DISCUSSION

We surveyed a broad swathe of geomorphically similar rivers across south eastern Australia and found that functional diversity in riparian vegetation communities, as described by functional dispersion, exhibits strong relationships with local patterns of hydrology. We used an ecologically relevant set of quantitative functional traits to capture variation in ecological strategy within communities. To our knowledge, this is the first study to examine relationships between hydrological conditions and the functional ecology of riparian vegetation communities using a quantitative trait dataset. The overarching pattern across these relationships can be summarised as “heterogeneous flows breed hetereogenous communities”.

This pattern fits within existing understanding of the processes which generate and maintain biological diversity in the riparian environment. Briefly stated, this paradigm holds that riparian biodiversity is a function of landscape complexity generated by hydrogeomorphic processes, overlaid by feedback interactions between these processes and biotic components of the riparian environment (Tabacchi *et al.* 1996; Naiman & Decamps 1997; Palmer & Poff 1997; Stromberg 2001; Corenblit *et al.* 2007; Bornette *et al.* 2008; Steiger & Corenblit 2012). We note that the following argument assumes that functional diversity is a property of riparian communities at the reach scale, and that influx of species from more physically complex adjacent patches is responsible for the diversity we observed on comparatively homogenous sloping bank sections.

The sites surveyed in this study spanned a spectrum of flooding intensity: at the lower bound, the calculated 20 year average return interval (ARI) flood was just 18 times the mean daily flow for that river; at the upper bound, flows 210 times greater than the mean daily flow occur approximately every 20 years. Higher magnitude flow events such as this are likely to be geomorphically effective across a greater extent of the fluvial landscape (Huang & Niemann 2006). The strong positive relationship between functional diversity and 20 year ARI flood magnitude supports the supposition that disturbance retards competitive exclusion as a diversity limiting process (*sensu* Huston 1979). Notably, no significant relationships were found between functional diversity and metrics describing mean high flow conditions, whereas metrics describing variability had high explanatory power. Interannual variability in high flow magnitude showed the strongest relationship with functional diversity in this study. If a causal relationship exists, it could be because the average high flow magnitude determines what proportion (in terms of elevation above the main channel) of the riparian zone experiences flooding in a given year. Variability in high flow magnitude, combined with geomorphic heterogeneity, will produce variability in the time since last inundation (without significant disturbance), or combined inundation and disturbance, for a given patch of vegetation. Since flood flows also function as an important dispersal pathway for propagules (Merritt, Nilsson & Jansson 2010), variability in high flow magnitude should influence recruitment processes in a similar manner. Likewise, variability in the frequency of flood flows also results in variable time since last inundation or disturbance. Interannual variability in flood rise and fall rates was also positively associated with functional diversity. Flood rise and fall rates may determine entrainment of woody debris into the flood channel and subsequent bank deposition (Cadol & Wohl 2010). Debris entrainment in turn increases the erosive potential of floods, but its deposition provides structural heterogeneity, and resources for fungal and animal communities (Harmon *et al.* 1986). Overall, the combination of occasional high intensity flooding disturbance with year-to-year variability in patterning of high flow events results in a mosaic of bare, disturbed and colonised substrate. This environmental heterogeneity provides a broad range of niches, facilitating the success of a diversity of ecological strategies (Bornette *et al.* 2008).

We can extend this framework to account for the observed relationships between functional diversity and variability in seasonal water availability. Our sites were distributed across a gradient of flow seasonality: at one end, rivers exhibited weak but stable patterns of seasonality; at the other, rivers were characterised by high interannual variability and spiked, inconsistent temporal distributions of flow. Once again, communities with higher functional diversity tended to be located towards the ‘variable’ end of the spectrum. South eastern Australian plants do exhibit characteristic species-level responses to seasonality, although there is no mass coordination of growth and reproduction phenologies as in the northern hemisphere. Flowering times within the Myrtaceae (a dominant family in riparian plant communities of south-eastern Australia) are often staggered where species are sympatric (Beardsell, Obrien & Williams 1993). Often, growth and reproduction of riparian plants are associated with the arrival of favourable conditions (Woolfrey & Ladd 2001; Robertson 2001; Siebentritt, Ganf & Walker 2004). High coefficients of variation in seasonal mean daily flows may act to temporarily provide species with favourable conditions according to their seasonal biology. Exceptions to these patterns included the quadratic fit for variability in summer mean daily flows, with high values being associated with a reduction in functional diversity, and mean daily flow for summer, which was positively associated with functional diversity, and broke the trend of associations with seasonal means being either non-significant or negative. A meta-analysis of the effect of drought on riparian vegetation showed reduced species richness and a shift towards drought tolerant species following climate-induced increases in the intensity and duration of drought, and that this effect was exacerbated by high temperatures (Garssen, Verhoeven & Soons 2014). Higher temperatures in the absence of drought were associated with higher rates of primary production. Higher mean daily flows in summer, then, potentially alleviate the water stressed induced by hot weather while stimulating plant growth. We did investigate whether sites at subtropical latitudes simply had higher functional diversity than temperate sites, according to well known latitudinal patterns of species richness (Willig, Kaufman & Stevens 2003), and found no relationship between latitude and FDis.

The multiple regression model selected according to AICc explained a high proportion of variation in FDis. This model described functional diversity as a function of variability in flood frequency and magnitude, and summer mean daily flow. The combination of flow heterogeneity with extra watering during summer appears to provide optimal conditions for functionally diverse communities. The coefficient of the interaction term between variability in flood magnitude and summer mean daily flow was significant but negative, indicating that the additive effect is subject to diminishing returns at high values of both terms. The key finding here is that these three metrics of hydrological conditions are able to account for almost all of the variation in FDis. We used traits in our analysis which capture a broad spectrum of ecological strategies, rather than solely traits associated with riparian specialist strategies, which might be expected to results biased towards flow response. No contribution from other environmental variables such as latitude, altitude, catchment area etc. was necessary, and in any case, such contributions would likely reduce the parsimoniousness of the model. We caveat, however, that this model does not account for the effect of plot-scale geomorphic variability on diversity, as this was controlled for in the site selection process.

Two sites had anomalous values for FDis which do not fit within this conceptual model of disturbance and flow variability providing high niche heterogeneity and therefore functional diversity. These sites experience highly variable flows but had low functional diversity. We experimentally adjusted the abundances of dominant species at these sites, and the low values for FDis appear to result from dominance of a single species at each site (the medium sized tree *Acmena smithii* at Mammy Johnson’s Creek, and the liana *Ripogonum album* at Jilliby Creek). These sites may represent cases in which species with ‘variability’ specialist strategies have become dominant. *Acmena smithii* has a relatively large seed and is shade tolerant (Melick 1990), but once established, develops a lignotuber and is highly resistant to drought and disturbance (Ashton & Frankenberg 1976). With respect to *Ripogonum album*, there is evidence to suggest that abundance lianas may be associated with disturbance (Laurance & Pérez-Salicrup 2001) and have a competitive advantage over trees in dry conditions (Swaine & Grace 2007; Cai, Schnitzer & Bongers 2009), although see Nepstad *et al.* 2007. These sites notwithstanding, we believe the relationships we have described form a strong case for our argument.

It was not possible with our dataset to dissect out which specific aspect of hydrology drove variation in functional diversity. Rather, it makes more sense to think about functional diversity as it relates to the correlated spectra of hydrological variability and disturbance intensity. The identification of such a strong relationship between environmental variability and functional diversity has significance for lotic ecology (Palmer & Poff 1997), as well as ecology in general, as it provides quantitative, real-world support for findings based on theoretical simulations (Schwilk & Ackerly 2005).

Our findings are also important from an applied river management and conservation perspective. Widespread anthropogenic river modification has altered hydrologies throughout the world, and the changing climate has the potential to exacerbate the impacts of flow modification as well as affecting unaltered river systems. The key issue with river modification is that it reduces flow heterogeneity. Dams flatten flood peaks, alter seasonality and increase predictability of flows (Graf 2006). Flow regulation and diversion for irrigation and hydropower has resulted in a complete reversal of flow seasonality on the Sacramento River (California, United States) from heterogeneous winter dominated flows to a comparatively homogenous summer dominated regime (Singer 2007). Likewise, in south eastern Australia, the River Murray’s hydrographs have been flattened by regulation, and its once highly variable flows are now stored for prescribed release during summer (Maheshwari, Walker & McMahon 1995). Dams also interrupt hydrochorous transport of propagules (Merritt *et al.* 2010), such that when flood flows do occur, less seed material is dispersed to patches of fresh substrate. When designing environmental flows (e.g. Howell & Benson 2000), river managers typically consider magnitude, frequency and seasonality of flows. We urge managers to consider simulating the natural variability in flow regime in their designed flows.

Reductions in mean summer precipitation have already occurred over large areas of Australia, coinciding with a warming of 0.4 – 0.7 oC since 1950 (Hennessy *et al.* 2007). Further changes of this nature are projected for Australia as well as other regions of the globe (Stocker *et al.* 2013). Lower average flows during hotter summers may stress riparian communities and constrain functional diversity. Alternatively, greater climatic variability associated with future climates (Hennessy *et al.* 2008) may promote hydrological heterogeneity for rivers in regions which were previously associated with more stable flow conditions. Thus we should be careful not to promote high functional diversity as an ecological ‘good’ which must be maximised. In conservation, preserving ecosystem function requires preserving the characteristic functional composition of communities. Climate change induced increases in flow variability in systems which are not naturally highly variable may open up niche space to favour opportunistic species and promote invasion by exotic species.

Our study emphasises the importance of flooding disturbance and hydrological heterogeneity as drivers of functional composition in riparian plant communities. These findings should be general to river systems in other regions and biomes, given the profound influence of hydrology in shaping the structure of fluvial landscapes and determining the ecological strategies of plants that are able to persist and thrive in the riparian environment. Comparisons with datasets from regions with hard, highly predictable seasonal patterns of hydrology, for example monsoonal or nival regimes, are needed to confirm this assertion. In the south eastern Australian context, at least, alterations to flow variability and disturbance regimes by dams and the changing climate may have significant consequences for the composition and functioning of riparian vegetation communities.