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, blunting of natural environmental heterogeneity by human modification of river flow regimes and catchment landscapes would result in lower diversity. This niche-oriented model of riparian plant diversity received mixed support in our study: species richness in fact decreased as hydrological conditions became more heterogeneous, and flow homogenisation by dams 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 hydrological heterogeneity. The proportion of variation in functional diversity explained by environmental variables was comparatively lower than species richness or exotic abundance. 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 regime was nevertheless the most consistently powerful predictor of diversity in our study. Models derived from flow regime metrics explained more total and independent variation in species richness (SR), exotic abundance and FRic.SES than any other group of environmental variables. Of the individual environmental variables with significant relationships to FDis.SES, the hydrological metric describing consistency in monthly maximum flows (C\_MaxM) explained the most variation. Variation in diversity metrics and exotic abundance were co-explained by soil and climatic variables, however, and any attempt to disentangle the effects of different environmental conditions inevitably leads to the question: is it possible to attribute flow regime as the dominant control on diversity? There is some evidence to support this assertion: SR increased with contingency of minimum flows (M\_MinM, Fig Xx), and also increased when M\_MinM was increased by flow modification (M\_MinM.mod, Fig Xx). SR had no direct relationship with the degree of modification of contingency of minimum flows (i.e. C\_MinM.mod) did increase as dry season flows (MDFMDFDry.mod, Fig Xx) were upregulated, which would increase constancy of minimum flows. Removal of the outlying pair of sites which had experienced extreme modification strengthened the relationship of MDFMDFDry.mod with SR (R2 = 0.117 vs 0.283). Likewise, greater high flow frequency (MDFAnnHSNum) was associated with lower FRic.SES and FDis.SES, and communities with altered high flow frequency followed the same trend. Extent of flow modification independently explained variation only in species richness, however, and changes to only a fraction hydrological metrics were important. As such it was not possible to answer this question conclusively; 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. Nevertheless, the importance of hydrological metrics in our optimal models of species richness, exotic abundance FRic.SES and FDis.SES lends weight to the case that hydrology was an important control on diversity.

Species richness had a more complicated relationship with hydrological heterogeneity than that expected, however. Richness was highest along rivers which experienced regular seasonal patterns of low flows, and short but frequent flood flows. These short flood flows may enhance diversity by generating habitat complexity (Tabacchi et al. 1998), with longer flood durations acting as an environmental filter favouring species with inundation tolerance traits. An international meta-analysis of the ecology of tropical riverscapes showed that consistent, seasonal flow regimes support communities with higher net primary and higher species richness in bird and fish assemblages than rivers with arrhythmic flow regimes (Jardine et al. 2015). Lundholm (2009) found in a meta-analysis of studies describing relationships between SR, spatial EH and energy availability, that energy availability was a better predictor of SR than EH. Rhythmicity in temporal patterns of energy and resource availability (water, nutrients, fresh sediment and newly disturbed habitat) appears to be competing with EH as a control on riparian plant diversity in this system.

Further insight about 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 EH increases. Comparison of patterns of FRic.SES and species richness reveals an interesting effect along gradients of flood frequency and duration: the relationship of mean duration (HSMeanDur) and frequency (MDFAnnHSNum) of high flow periods with FRic.SES was the inverse of that with SR. Thus community convex hulls retained their volume in traitspace as EH increased, but became more sparsely populated.

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. 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 the opposite relationships with high flow frequency, climate and soil variables, 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 in this study accounted for only part of the total variation in functional diversity. 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 2015). A fraction of this variation was independently explained by climate, and none was independently explained by soil variables **(Lawson 2015).** In contrast, much of the variance in functional diversity metrics in the current study was jointly explained by hydrological, climate and soil models. The single weak relationship observed between functional diversity and flow modification 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).

A substantial amount of variance in exotic abundance was jointly explained by hydrological and land use models. The proportion of catchment land-use associated with irrigated agricultural production was typically low, but production from natural environments (forestry etc.) was common and dominated a number of catchments. The rationale for our hypotheses was that environmental heterogeneity should result in structural complexity of habitat and therefore limit competitive exclusion by invasive species. We found that exotic abundance was associated with more hydrologically heterogeneous sites, and a greater proportion of catchment used for forestry. It is possible that invasive species are competitive in colonising niches opened by flooding or land management disturbance, the resulting assemblages being characterised by acquisitive, ruderal ecological strategies (kyle & leishman?). However post-hoc analysis of our data reveals that sites with high exotic abundance had higher community weighted mean (CWM) wood density (R2 = 0.338, p < 0.0001) and lower CWM leaf area (R2 = 0.325, p < 0.0001) (see Supporting Information). Higher wood density in riparian plant communities has been previously linked with flow heterogeneity and is indicative of conservative resource use and stress tolerance (Lawson et al. 2015), and small leaves are also characteristic of plants adapted to harsh environments (REF). All four sites where exotic proportional abundance exceeded 0.4 (0.41, 0.48, 0.58, 0.86) supported dense thickets of *Macfadyena unguiscati*, a tall liana native to Brazil and Argentina. A wood density value for this species could not be found, but its leaves are small compared with the average leaf area of species in this study (14 cm2 vs 27 cm2). There is also evidence to suggest that lianas have a competitive advantage over trees in dry conditions (Swaine and Grace 2007; Cai et al. 2009), and thus may be favoured by variable flow regimes. *Leucaena leucocephala,* which has very small leaves (0.2 cm2) and dense wood (0.76 g/cm3), was co-dominant with *M. unguiscati* at the most invaded site. High abundance at two of these sites of *Lantana camara*, which has average sized leaves and high specific leaf area (i.e. fast relative growth rate and resource acquisitive resource use) and is a well-known colonist of disturbed niches, suggests that multiple invasion strategies are at play. Three of these four sites had greater than expected functional divergence (FDis.SES), demonstrating that the traits of the most abundant species (i.e. the exotics) diverged from community trait averages. This could indicate either a.) division of niche space between conquerors (*M. unguiscati* and *L. camara*) where trait averages do not actually represent any real species, or b.) that the niches occupied by invasive species were previously unfilled. The most invaded site did not follow this trend: in this case, the *M. unguiscati* and *L. leucocephala* were dominant to the point that their average trait values were not different from the community average. A final note to make is that it matters when communities were sampled, in terms of how much time has elapsed since the last geomorphically effective flood, due to the temporal sequence inherent in community response to disturbance. This aspect was not quantified here, although it would be mostly pertinent for ruderal-type ecological strategies (i.e. *L. camara* but not *M. unguiscati* or *L. leucocephala*).

Environmental conditions may also have interactive effects on exotic abundance and riparian plant diversity. We originally intended to model a set of competing hypotheses about the effects of interactions between environmental conditions on diversity and exotic abundance, but the analyses described in 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.

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 et al. 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 deleterious 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 inherent 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. 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 2015), but 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. 2015). The current study confirms the general importance of flow regime in shaping riparian plant assemblages, but we found little evidence that environmental heterogeneity *per se* was the key control on diversity in this system. Rather, generation of diversity by the ‘flood rhythm’ appears to dominant here (Jardine et al. 2015). 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. An interesting avenue for future research would be to investigate how spatial scale affects the relative influence of flow rhythmicity and environmental heterogeneity on diversity (Lundholm 2009). Functional ecology is being increasingly used to characterise riparian plant communities, and in the future, a comparative synthesis of different systems may shed light on how the interplay between environmental heterogeneity and flood rhythmicity controls community assembly.