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Does stream flow structure woody riparian vegetation in highly modified subtropical catchments?

1   **Does stream flow structure woody riparian vegetation in highly modified**

2   **subtropical catchments?**

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26 **SUMMARY**

27 1.   Hydrology is recognised globally as the principal driver of riparian vegetation

28 composition and structure. This relationship underpins restoration efforts that aim to conserve

29 and enhance riparian vegetation communities using flow. As catchment restoration often occurs

30 in modified landscapes, flow-ecology relationships should be robust to the potential impacts of

31 land use and other anthropogenic pressures.

32 2.   The strength of flow-ecology relationships was investigated for woody riparian

33 vegetation in a sub-tropical landscape highly modified for agriculture. We used a predetermined

34 stream flow classification to select 44 riparian sites across the major flow gradients in subtropical

35 southeast Queensland, Australia. We applied multiple regression analysis using a multi-model

36 inference approach and multivariate analysis to investigated key drivers of riparian vegetation

37 structure (i.e. depth to water table, stream specific power, climate, substrate type and degree of

38 hydrologic alteration) on riparian vegetation assemblages and metrics.

39 3.   Over 190 species and 15, 500 individuals were recorded from 44 sites. Flow was weakly

40 correlated with assemblage composition and metrics. Variation in structural metrics, common

41 species abundances and overall vegetation assemblages between flow classes was explained

42 largely by climate, particularly annual rainfall. Hydrologic alteration and stream specific power

43 were correlated with assemblage structure when the effects of climate were partialled out. No

44 relationships were found between land use and, riparian vegetation composition and structure.

45 4.   The relatively minor role of flow in structuring riparian vegetation assemblages may have

46 been due to the relatively long lived nature of woody riparian species, extent of overall landscape

47 modifications in the catchments and lack of specialist riparian species in subtropical landscapes.

48   5.   **Synthesis and Applications** - Our results highlight some of the difficulties in

49   determining flow-ecology relationships in subtropical agricultural landscapes, especially

50   disentangling the effects of multiple, co-varying drivers. Controlled experiments, including those

51   conducted as part of an adaptive management strategy, may better inform environmental flow

52   planning in such complex systems. A functional, trait-based approach to understanding

53   vegetation patterns in relation to flow characteristics and other drivers may also prove

54   informative.

55

56

57   **INTRODUCTION**

58   Hydrology is widely recognised as the principal driver of riparian vegetation composition

59   and structure throughout the world (Nilsson & Svedmark 2002; Naiman *et al.* 2005). Riparian

60   species' pools commonly reflect a combination of plant tolerances to the stresses imposed by

61   surface water flow regimes, their capacity to capitalise on the subsidies provided by flow and

62   their ability to regenerate after hydrologic disturbance (Naiman & Decamps 1997). Riparian

63   vegetation assemblages vary mainly in relation to flow as well as geomorphology, which

64   together largely determine patterns of water availability and fluvial disturbance (Merritt *et al.*

65   2010; Bendix & Stella 2013). Consequently, flow modification, such as that resulting from dams,

66   is often associated with changes in riparian vegetation which, given its disproportionate

67   functional importance in the landscape, can have significant environmental and socio-economic

68   ramifications across multiple scales (Capon *et al.* 2013). Knowledge of relationships between

69   flow and vegetation ecology are therefore fundamental to making decisions concerning the

70   restoration and conservation of river ecosystems, especially the delivery of environmental flows

71   for ecological purposes.

72   In highly modified agricultural and urban regions, riparian vegetation frequently

73   represents the sole native vegetation remaining in the landscape (Maisonneuve & Rioux 2001).

74   Often persisting as thin and fragmented strips, riparian vegetation within such landscapes is

75   likely to be vulnerable to a wide range of anthropogenic pressures associated with the direct

76   effects of human activities in the riparian zone (e.g. clearing, grazing, cropping and burning) as

77   well as indirect effects of land uses in surrounding catchments (e.g. pollution from

78   agrochemicals, invasion by pastoral species and changes to runoff and sediment transport

79   patterns; Richardson *et al.* 2007; Bowers & Boutin 2008). Such pressures can result in greater

80 cover of exotic species, reduced native species diversity, altered plant density or disrupted

81 successional patterns (e.g. Johnson 1999; Corbacho, Sanchez & Costillo 2003; Aguiar & Ferreira

82 2005; Lopez, Harper & Drapeau 2006; Bruno *et al.* 2014). The role of flow in structuring

83 riparian vegetation in highly modified landscapes may therefore be masked, diminished or

84 amplified by many anthropogenic pressures and their effects.

85 Studies of flow-ecology relationships rarely address the influence of catchment

86 modification and land use change (Stewart-Koster *et al.* 2010; Arthington *et al.* 2014). Indeed, in

87 many cases, study designs may actively avoid potentially confounding effects of land use on

88 flow regimes and riparian/aquatic ecosystems. Nevertheless, environmental flow management

89 inescapably occurs within this context and knowledge of flow-vegetation ecology relationships

90 in modified landscapes is still needed to guide decision-making. Furthermore, environmental

91 flow management has the potential to promote improvements in riparian condition and river

92 health even where land use has an overwhelming influence on riparian ecology (Johnson 1999).

93 The ELOHA (Ecological Limits of Hydrological Alteration) method is a new framework

94 for exploring flow-ecology relationships and the effects of flow modification to inform

95 environmental flow management (Arthington *et al.* 2006; Poff *et al.* 2010). The framework is

96 underpinned by the principle that flow is a key determinant of the ecological characteristics of

97 rivers and their riparian zones and that these should therefore vary spatially in relation to river

98 types (i.e. river segments with similar flow regime properties) (e.g. Mackay, Arthington & James

99 2014). We tested this assumption for woody riparian vegetation in southeast Queensland as part

100 of a regional ELOHA trial. Because this region is intensively settled and highly modified for

101 agriculture, we were particularly interested in whether or not riparian vegetation in this landscape

102 would still exhibit strong relationships to flow given other pressures.

103   We surveyed woody riparian vegetation in 44 sites across the region selected to represent

104   the characteristics of flow classes identified for the ELOHA trial (Mackay, Arthington & James

105   2014) as well as a variety of agricultural land uses. We investigated the effects of flow class,

106   land use and a selection of other potential drivers (i.e. bank height, stream specific power,

107   substrate type, climate and the degree of hydrologic alteration) on riparian vegetation

108   assemblages and structural metrics characterising them.

109

110   **METHODS**

111   **Study area**

112   The study was conducted in southeast Queensland, Australia (Fig. 1). Climatically, the

113   region is subhumid and subtropical. Rainfall occurs throughout the year but declines strongly

114   along an east-west gradient with mean annual rainfall ranging from 1400 mm on the coast to 800

115   mm inland (Bridges, Ross & Thompson 1990). The region comprises seven major river

116   catchments. Higher mean annual runoff per unit area occurs in the eastern coastal catchments.

117   Due to the irregularity of rainfall across the region, flow regimes in all of the region's rivers and

118   streams are highly variable.

119   The region exhibits considerable topographic and geomorphologic variation and is

120   associated with complex geology and associated soils. Distinct topographic areas in the region

121   include coastal plains, river floodplains and large estuaries in the east and foothills and

122   mountains with plateaux over 300 m a.s.l. to the west, north and south. Land use in the region is

123   predominantly agricultural (~ 60 % of land area), mainly comprising grazing on relatively

124   natural pastures. Much of the region has also been extensively cleared of native vegetation,

125   mostly by the 1940s, but with clearing continuing in recent decades (Bradshaw 2012).

126   There are twenty-four dams with crest heights over 15 m in the study region, most of

127   which were constructed in the early to mid-1970s to support irrigated agriculture and urban

128   development. Although dams have had significant effects on downstream flow regimes, many

129   pre-development hydrological characteristics persist in the region (Mackay, Arthington & James

130   2014). The main changes to flow regimes from pre-development conditions include a loss of

131   natural flow diversity and an increase in the duration of low flow spells (Mackay et al. 2014).

132 **Site selection**

133   Sites were selected as part of a regional trial of the ELOHA framework that also

134 considered flow-ecology relationships for fish and aquatic macrophytes (Arthington *et al.* 2014;

135 Mackay, Arthington & James 2014). To provide the 'hydrological foundation' of this trial, a

136 classification of historic flow regimes was conducted using stream gauge data which identified

137 five flow classes across the region (Table 1; Mackay et al. 2014). Flow classes were

138 distinguished from each other mainly by hydrologic metrics associated with flow magnitude,

139 high spell duration and flow constancy (Mackay et al. 2014). Flow classes 2 to 5 reflect similar

140 'reference' flow classes developed from modelled pre-development hydrologic data while flow

141 class 1 is an artificial flow class reflecting conditions associated with river regulation by dams

142 and other flow modification (Table 1; Mackay et al. 2014).

143   We selected 44 sites, spread across the five flow classes, based on criteria including

144 proximity to stream gauges, accessibility and limited direct modification of riparian vegetation

145 from activities such as clearing, burning and/or grazing (Fig. 1). All sites were positioned in mid-

146 and lowland stream reaches of < 300 m elevation and regulated and non-regulated reaches were

147 included. While we excluded sites that had been directly impacted by clearing in the last 20-30

148 years, all of our sites had more than 24% (and up to 92 %) of their catchment area subject to

149 agricultural activity. To minimise within-site variation in stream morphology, geology and

150 adjacent land use, but still include multiple in-stream habitats, field sites comprised 100 m long

151 stream reaches.

152 **Data collection**

153 *Vegetation survey*

154   We surveyed woody riparian vegetation in three randomly positioned 5 m wide belt

155   transects at each site. All transects were located on the same bank so that land use impacts were

156   similar within a site. Up to three additional transects were surveyed at three sites due to very low

157   plant densities (i.e. <100 individuals) in initial transects. Transects extended up to 70 m from the

158   water's edge to the edge of the remnant riparian vegetation. In the few cases where land use

159   change did not occur within 50 m of the water's edge, landform change (e.g. a distinct change in

160   bank slope) was used to delineate the upland extent of each transect. Transects ranged from 12.5

161   m to 69 m with a median length of 32.4 m. We recorded the presence and diameter at breast

162   height (dbh) of all trees and shrubs greater than 50 cm tall within each belt transect. Field work

163   was undertaken between 2008 and 2010.

164   *Environmental variables*

165   For each site, we calculated a range of environmental variables selected because of their

166   potential to influence vegetation. To characterise the substrate at each site, we collected soil

167   samples along each transect at the stream edge, midway along the transect and bankfull (i.e. the

168   point at which water begins to over flow onto a floodplain or surrounding landscape; Rosgen

169   1996). Additional soil samples were taken where cross-sections intersected other distinct

170   landforms (e.g. benches and bars), although these were not common at selected sites. A

171   hydrometer was used to determine the proportion of silt, clay and sand in each sample and mean

172   values were calculated for the site. Mean annual temperature and mean annual rainfall for each

173   site were determined from national datasets (Bureau of Meteorology 2009; Stein *et al.* 2009).

174   We used bank height above the waterline, measured via two or three cross-sectional

175   surveys with a dumpy level at each site, as a proxy for depth to the water table because

176   groundwater can have a significant influence on riparian vegetation assemblages. To characterise

177   the degree of fluvial disturbance and therefore the potential for mechanical damage to plants

178   (Bendix 1999), we also calculated stream specific power (SSP, W m^{-2}) for each site using the

179   formula SSP = yQS/w, where y is the unit weight of water (9 800 N/m^3), Q is discharge (m^3/s), S

180   is energy slope (m/m) approximated by bed slope and w is channel bankfull width (m) (Bizzi &

181   Lerner 2015). We used two year annual return interval (ARI) floods as the reference discharge as

182   this is approximately equal to bankfull discharge (Wharton 1995). The 2 year ARI floods may

183   not reach all the riparian vegetation at every site, however this ARI is highly correlated with

184   larger flood magnitudes (i.e. 10 year ARI correlation coefficient > 0.99) and it is therefore

185   unlikely to affect the overall results. Stream slope and channel bankfull width were obtained

186   from field surveys using a dumpy and level except for three sites for which channel slope was

187   estimated from 25 000 scale mapping due to constraints accessing sites.

188   We determined the proportion of each site's catchment under agriculture using land use

189   data from the Queensland Land Use Mapping Program, generated from 1999 baseline surveys

190   (Witte *et al.* 2006). Draft updates available from 2006 land use surveys for the Maroochy and

191   Logan-Albert were also incorporated (DERM, 2010). Because land use closer to streams may

192   have a disproportionate influence on stream condition relative to distal land uses, we calculated

193   an inverse-distance weighting *(d+1)$^{-1}$* metric following Peterson et al. (2011).

194   We also determined the degree of hydrologic alteration for each site, represented by a

195   Gower dissimilarity metric which was based on the difference between modelled pre-

196   development (i.e. natural) flows and actual, historic flows as described by Mackay et al. (2014).

197   Modelled, natural flow data was unavailable for four sites but since none of these were regulated,

198   flow modification at these sties was assumed to be similar to nearby non-regulated streams.

199   **Data analysis**

200   We calculated vegetation metrics based on the cumulative survey data for each site

201   (Table 2). We determined species richness and abundance per hectare (ha) (Table 2). Variation in

202   fluvial disturbance may result in different successional vegetation patterns with high

203   disturbances constraining species assemblages to vegetation of early successional stages. Each

204   species was therefore assigned a successional stage characterised as early (E), intermediate (M)

205   or late (L) and combinations of these stages, i.e. where the species occurred in more than one

206   successional stage, as EM, ML or EML, following Kanowski et al. (2010). Proportions of

207   individuals classified as early, intermediate and late successional stages were determined as a

208   percentage of the total abundance. Because many species are classified as combinations of these

209   stages, the total percentage of early, intermediate and late can sum to more than 100 %.

210   Proportions of exotic trees and shrubs were determined for each site. Trees with a dbh ≤10 cm

211   were all categorised as regenerating (Kariuki & Kooyman 2005).Vegetation metrics and

212   assemblage data were calculated for both the whole transect width, hereafter 'bank full', and for

213   the 'near stream' zone which included the transect area <5 m from the water's edge because

214   regional floristic surveys suggest that is where most rheophytic species are confined.

215   We used Kruskal-Wallis tests and Tukey's HSD tests to examine differences in

216   vegetation metrics and common species' abundances (i.e. species occurring at more than 20

217   sites) across flow classes. We adjusted the p value to take account of the multiple comparisons

218   between flow classes using a more conservative significance value of $p<0.005$.

219   We explored relationships between vegetation metrics and environmental variables using

220   the glmutli package in R (Calcagno & de Mazancourt 2010). This approach uses linear

221   modelling to fit all possible models which are then compared using various criteria. We

222   restricted our model selection to main effects only, due to the relatively small number of sites,

223 and compared models using the AICc criterium, which adjusts for small sample sizes. We

224 assumed a Gaussian distribution for all response variables apart from proportional data

225 (successional stages and exotics as a proportion of total individuals) for which we used the

226 binomial family with a logit link function. All data was checked to make sure it fitted the

227 assumptions of linear models and transformed where necessary. Square root transformation was

228 applied to the total abundance (D_ALL) and the abundance of regenerating native

229 (D_REGEN_NATIVE) and the basal area (BA_ALL) of trees and shrubs. Species richness per

230 ha (D_SPECIES) was not transformed. We then undertook a similar set of analyses to the

231 riparian metrics (detailed above) using common species' abundances for the full bank data set.

232 Species abundance data was log transformed and the Gaussian distribution assumed.

233   To assess the effects of flow class on vegetation assemblages, we conducted

234 permutational Multivariate Analysis of Variance using Bray-Curtis distance matrices with the

235 Adonis function in R's vegan package (Oksanen *et al.* 2010). Prior to this analysis, species

236 abundance data were $\log10(x)+1$ transformed and rare species (i.e. those occurring in less than 3

237 sites) removed. We were unable to analyse pairwise differences between group means because

238 groups were unbalanced. Instead, we explored differences between flow classes using Analysis

239 of Multivariate Homogeneity of group variances with a test analogous to Levene's test of the

240 equality of variances followed by pairwise comparisons using Tukey HSD. We also calculated

241 the indicator values of species for each flow class as the product of the relative frequency and

242 relative average abundance in flow classes. Indicator value is maximised (i.e. 1) when all

243 individuals of a species are found in a single flow class (high fidelity) and when the species

244 occurs in all sites in that class (high constancy). This analysis was conducted using Duferene-

245 Legendre indicator species analysis with the indval function in the 'Labdsv' package of R.

246   Differences in assemblages across flow classes were visualised using non-metric

247   multidimensional scaling (nMDS) based on Bray-Curtis distance matrices.

248   We then used the bioenv procedure in the vegan package in R to identify the best subset

249   of environmental variables, including flow class, that minimized the Gower distances of scaled

250   environmental variables to have the maximum rank correlation with the community dissimilarity

251   matrix (Clarke & Ainsworth 1993). Gower distances were used because the environmental

252   variables included both quantitative and categorical predictors (i.e. flow class). We added a

253   climate-based distance matrix between sites as a partial predictor in the bioenv procedure in a

254   second analysis because differences in climate may account for differences in vegetation

255   assemblages. Because SSP may covary with flow class we undertook this analysis with and

256   without flow class. Relationships between assemblage composition and significant

257   environmental variables identified from the bioenv procedure were visualised in ordination

258   space. We fitted smooth surfaces on the ordination using generalised additive models (GAM)

259   with thin plate splines using the ordisurf package in vegan. All analysis was performed in R

260   version 3.1.1 (R Development Core Team 2010).

261

262   **RESULTS**

263   Over 15 500 trees and shrubs, representing 191 species, were recorded during the

264   vegetation survey (Table S1). Exotic taxa comprised 26.5% of all individuals recorded. Riparian

265   vegetation associated with drier, inland sites was characterised by a relatively small suite of

266   species. Rainforest sites, which were particularly prevalent along coastal creeks and in the

267   northern Mary River catchment (Fig. 1), were typified by a diverse assemblage of rainforest

268   species including many not usually considered to be obligate riparian plants.

269   *Effects of flow class on vegetation*

270   Significant differences across flow classes were detected for species richness, species

271   abundance and abundance of native regeneration (D_SPECIES, D_ALL, D_REGEN_NATIVE

272   respectively), although no significant pairwise differences were detected (Fig. S1). Significant

273   differences between flow classes were detected in the distribution of three common species;

274   *Melaleuca viminalis*, *Casuarina cunninghamiana* and *Streblus brunonianus* (Fig. S2). *C.*

275   *cunninghamiana* was relatively common in flow class 1 but virtually absent from flow class 5

276   while *Streblus brunonianus* was common in flow class 3 but relatively uncommon in both flow

277   class 1 and 5. Significant pairwise differences were only found, however, for *Melaleuca*

278   *viminalis* between flow classes 2 and 5 with this species significantly less common in the latter

279   class (Tukey, p<0.005). No significant differences were found across flow classes for proportion

280   of different successional stages, proportion of woody exotic species or basal area.

281   An effect of flow class was detected for both bankfull ($F_{4, 39}$ = 3.66, p = 0.001) and near

282   stream ($F_{4, 39}$ = 2.63, p = 0.001) vegetation assemblages (Fig. S3). Site dispersion within each

283   flow class did not differ significantly between flow classes suggesting that the differences

284   detected between flow classes were due to means rather than within-class variation. Twenty-one

285   indicator species, mostly native, distinguished between vegetation assemblages of each flow

286   class (Table S2). Most of these indicator species were associated with flow class 5, four species

287   including one exotic species, *Celtis sinensis*, were associated with flow class 1 (i.e. the modified

288   flow class) and one species was associated with flow class 3 (*Streblus brunonianus*).

289   *Do other environmental variables vary across flow classes?*

290   Other environmental variables were found to vary significantly across historic flow

291   classes (i.e. annual rainfall, mean annual temperature, sand, clay, SSP and land use modification;

292 Fig. S4). Annual rainfall was significantly higher for sites in flow class 5 compared with sites in

293 flow classes 1 or 2. Proportion of clay was significantly higher in flow class 5 compared with

294 flow class 2 and SSP significantly higher in flow class 3 compared with flow class 2. Pairwise

295 differences were not detected for other metrics. No significant differences across flow classes

296 were found for bank height or the Gower metric of overall flow modification although the latter

297 tended to be higher for sites in flow class 1 compared to the other flow classes.

298 ***Effects of other environmental variables on vegetation***

299   Variation in all of the calculated vegetation metrics was overwhelmingly driven by

300 annual rainfall (Table 3). Annual temperature was also significant for D_SPECIES and

301 D_REGEN_NATIVE while bank height and proportion of clay were only significant for

302 D_SPECIES and BA_ALL_NS respectively (Table 3). None of the other environmental

303 variables had a significant influence on any of the vegetation metrics considered. Climate

304 variables were also the most important predictors of common species' abundances (Table 4). The

305 abundance of *Melaleuca viminalis* and *Casuarina cunninghamiana* were negatively related to

306 rainfall and that of *Ficus coronata* positively related to rainfall. *Cryptocarya triplinervis* and

307 *Ficus coronata* abundances were positively correlated with mean annual temperature (Table 4).

308 The abundance of the exotic species *Lantana camara* was negatively associated with the

309 proportion of clay substrate and *Melaleuca viminalis* abundances were negatively associated

310 with SPP (Table 4). For the remaining species, abundances were not significantly associated with

311 any of the environmental variables considered.

312   Multivariate analyses indicated that both bankfull and near stream vegetation

313 assemblages were most strongly correlated with annual rainfall, which varied strongly between

314 flow classes along the first ordination axis (Table 5, Fig. S5,). Annual temperature also

315   correlated significantly with ordinations of vegetation assemblages (Table 5, Fig. S5) and was

316   generally lower in flow class 1 compared with the other flow classes. Specific stream power

317   (SSP) was correlated with the ordination for bank full vegetation assemblages once the effects of

318   climate had been partialled out (Table 5, Fig. S5). The degree of hydrologic alteration, indicated

319   by the Gower metric, was also significantly correlated with the first ordination axis for near

320   stream, but not bankfull, assemblages once climate had been partialled out (Table 5, Fig. S5).

321   Other environmental variables were not identified as significant influences on riparian vegetation

322   assemblages.

323

324   **DISCUSSION**

325   The overriding influence of flow regime on riverine and riparian ecosystems has become

326   a central axiom in freshwater ecology and management (Poff *et al.* 1997; Bunn & Arthington

327   2002). Relatively few studies have addressed links between flow and riparian vegetation in

328   subtropical catchments, especially those in heavily modified landscapes where pressures

329   associated with agricultural and urban land uses may overwhelm hydro-ecological effects.

330   Furthermore, riparian vegetation in subtropical regions, in contrast to that in many arid,

331   temperate and boreal landscapes, tends to be less distinctive from adjacent upland vegetation and

332   generally comprises fewer specialised riparian species (Drucker, Costa & Magnusson 2008;

333   Heartsill Scalley, Crowl & Thompson 2009; Sirombra & Mesa 2010). Effects of stream flow on

334   riparian vegetation in subtropical landscapes may therefore be comparatively small if evident at

335   all.

336   In the agriculturally dominated catchments of subtropical southeast Queensland, we

337   found the influence of flow regime on woody riparian vegetation composition and structure to be

338 relatively weak. Indeed, the variation we detected between flow classes in structural vegetation

339 metrics, the abundance of common species and overall vegetation assemblages could be

340 explained largely by climate, particularly annual rainfall. Since rainfall co-varied strongly with

341 flow class, the relative effects of flow were difficult to isolate in our study. However, mean

342 annual temperature also emerged as a significant driver of overall riparian vegetation

343 assemblages, species richness, native regeneration and the distribution of several common

344 species, further emphasising the critical influence of local climatic variation on riparian

345 vegetation in this region. Additionally, many of the most common species recorded in these

346 riparian zones (e.g. *Cryptocarya triplinervis*) are not usually considered rheophytic and occur

347 across a range of terrestrial habitats, suggesting factors other than flow are significant in

348 determining their distributions and abundance.

349   Our results illustrate the clear overarching influence of climate on woody riparian

350 vegetation patterns in southeast Queensland. Although we detected an effect of flow class on

351 bankfull vegetation assemblages once the effect of climate had been partialled out, the

352 mechanistic role of flow is not clear from our results. Amongst the other variables considered,

353 bank height did have a significant negative influence on species richness, suggesting that access

354 to sub-surface water may play a role in shaping woody riparian vegetation composition in this

355 region.

356   Prior to this study, we hypothesised that fluvial disturbance is likely to be the main

357 mechanism via which flow influences riparian vegetation in subtropical catchments because

358 riparian zones in these landscapes are highly dynamic and prone to fluvial disturbance due to

359 their strongly seasonal stream flows and the occurrence of intense rainfall events throughout the

360 year. Conversely, effects of flow on moisture provision to riparian vegetation may be less

361 important in subtropical catchments, where water is more plentiful throughout the year than it is

362 in other climatic regions. Our measure of fluvial disturbance (specific stream power), however,

363 was only weakly correlated with bankfull vegetation assemblages and only when the effects of

364 climate had been partialled out. Furthermore no relationship with SSP was found for near bank

365 assemblages nor any of the selected riparian metrics. Stream specific power was found to be

366 significant for only one of the common species, *Melaleuca viminalis* which was negatively

367 related to stream power. *M. viminalis* is a rheophytic species found growing closely beside

368 creeks and rivers. Because of its proximity to the channel at study sites, it may be more

369 vulnerable to fluvial disturbance relative to species found further away from the channel edge.

370   Studies in other climatic regions have also failed to show effects of fluvial disturbance on

371 woody vegetation metrics (e.g. Lite, Bagstad & Stromberg 2005), despite the strong conceptual

372 basis for assuming such relationships. Descriptions of stream power determination in the

373 ecological literature, however, often belie the practical issues around estimating this parameter.

374 Stream power estimates are highly sensitive to the energy slope and the distance over which this

375 is calculated (Barker *et al.* 2009). It is possible that our field estimates of stream power based on

376 local field slopes (determined over less than 600 m stream lengths) may be capturing too much

377 local variation rather than the scale likely to influence riparian habitats (Jain *et al.* 2006).

378   Stronger relationships between flow and riparian vegetation assemblages in southeast

379 Queensland may be masked by flow modification and lagged responses of the vegetation to this

380 disturbance. Many of the species recorded in our survey are relatively long-lived (i.e. >100

381 years). Consequently, their current distribution and abundance may reflect flow conditions prior

382 to river regulation and the period for which historical records were available from which to

383 develop flow classes (i.e. post 1975; Mackay, Arthington & James 2014). Although we included

384   a measure of flow modification in our analyses, this Gower metric represents the full suite of

385   changes in flow attributes that have occurred while, individually, these changes varied in relation

386   to the type of dam, its location and its operational patterns (Mackay, Arthington & James 2014).

387   In other words, the same Gower estimate can result from alterations in different flow attributes

388   which may in turn trigger contrasting vegetation responses. Despite this, our results suggest that

389   overall flow modification, as indicated by the composite Gower metric, has had an influence on

390   the composition of near stream riparian assemblages in southeast Queensland, particularly in the

391   artificial flow class 1.

392   Somewhat surprisingly, we did not detect any effect on woody riparian vegetation

393   composition or structure of agricultural land use intensity (measured as proportional area) in the

394   surrounding catchment. Since all of the sites had a relatively large proportion of their catchment

395   under agriculture (i.e. mostly >45 % with only 4 sites having less than 45% of land use

396   modified), it is possible that riparian vegetation assemblages have been similarly affected by land

397   use across the region. Our results imply that even sites within the least disturbed catchments may

398   be affected by distal land uses and overall catchment modification in the region, potentially via

399   macro-ecological processes, e.g. teleconnections (McCluney *et al.* 2014). Land use intensity and

400   associated changes in land cover especially, are also very likely to have contributed, in addition

401   to dams and weirs, to overall modification of flow regimes in the region and, in turn, its effects

402   on riparian vegetation (Mackay et al. 2014).

403   Research on forest ecology in tropical and subtropical regions is hampered by their sheer

404   complexity and diversity (Pyke *et al.* 2001). In riparian habitats, the challenges of conducting

405   vegetation surveys are further compounded by the difficulty of acquiring complementary

406   hydrologic and hydraulic data as well as data for other significant environmental variables (e.g.

407   soil type, land use and clearance history etc.) with which to interpret floristic patterns. As a

408   result, relatively few studies have attempted to relate such a broad suite of potential drivers to

409   riparian vegetation in subtropical catchments. Our results highlight some of the difficulties in

410   determining hydro-ecological relationships in these landscapes, especially with regard to

411   disentangling the effects of multiple, co-varying drivers - in this case, climate and hydrology.

412   Controlled experiments, including those conducted as part of an adaptive management strategy,

413   may therefore be required, in addition to vegetation surveys, to better inform environmental flow

414   planning in such complex systems (Poff *et al.* 2003). A functional, trait-based approach to

415   understanding vegetation patterns in relation to flow classes and other drivers may also prove

416   informative (Burton, Samuelson & Mackenzie 2009; Merritt *et al.* 2010).

417

424

425   **Data accessibility**

426   Species and environmental data for each site: https://tropicaldatahub.org/

427

428

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566

567

568   **Table 1.** Descriptions of flow regimes characterizing each historic flow class (adapted

569   from Mackay et al. 2014).

570

Flow class	Description
1	(artificially) Perennial flow regime / high groundwater contribution to base flow, high 1 day annual maxima and constancy of mean daily discharge, relatively low magnitude of the 1 and 10 year annual return interval flood
2	Peak discharge in late summer and secondary peak in late autumn, high % zero flow days (~100), high spell duration and very low discharge magnitude
3	Peak discharge in late summer, secondary peak in autumn, relatively invariant in terms of major discriminating metrics, rapid flow recession at low flow end of flow duration curve
4	High variation in Mean number of zero flow days per but otherwise similar to Flow Class 2
5	Discharge late summer dominated, high discharge magnitude per unit catchment area, low discharge constancy

571

572 **Table 2**. Descriptions of vegetation metrics used in the analyses.

573

Metric	Description
D_SPECIES	Species richness per ha
D_ALL	Abundance of trees and shrubs per ha
EARLYPER	Proportion of early successional species
INTERPER	Proportion of intermediate successional species
LATEPER	Proportion of late successional species
EXOTICPER	Proportion of exotic trees and shrubs
D_REGEN_NATIVE	Abundance of native regenerating (DBH <10cm) trees and shrubs per ha
BA_ALL	Basal area of trees and shrubs per ha

574

575   **Table 3.** Significant parameters of best model for riparian metrics for full bank and near stream (with suffix NS).

576

Riparian metric	A_RAIN		A_TEMP		BANK.HT		CLAY	
	Estimate	Std. error	Estimate	Std. error	Estimate	Std. error	Estimate	Std. error
D_SPECIES	0.0142***	0.004	0.011**	0.0037	-0.010*	0.004		
D_ALL	12.933**	3.824						
D_REGEN_NATIVE	13.904***	3.314	9.209**	3.314				
BA_ALL	0.631*	0.299						
D_SPECIES_NS	0.025**	0.008						
D_REGEN_NATIVE_NS	10.207*	4.020						
BA_ALL_NS							0.199**	0.068

577   *$***p < 0.001$, $**p<0.01$, $*p<0.05$*

578

579 **Table 4.** Significant parameters of best model for riparian species abundances

580 (log+1 transformed) for full bank data.

581

Species	A_RAIN		A_TEMP		CLAYS		SPP	
	Estimate	Std. error	Estimate	Std. error	Estimate	Std. error	Estimate	Std. error
Mel_vim	-1.76***	0.35					-0.77*	0.33
Cas_cun	-1.12***	0.31	-0.86**	0.29				
Cry_tri			1.49***	0.41				
Fic_cor	1.01**	0.31	0.75*	0.30				
Str_bru			0.91*	0.43				
Lan_cam					-0.61*	0.30		

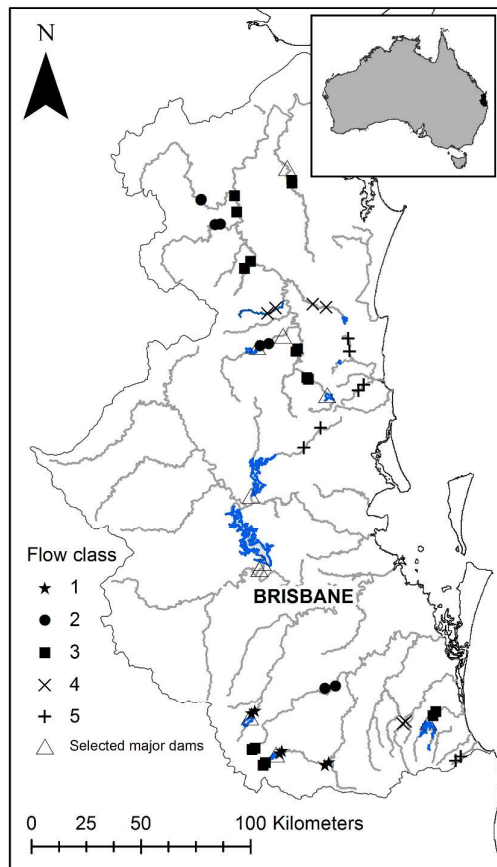582 ****p < 0.001, **p<0.01, *p<0.05*

583

584   **Table 5**. BIOENV results showing the correlation of combinations of

585   environmental variables with riparian vegetation assemblages.

586

Vegetation dataset	Environmental variables	Correlating variables	Correlation
Bankfull	Full set	A_RAIN, A_TEMP	0.47
	Climate partialled out	FLOW CLASS, SPP	0.13
	Climate partialled out, without flow class	SSP	0.06
Near stream	Full set	A_RAIN, A_TEMP	0.36
	Climate partialled out	FLOW CLASS, GOWER	0.09
	Climate partialled out, without flow class	GOWER	0.08

587

588   **Figure1.** The south east Queensland study region and site locations. Grey lines

589   are major rivers and the solid black line is the study extent.

590

591