

<i>metric</i>	<i>PC1</i>	<i>PC2</i>	<i>PC3</i>	<i>PC4</i>	<i>PC5</i>
MDFMDFWet	-0.068	0.127	-0.647	-0.183	0.210
MDFMDFDry	0.261	-0.226	-0.132	-0.141	0.243
CVMDFWet	-0.300	-0.102	0.242	-0.194	0.210
CVMDFDry	-0.331	-0.134	0.043	0.125	-0.046
HSPeak	-0.307	-0.001	-0.272	0.190	-0.018
HSMeanDur	0.261	-0.313	-0.046	0.068	-0.016
CVAnnHSPeak	-0.296	0.063	-0.210	0.082	0.131
CVAnnHSMeanDur	0.141	-0.367	0.150	0.312	0.029
LSPeak	-0.137	0.384	-0.023	0.314	0.257
LSMeanDur	-0.283	-0.193	-0.067	-0.336	0.205
CVAnnLSPeak	0.095	-0.342	0.069	-0.350	0.330
CVAnnLSMeanDur	-0.121	-0.242	-0.199	0.130	0.311
BFI	0.334	-0.020	-0.026	0.205	0.215
CVAnnBFI	-0.250	-0.286	-0.139	0.160	-0.235
C_MinM	0.200	-0.225	-0.403	0.394	-0.045
M_MinM	0.172	0.159	-0.211	-0.233	-0.451
C_MaxM	-0.154	-0.345	-0.155	-0.202	-0.456
M_MaxM	0.259	0.175	-0.246	-0.283	0.066

Table 2.3: Summary statistics for trait data.

<i>trait</i>	<i>mean</i>	<i>SD</i>
flowering duration (months)	4.72	2.58
leaf area (cm ²)	28.61	28.05
maximum height (m)	19.79	13.98
seed mass (mg)	365.99	2078.8
SLA (cm ² /g)	15.3	7.42
wood density (g/cm ³)	0.609	0.13

Table 2.4: Proportional abundance of plants represented in the functional diversity analysis at each site.

<i>site</i>	<i>Total cover (individuals Ha⁻¹)</i>	<i>Represented cover (individuals Ha⁻¹)</i>	<i>Proportion represented</i>
1	8365	8219	0.983
2	13698	13643	0.996
3	28142	22487	0.799
4	9567	8177	0.855
5	3193	3179	0.996
6	25237	25140	0.996
7	14409	12887	0.894
8	9458	9384	0.992
9	16578	15068	0.909
10	12505	11118	0.889
11	42275	35464	0.839
12	9320	9320	1.000
13	25981	23881	0.919
14	12954	12007	0.927
15	11103	10882	0.980
16	20669	16540	0.800
17	25177	18199	0.723
18	4613	4219	0.915
19	3657	3443	0.942
20	27249	23889	0.877
21	23301	23008	0.987
22	15639	13730	0.878
23	10855	6067	0.559
24	17888	15538	0.869
25	3869	2603	0.673
26	14070	11862	0.843
27	17238	14213	0.825
28	13756	9638	0.701
29	7249	7208	0.994
30	21555	21483	0.997
31	7296	7227	0.991
32	5307	5307	1.000
33	19417	19046	0.981
34	9942	9782	0.984
35	8202	8185	0.998
36	3745	3607	0.963
37	13851	13535	0.977
38	18326	15187	0.829
39	8410	5840	0.694
40	5360	5283	0.986

Table 2.5: Proportion of species included in the functional diversity analysis for which trait values were available.

<i>trait</i>	<i>data density</i>
flowering duration	0.891
growth form	1
leaf area	0.983
maximum height	0.971
seed mass	0.868
SLA	0.661
wood density	0.672

Table 2.6: Error estimates for imputation of missing data. Note that these error estimates refer to transformed data.

<i>trait</i>	<i>normalized root mean squared error</i>
flowering duration	0.263
growth form	0
leaf area	4.351
maximum height	1.346
seed mass	0.745
SLA	0.022
wood density	0.007

3 Supplementary Information S2 (Univariate regression statistics)

Linear regression model statistics						Quadratic regression model statistics										
metric	p	R2.linear	est	stderr	t	metric	p	R2.adj	est	stderr	t	p.term	est.quad	stderr.quad	t.quad	p.term.quad
C_MinM	0.049	0.098	-74.979	36.805	-2.037											
clim_pdry	0.000	0.373	0.425	0.089	4.758	clim_pdry	0.000	0.367	1.523	0.866	1.758	0.087	-0.004	0.003	-1.274	0.210
clim_pwet	0.000	0.438	0.124	0.023	5.446	clim_pwet	0.000	0.424	0.310	0.188	1.655	0.106	0.000	0.000	-1.003	0.323
						clim_tcid	0.004	0.218	288.046	94.845	3.037	0.004	-9.764	3.281	-2.976	0.005
clim_tsea	0.000	0.349	-0.415	0.092	-4.517	clim_tsea	0.000	0.316	-1.248	2.759	-0.452	0.654	0.001	0.003	0.302	0.764
						CVAnnHSPeak	0.020	0.147	-275.048	93.115	-2.954	0.005	173.858	59.605	2.917	0.006
CVAnnBFI	0.023	0.129	-49.174	20.735	-2.372											
CVAnnBFI.mod	0.039	0.108	-35.956	16.803	-2.140											
CVMDFWet.mod	0.042	0.104	-25.905	12.340	-2.099											
exotics	0.013	0.152	-42.132	16.162	-2.607	exotics	0.027	0.132	-81.399	40.361	-2.017	0.051	59.284	55.853	1.061	0.295
						FDIs.SES	0.010	0.180	-9.141	3.459	-2.643	0.012	7.080	2.775	2.552	0.015
FRic.SES	0.042	0.104	-20.651	9.823	-2.102	FRic.SES	0.034	0.122	-22.521	9.663	-2.331	0.025	42.618	25.469	1.673	0.103
						HSMeanDur	0.003	0.232	-55.755	15.341	-3.634	0.001	4.707	1.337	3.520	0.001
						leaf.area	0.041	0.113	31.227	14.123	2.211	0.033	-2.520	1.319	-1.911	0.064
M_MaxM	0.015	0.147	384.485	150.292	2.558	M_MaxM	0.005	0.207	2149.057	807.190	2.662	0.011	-12483.214	5619.940	-2.221	0.033
						M_MaxM.mod	0.002	0.243	32.559	8.657	3.761	0.001	-11.333	3.060	-3.704	0.001
M_MinM	0.022	0.130	311.753	130.876	2.382	M_MinM	0.047	0.107	1326.588	1027.966	1.290	0.205	-4634.497	4656.253	-0.995	0.326
M_MinM.mod	0.000	0.327	27.398	6.382	4.293	M_MinM.mod	0.000	0.342	43.881	11.534	3.804	0.001	-17.368	10.229	-1.698	0.098
						MDFMDFDry.mod	0.039	0.115	-64.401	25.458	-2.530	0.016	38.306	17.945	2.135	0.039
						production_dryland	0.013	0.167	209.817	68.832	3.048	0.004	-385.724	146.482	-2.633	0.012
production_irrigated	0.014	0.150	-437.291	169.178	-2.585	production_irrigated	0.045	0.109	-208.657	509.173	-0.410	0.684	-5186.056	10879.298	-0.477	0.636
						seed.mass	0.006	0.198	64.569	18.933	3.410	0.002	-18.902	5.733	-3.297	0.002
soil_awc	0.003	0.214	-12.729	3.952	-3.220	soil_awc	0.011	0.175	30.966	121.684	0.254	0.801	-1.571	4.373	-0.359	0.721
soil_bdw	0.004	0.200	-111.358	36.143	-3.081	soil_bdw	0.014	0.163	251.956	673.837	0.374	0.711	-155.143	287.322	-0.540	0.592
soil_ece	0.000	0.373	-4.018	0.845	-4.755	soil_ece	0.000	0.339	-4.458	5.559	-0.802	0.428	0.019	0.242	0.080	0.937
soil_phc	0.000	0.369	-35.936	7.631	-4.709	soil_phc	0.000	0.339	99.027	255.470	0.388	0.701	-13.265	25.098	-0.529	0.600
soil_slt	0.049	0.098	2.570	1.263	2.034											
soil_soc	0.001	0.252	16.169	4.515	3.581	soil_soc	0.004	0.214	7.251	31.348	0.231	0.818	1.218	4.235	0.288	0.775

Figure 3.1: Univariate OLS regression statistics for species richness.

Linear regression model statistics						Quadratic regression model statistics									
<i>metric</i>	<i>P</i>	<i>R2.linear</i>	<i>est</i>	<i>stderr</i>	<i>t</i>	<i>metric</i>	<i>p</i>	<i>R2.adj</i>	<i>est</i>	<i>stderr</i>	<i>t</i>	<i>p.term</i>	<i>est.quad</i>	<i>stderr.quad</i>	<i>t.quad</i>
C_MaxM	0.033	0.114	1.155	0.523	2.209	C_MinM	0.045	0.109	3.528	1.669	2.114	0.041	-7.163	4.845	-1.478
C_MinM	0.042	0.104	1.207	0.573	2.104	clim_pdry	0.015	0.161	-0.006	0.016	-0.389	0.699	0.000	0.000	0.075
clim_pdry	0.003	0.203	-0.005	0.002	-3.116	clim_pwet	0.005	0.205	-0.001	0.003	-0.346	0.732	0.000	0.000	-0.076
clim_pwet	0.001	0.246	-0.001	0.000	-3.518	clim_tsea	0.004	0.215	0.069	0.046	1.494	0.144	0.000	0.000	-1.384
clim_tsea	0.002	0.217	0.005	0.002	3.242	CVAnnBFI	0.012	0.170	6.141	2.246	2.734	0.010	-5.396	2.171	-2.486
CVAnnHSMeanDur	0.004	0.200	1.179	0.382	3.084	CVAnnHSMeanDur	0.009	0.182	4.169	2.831	1.473	0.149	-3.137	2.943	-1.066
CVAnnHSNum	0.025	0.125	0.303	0.130	2.326	CVAnnHSNum	0.023	0.141	2.223	1.169	1.902	0.065	-0.726	0.439	-1.652
FDis.SES	0.005	0.191	0.156	0.052	2.994	FDis.SES	0.011	0.175	0.173	0.054	3.193	0.003	-0.048	0.044	-1.108
HSMeanDur	0.007	0.178	0.086	0.030	2.865	HSMeanDur	0.005	0.213	0.551	0.243	2.272	0.029	-0.041	0.021	-1.932
LSPeak	0.010	0.163	-6.065	2.234	-2.715	LSPeak	0.031	0.127	-13.083	11.086	-1.180	0.245	49.502	76.569	0.647
MDFAnnHSNum	0.000	0.292	-0.254	0.064	-3.958	MDFAnnHSNum	0.001	0.284	0.143	0.321	0.446	0.658	-0.088	0.069	-1.262
MDFAnnHSNum.mod	0.017	0.142	-0.457	0.182	-2.507	MDFAnnHSNum.mod	0.039	0.115	-0.824	0.444	-1.854	0.072	-0.658	0.727	-0.905
richness	0.050	0.098	-2.052	1.012	-2.029	MDFMDFDry.mod	0.020	0.147	1.135	0.391	2.906	0.006	-0.712	0.275	-2.584
soil_nto	0.016	0.144	-3.177	1.259	-2.525	soil_nto	0.043	0.110	3.699	9.453	0.391	0.698	-18.071	24.619	-0.734
soil_phc	0.007	0.178	0.391	0.136	2.873	soil_phc	0.019	0.150	4.214	4.528	0.931	0.358	-0.376	0.445	-0.845
soil_soc	0.001	0.257	-0.255	0.070	-3.628	soil_soc	0.004	0.218	-0.362	0.489	-0.741	0.464	0.015	0.066	0.221

Figure 3.2: Univariate OLS regression statistics for FRic.SES.

Linear regression model statistics						Quadratic regression model statistics									
<i>metric</i>	<i>P</i>	<i>R2.linear</i>	<i>est</i>	<i>stderr</i>	<i>t</i>	<i>metric</i>	<i>p</i>	<i>R2.adj</i>	<i>est</i>	<i>stderr</i>	<i>t</i>	<i>p.term</i>	<i>est.quad</i>	<i>stderr.quad</i>	<i>t.quad</i>
C_MaxM	0.030	0.118	3.287	1.457	2.257	C_MaxM	0.000	0.321	39.627	9.921	3.994	0.000	-52.868	14.316	-3.693
clim_pwet	0.017	0.140	-0.003	0.001	-2.492	clim_pwet	0.028	0.131	0.009	0.010	0.943	0.352	0.000	0.000	-1.256
CVAnnHSMeanDur	0.025	0.126	2.612	1.116	2.341										
CVAnnHSNum	0.038	0.108	0.789	0.367	2.149										
flowering.duration	0.029	0.120	1.598	0.703	2.274										
FRic.SES	0.005	0.191	1.220	0.407	2.994	FRic.SES	0.000	0.334	1.357	0.367	3.693	0.001	-3.118	0.968	-3.219
HSMeanDur	0.028	0.121	0.197	0.086	2.285										
LSPeak	0.011	0.158	-16.695	6.254	-2.670	LSPeak	0.033	0.124	4.252	31.016	0.137	0.892	-147.752	214.215	-0.690
maximum.height	0.000	0.277	-0.573	0.150	-3.813	maximum.height	0.000	0.302	1.220	0.983	1.241	0.223	-0.258	0.140	-1.844
MDFAnnHSNum	0.035	0.112	-0.439	0.201	-2.191										
MDFAnnHSNum.mod	0.016	0.144	-1.284	0.508	-2.524	MDFAnnHSNum.mod	0.023	0.141	-2.802	1.222	-2.293	0.028	-2.726	2.000	-1.363
seed.mass	0.005	0.193	-0.694	0.230	-3.013	seed.mass	0.002	0.245	-2.362	0.802	-2.946	0.006	0.525	0.243	2.164
soil_nto	0.046	0.101	-7.426	3.601	-2.062	soil_nto	0.043	0.111	33.457	26.387	1.268	0.213	-107.448	68.723	-1.563
soil_soc	0.001	0.243	-0.692	0.198	-3.491	soil_soc	0.000	0.344	2.803	1.250	2.242	0.031	-0.477	0.169	-2.826

Figure 3.3: Univariate OLS regression statistics for FDis.SES.