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1 **TITLE** Biogeographic determinants of Australian freshwater fish life-history indices assessed within a  
2 spatio-phylogenetic framework

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16

17 **RUNNING TITLE** Functional composition of Australian fish assemblages

18

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24 **ABSTRACT**

25 **Aim** This study aims 1) to quantify broad scale patterns of functional diversity and life-history  
26 strategies of freshwater fish in relation to environmental variation across Australian river basins; and  
27 2) identify key life-history traits associated with species extinction risk in order to determine how  
28 fish communities and extinction prone species may respond to future environmental change.

29 **Location** 123 river basins across eastern-Australia

30 **Methods** Based on 10 key life-history traits for 194 freshwater fish we used a novel analytical  
31 approach to quantify multivariate life-history indices in relation to environmental variation within a  
32 spatio-phylogenetic framework. We assessed the utility of our analytical framework by contrasting  
33 final models against best performing candidate models from both and quantified the degree of  
34 autocorrelation in all model residuals.

35 **Results** Temperature, habitat heterogeneity/availability, flow variability, and primary productivity  
36 accounted for between 55 % and 80% of the variation in life-history indices. Best performing models  
37 were all derived from the addition of spatial and phylogenetic co-variates to the analytical  
38 framework which consistently produced more parsimonious final models with higher explanatory  
39 power and insignificant levels of autocorrelation in the model residuals.

40 **Main conclusion** The life-history functional diversity of fish assemblages and the composition of life-  
41 history strategies across Australian river basins is in-part determined by environmental variability,  
42 stability and seasonality which highlights both the importance of environmentally driven community  
43 assembly processes and the potential changes to freshwater fish biodiversity in response to climate  
44 change. A spatio-phylogenetic analytical framework is a key component of effectively managing  
45 autocorrelation in ecological data and for deriving more rigorous trait-environment relationships.

## 46 INTRODUCTION

47 The need to understand the potential impacts of anthropogenic changes on biological communities  
48 and ecosystems continues to grow in light of increasing evidence suggesting that landscape and  
49 climate change are among the major threats to species extinction and global biodiversity (Olden *et al.*, 2010). Recent evidence suggests that freshwaters are among the most endangered ecosystems  
50 worldwide (Vörösmarty *et al.*, 2010). Threats to freshwater biodiversity from flow modification,  
51 water pollution, species invasions and habitat degradation emphasize the importance of  
52 understanding the functional links between species and their environment and the ability to predict  
53 community response to environmental change (Mouillot *et al.*, 2013).

55 Functional traits (characteristics of an organism that are linked with its fitness or  
56 performance) can provide a mechanistic basis to understand and predict patterns of community  
57 composition across gradients of environmental variation (Poff *et al.* 2006). Quantifying trait-  
58 environment relationships can, therefore, be useful for quantifying biogeographic patterns of  
59 species distribution and for predicting the functional change in biotic communities in response to  
60 changing environmental conditions. Life-history traits have been shown to be particularly good  
61 predictors of extinction-colonisation dynamics and for understanding the effects of environmental  
62 filtering (Olden *et al.*, 2006; Erös *et al.*, 2009). The presence or absence of a species in a given  
63 location (i.e. community assembly) is related to its ability to survive under existing abiotic and biotic  
64 conditions (i.e. species fitness) and is largely a product of life history traits relating to survival,  
65 reproductive success and population growth (Frimpong & Angermeier, 2010). Based on mechanistic  
66 life history trade-offs among these components, and on observed patterns of life history variation in  
67 fish, three reproductive strategies have been identified as endpoints of a triangular continuum  
68 resulting from adaptive responses to environmental conditions: periodic, opportunistic and  
69 equilibrium (Winemiller, 2005). These strategies optimize fitness within environmentally predictable,  
70 unpredictable and stable systems, respectively.

71 Life-history theory, therefore, offers explicit predictions regarding the relationships between  
72 the extant distribution of life-history strategies and the environment that may be useful for  
73 identifying the potential response of communities to environmental change. Studies concerned with  
74 patterns of biodiversity have increasingly focused on the use of functional diversity indices to  
75 quantify the range and value of organismal traits in a given assemblage and highlight their potential  
76 response to gradients of environmental variation (Kraft & Ackerly, 2010; Schleuter *et al.*, 2010;  
77 Mouilott *et al.*, 2013). Indeed, there is a growing body of literature demonstrating the relationship  
78 between aspects of functional diversity and variation in climatic factors such as temperature and  
79 precipitation (e.g. Pool *et al.*, 2010; Schleuter *et al.*, 2012), habitat heterogeneity/availability (e.g.  
80 Erös *et al.*, 2009; Villegger *et al.*, 2010) and flow variability (e.g. Olden *et al.*, 2006; Pease *et al.*, 2012).  
81 These studies provide important insight into the functional links between the environment and  
82 community driven ecosystem processes. Quantifying these measures of assemblage diversity and  
83 resilience to change in terms of key life-history traits known to influence species survival,  
84 reproductive success and population growth could potentially identify novel life-history trait-  
85 environment relationships and provide greater insight into the potential response of focal  
86 assemblages to environmental change.

87 This study aims to: 1) quantify broad scale patterns in the life-history functional diversity of  
88 freshwater fish assemblages in relation to environmental variation across Australian river basins. We  
89 anticipate that measures of freshwater fish life-history functional diversity will be related to  
90 variation in climatic factors, habitat heterogeneity/availability, and flow variability across Australian  
91 river basins; and 2) quantify broad scale freshwater fish life-history strategy-environment  
92 relationships across Australian river basins. We anticipate that periodic, opportunistic and  
93 equilibrium life-history strategies will be related to aspects of environmental predictability,  
94 unpredictability and stability, respectively (Winemiller, 2005). We achieve these aims using a novel  
95 analytical approach to quantify multivariate life-history indices in relation to environmental variation  
96 within a spatio-phylogenetic framework to account for autocorrelation in the modelling procedure.

97 Our approach has general applicability to a range of ecological disciplines and emphasises a holistic  
98 functional perspective based on multivariate combinations of life-history traits to define key trait-  
99 environment relationships in light of future environmental change.

100

## 101 **METHODS**

102

### 103 **Study area, fish distribution and functional trait information**

104 We assembled functional trait information for freshwater fish occurring in 123 river basins within six  
105 primary Australian drainage divisions: North-East Coast, South-East Coast, Murray-Darling Basin,  
106 Lake Eyre Basin, Timor Sea, and Gulf of Carpentaria. The region encompasses 4,300,000 km<sup>2</sup> (56%) of  
107 the Australian continent and is characterised by a diversity of landforms, climate, flow regimes, and  
108 aquatic habitat types. The region also contains over 90% of the freshwater fish species found in  
109 Australia (the majority of the remainder belonging to the family Galaxiidae and occurring in the  
110 Tasmanian drainage division) (Allen *et al.*, 2003)

111 We collated present day species distribution data for 194 native freshwater fish species (35  
112 families and 81 genera) using information from published sources (Allen *et al.*, 2003; Pusey *et al.*,  
113 2004; Lintermans, 2007; Unmack 2013) and our own unpublished surveys. Following Allen *et al.*  
114 (2003), we define a freshwater fish as one that can reproduce in freshwater and those diadromous  
115 species that spend the majority of their life cycle in fresh waters.

116 We quantified 10 life-history traits based on our current state of knowledge and the  
117 information available for the majority of focal species. These traits described longevity, age at  
118 maturation (female), length at maturation (female), spawning substrate, spawning frequency,  
119 reproductive guild (following Balon, 1975), total fecundity, egg size, degree of parental care (PC)  
120 (following Winemiller, 1989), and maximum length (Table 1). Trait assignments were based on  
121 multiple sources of information including species accounts in comprehensive texts (i.e. McDowall,  
122 1996; Allen *et al.*, 2003; Pusey *et al.*, 2004; Lintermans 2007) and species descriptions from the

123 primary literature. In a few cases, this information was supplemented with information from state  
124 agency reports, university reports and graduate theses and, electronic databases available on the  
125 World Wide Web (e.g. FishBase). All trait information was assigned based on a majority of evidence  
126 rule with preference given to adult female measurements where possible (see Olden & Kennard,  
127 2010 for more details on trait assignments). Ordinal data were assigned a single trait state and  
128 median values were recorded when ranges were presented for continuous data. Existing information  
129 for species traits can be confounded by imprecise measurement, inconsistency among  
130 measurements and studies, missing data, intraspecific variation in trait expression and ontogeny.  
131 Where such issues arose we employed our own expert knowledge to assign trait values (as per  
132 Tedesco & Hugueny, 2006; Sternberg and Kennard 2013a, 2013b).

133

#### 134 **Functional diversity indices, life-history strategies**

135 We investigated two independent facets of functional diversity: functional dispersion (FDis) and  
136 functional evenness (FEve) based on life-history trait information. Although a range of functional  
137 diversity indices exist, we chose FDis and FEve because they are unaffected by species richness, not  
138 affected by outliers, and have no loss of information associated with reduced space ordination and  
139 subsequent calculation (Villegger *et al.*, 2008; Laliberte & Legendre, 2010). Further, fish life-history  
140 traits have been shown to be particularly good predictors of extinction-colonisation dynamics and  
141 for understanding the effects of environmental filtering (Olden *et al.* 2006; Erös *et al.* 2009). Life-  
142 history FDis and FEve are thus appropriate for our aim to quantify patterns of life-history functional  
143 diversity across gradients of environmental variation and infer community vulnerability to potential  
144 environmental change. We computed functional diversity using the FD package and the function  
145 dbFD (Laliberte & Legendre, 2010) in R version 2.14.0 (The R Foundation for Statistical Computing  
146 2011). Firstly, a principle coordinates analysis (PCoA) was performed on a square-root corrected  
147 species-species Gower distance matrix, wherein the resulting PCoA axes were used to calculate FEve  
148 for each river basin as per Villegger *et al.* (2008). Secondly, FDis for each basin was computed from

149 the uncorrected species-species Gower distance matrix with negative eigenvalues corrected  
150 following the approach of Anderson (2006). Given that our species had equal abundances (i.e.  
151 presence-absence), FDis was simply computed as the average distance of each species to the  
152 centroid of all species as originally described by Anderson (2006) as a measure of multivariate  
153 dispersion.

154         As per Winemiller and Rose (1992), we plotted species position in trivariate life-history space  
155 according to three major axes of strategy variation: 1) ln length at maturation; 2) ln total fecundity;  
156 and 3) investment per progeny calculated as  $\ln(\text{egg size} + 1) + \ln(\text{parental care} + 1)$ . We then  
157 assigned each species to one of three life-history strategies (opportunistic, periodic, or equilibrium)  
158 by selecting the minimum Euclidean distance from each species' position to each endpoint strategy  
159 (Olden & Kennard, 2010). These endpoints were defined by: opportunistic (minimum fecundity,  
160 minimum juvenile investment, and minimum maturation size), periodic (maximum fecundity,  
161 minimum juvenile investment, and maximum maturation size), and equilibrium (mean fecundity,  
162 maximum juvenile investment, and maximum maturation size). These calculations were performed  
163 on normalised trait values to ensure equal contribution from each of the three life-history  
164 parameters (Olden & Kennard, 2010). We then calculated the number of species in each river basin  
165 of a given life-history strategy as a proportion of river basin level species richness to give the  
166 proportion of each life-history strategy in each river basin.

167

168

### 169 **Environmental characterisation of river basins**

170 Basin level environmental variables were chosen *a priori* based on their demonstrated relationship  
171 with functional diversity and fish life-history strategies (e.g. Winemiller & Rose, 1992; Mason *et al.*,  
172 2005; Olden & Kennard, 2010; Schleuter *et al.*, 2012) and their sensitivity to potential climate change  
173 (e.g. Hobday & Lough, 2011). For each river basin, we quantified six environmental variables that  
174 describe extant habitat availability (stream density and river basin area), climate (basin average



175 annual mean temperature), productivity (basin average net terrestrial primary productivity) and  
176 hydrology (mean annual runoff magnitude and variability) using the National Catchment and Stream  
177 Environment Database at the 1:250,000 scale (Stein, 2012) (Table 2). We also chose to exclude river  
178 basin species richness as a predictor variable after additional analysis for the model validation and  
179 sensitivity analysis showed that total species richness was not selected for in our final models or in  
180 the best supporting models. We normalised all environmental variables prior to analysis and tested  
181 for collinearity by calculating the variance inflation factor (VIF). All variables in the final analysis had  
182 a VIF less than 5 (VIF values greater than 10 indicate strong collinearity; Quinn & Keough, 2002).

183

184 **Quantifying environmental correlates of spatial variation in functional diversity indices and life**  
185 **history strategies**

186 Multiple linear regression was used to relate basin-scale measures of functional diversity indices and  
187 life history strategies with environmental variables. Prior to this analysis, we recognised that  
188 autocorrelation (i.e. non-independence of samples related in space, time or phylogenetic history) in  
189 traits-based comparative analyses is a commonly encountered ecological phenomenon (reviewed in  
190 Dormann *et al.*, 2007). Trait-environment analyses are particularly prone to both spatial and  
191 phylogenetic autocorrelation because fish communities tend to be more similar in neighbouring  
192 river basins than distant basins (e.g. due to biogeographic filtering), and trait characteristics are  
193 more similar in closely related species than in those from disparate phylogenetic backgrounds.  
194 Methods that extract eigenvectors from a matrix of spatial, temporal or phylogenetic information to  
195 be included as synthetic predictor variables in a modelling procedure are capable of reducing  
196 autocorrelation in model residuals and explaining additional spatial/evolutionary variation  
197 associated with trait-environment relationships.

198 We used this procedure to account for spatial and phylogenetic autocorrelation in the  
199 patterns of functional diversity and the distribution of life-history strategies across Australian river  
200 basins (see Fig. 1). Following Kuhn *et al.* (2009), we used a combination of spatial and spatio-

201 phylogenetic eigenvector filtering to reduce the residual autocorrelation in a multiple linear  
202 regression model to predict the functional response variables. This procedure begins by introducing  
203 a species by phylogeny matrix (**P**), a species by river basin matrix (**S**), a species by trait matrix (**T**), a  
204 matrix of spatial coordinates (**C**) and a matrix of environmental variables per basin (**E**) (Fig. 1). To  
205 construct **P**, a taxonomic phylogeny of Australian freshwater fish was generated as a rooted  
206 neighbour-joining tree with unity branch lengths and polytomies at lower taxonomic resolutions  
207 (Sternberg & Kennard, 2013a). The phylogenetic relationships among extant species were  
208 reconstructed with taxonomic information because detailed genetic information was unavailable for  
209 the majority of Australian fish species. This is an appropriate method when branch length  
210 information is missing (Schweiger *et al.*, 2008). The patristic distance from each species to the root  
211 of this phylogeny was then extracted to give an estimate of the level of divergence in each species  
212 from a common ancestor (Fig. 1). To construct **C**, we recorded the latitude and longitude of each  
213 river basin outlet to generate a matrix of spatial distances (Fig. 1). As stream capture is considered to  
214 be a relatively rare event and not a major determinant of extant freshwater fish distributions in  
215 Australia (Unmack, 2013), we considered it more appropriate to use basin outlet as a measure of  
216 potential historic connectivity among river basins (e.g. via formerly connected river networks at  
217 lower sea levels). **S**, **T** and **E** matrices were constructed as per the methods outlined in previous  
218 sections. A matrix of response variables (**U**; functional diversity indices, and the proportion of each  
219 life-history strategy, for each river basin) was also generated from the **S** and **T** matrices as per the  
220 methods outlined in previous sections and checked for normality to satisfy the assumptions of the  
221 multiple linear regression procedure. A matrix of phylogenetic distances among river basins (**M**) was  
222 constructed by multiplying the **P** and **S** matrices to produce a matrix of spatially structured  
223 phylogenetic information (Fig. 1) (Kuhn *et al.*, 2009). This matrix was then subjected to a principle  
224 coordinates analysis (PCoA) on a double-centred Euclidean distance matrix (Diniz-Filho *et al.*, 2012)  
225 and the resulting eigenvectors that were significantly correlated with the chosen response variable  
226 (**U**) were retained for inclusion in the final modelling procedure (Diniz-Filho *et al.*, 2009) (Fig. 1). This

227 selection procedure is an appropriate method given that orthogonal eigenvectors are uncorrelated  
228 with each other and it is possible to control for over fitting parameters in the final model with the  
229 Moran's I coefficient. Purely spatial eigenvector filtering followed a similar method to above,  
230 however, geographic coordinates were first converted to a binary connectivity matrix using  
231 Delaunay triangulation and globally standardised (C-scheme; Thayn & Simanis, 2014) to produce a  
232 centred connectivity matrix (Griffith & Peres-Neto, 2006). Prominent eigenvectors were then  
233 selected using an iterative semi-parametric procedure that derives a single eigenvector reducing the  
234 standard variate of Moran's I for regression residuals most, and continuing until no candidate  
235 eigenvector reduces the value by more than 0.1 using the function 'SpatialFiltering' in the R package  
236 'spdep' (R; v2.14.0; The R Foundation for Statistical Computing, 2011). Moran's I values typically  
237 range between 1 and -1 where departures from 0 indicate either positive or negative  
238 autocorrelation in the residuals from the full model and tend to indicate that too few, or too many  
239 eigenvectors have been selected from the filtering procedure, respectively. Finally, the chosen  
240 subset of spatial and spatio-phylogenetic eigenvectors were checked for collinearity (and removed  
241 where appropriate) and added to the multiple linear regression model as co-variables to account for  
242 the inherent levels of spatial and phylogenetic autocorrelation in the response variable (**U**) (Fig. 1).

243 To avoid overfitting we tested the relationship between environmental predictor variables  
244 and river basin functional diversity and life-history strategy composition in the multiple linear  
245 regression using a variable subset selection procedure. Initially, all environmental predictor variables  
246 were normalised prior to analysis to remove the influence of units of measure. We then performed  
247 an exhaustive model selection procedure (Quinn & Keough, 2002) and employed the Bayesian  
248 Information Criterion (BIC) to inform the best-performing model for each response variable using the  
249 function 'regsubsets' in the R package 'leaps'. Spatial and spatio-phylogenetic eigenvector filters  
250 were forced into the exhaustive selection procedure so that only the best subset of additional  
251 environmental predictors was chosen. The BIC was chosen because it provides a more robust test of

252 model support and protects from overfitting by penalising models based on the number of predictor  
253 variables (Quinn & Keough, 2002).

254 We used the change in BIC ( $\Delta$ BIC) to assess the utility of our final model by quantifying  
255 the difference between the best approximating model and all models with similar levels of  
256 support (i.e.  $\Delta$ BIC <2; *sensu* Burnham and Anderson 2002).

257

## 258 **Model validation**

259 We assessed the validity of including a spatio-phylogenetic filtering procedure in our  
260 analytical framework by performing classical multiple linear regression excluding  
261 autocorrelative terms. The MLR model selection procedure followed an exhaustive search  
262 among all possible combinations of predictor variables (Quinn and Keough 2002) with the  
263 best approximating model chosen by minimising the BIC. We then quantified the amount of  
264 autocorrelation in the best approximating model residuals by calculating the Moran's I  
265 coefficient. A significant amount of residual autocorrelation was estimated using the  
266 standard deviate of Moran's I at the  $\alpha=0.05$  significance level.

267 We used the change in BIC ( $\Delta$ BIC) to assess the utility of our final models by  
268 quantifying the difference between the best approximating model and all models, both with  
269 and without the eigenvector filtering procedure, with similar levels of support (i.e.  $\Delta$ BIC <2;  
270 *sensu* Burnham and Anderson 2002).

271

272

## 273 **RESULTS**

### 274 **Spatial patterns of functional diversity and life-history strategy composition**

275 Life-history indices varied markedly among river basins (Fig. 2). Life-history FDis was highest  
276 in eastern and south-eastern coastal river basins and lowest in inland and some north-west  
277 coastal basins (Fig. 2a). Life-history FEve was lowest in inland river basins and smaller  
278 coastal basins across the north. Highest values of life-history FEve occurred in southern  
279 coastal draining river basins (Fig. 2b). Classification of life-history strategies of Australian fish  
280 species in this study showed that >60% show an affinity for the opportunistic strategy,  
281 around 25% with the periodic strategy and <15% with the equilibrium strategy. Inland river  
282 basins contained a higher proportion of fish associated with the 'opportunistic' life-history  
283 strategy, while south-east and northern coastal draining river basins appeared to have the  
284 lowest proportion of opportunistic strategists (Fig. 2c). The proportion of periodic species in  
285 each river basin was highest in coastal south-east river basins and lowest in river basins  
286 scattered throughout inland and some northern coastal draining river basins (Fig. 2d).  
287 Species associated with the 'equilibrium' strategy were more common in coastal draining  
288 river basins across the northern tropics and less common in some inland and south-east  
289 river basins (Fig. 2e).

290

### 291 **Environmental correlates of functional diversity and life-history strategy composition**

292 After accounting for spatial and spatio-phylogenetic autocorrelation, the multiple linear regression  
293 and BIC variable selection procedure revealed strong relationships between environmental predictor  
294 variables and life-history indices (Table 3). FDis was negatively associated with river basin area and  
295 temperature, and positively associated with NPP, runoff and inter-annual flow variability (CV)  
296 (Adjusted  $R^2 = 0.591$ ;  $p < 0.001$ ; Table 3). FEve was positively associated with basin area and CV, and  
297 negatively associated with temperature, NPP (Adjusted  $R^2 = 0.800$ ;  $p < 0.001$ ; Table 3). River basins  
298 containing proportionally more opportunistic strategists were positively associated with basin area,

299 temperature and NPP, and negatively associated with runoff and CV (Adjusted  $R^2=0.564$ ;  $p<0.001$ ;  
300 Table 3). The proportion of periodic strategists was significantly higher in river basins with smaller  
301 area, low temperature and higher inter-annual flow variability (CV) (Adjusted  $R^2=0.786$ ;  $p<0.001$ ;  
302 Table 3). Equilibrium strategists appeared significantly more common in river basins characterised by  
303 small area, low stream density, low NPP and high runoff (Adjusted  $R^2=0.684$ ;  $p<0.001$ ; Table 3).

304 The number of eigenvectors included in the multiple linear regressions as spatial and spatio-  
305 phylogenetic filters ranged between 9 and 16. Residual autocorrelation, quantified by the Moran's I  
306 coefficient in the final model, was low, ranging between -0.060 and 0.014. Thus, the eigenvector  
307 filtering procedure effectively reduced autocorrelation while only slightly over-fitting the multiple  
308 linear regression model (Table 3).

309

### 310 **Model Validation**

311 Classical multiple linear regression excluding autocorrelative terms yielded relatively similar  
312 estimates for the partial regression coefficients with the rejection of a number of environmental  
313 predictors in the best supporting models (Table 4). Estimates of the Moran's I standard deviate were  
314 all high and significant suggesting there was a large amount of residual spatial and/or phylogenetic  
315 autocorrelation in the final models where eigenvector filters were excluded (Table 3).

316 Comparisons among the best supporting models, both with and without autocorrelative  
317 terms, indicated that FDis and FEve each had two and four supporting models, respectively, while  
318 the proportion of opportunistic, periodic and equilibrium species were supported by a single best  
319 performing model each (Table 5). All best performing models and models with similar levels of  
320 support were derived from the spatio-phylogenetic filtering procedure suggesting that this analytical  
321 framework consistently produced the most parsimonious models (i.e. lowest BIC) (Table 4).

322

323

### 324 **DISCUSSION**

325 Evaluating and predicting the potential impacts of anthropogenic changes on ecological communities  
326 is a major conservation challenge given the growing threats to global biodiversity and species  
327 extinction (Olden *et al.*, 2010). Central to this challenge is quantifying the ways in which life-history  
328 indices respond to environmental variation. We show that gradients of variation in temperature,  
329 habitat heterogeneity, flow variability, and primary productivity are strongly related to variations in  
330 the life-history functional diversity of Australian freshwater fish communities and highlight a number  
331 of strong life-history strategy-environment relationships that provide a basis to understanding the  
332 associations between life-history traits, environmental variation, and species conservation. This  
333 study is the first to quantify multivariate functional diversity and life-history strategy indices in  
334 relation to environmental variation within a spatio-phylogenetic framework and has advanced our  
335 understanding of the relationship between patterns of assemblage composition and broad-scale  
336 environmental variation.

337         Functional dispersion is a multivariate measure of the range of life-history traits present in a  
338 community and has been linked with community resistance to disturbance (Anderson *et al.*, 2006).  
339 In this study, we found that higher functional dispersion was observed in sub-tropical and temperate  
340 coastal river basins and was associated with relatively smaller basins with lower temperatures and  
341 greater NPP, runoff and inter-annual variability in flows. High productivity, runoff and flow variability  
342 likely increases the available niche space in these areas thus supporting a greater diversity of life-  
343 history traits in those river basins. Long-term variation in environment conditions applies differential  
344 selection pressure on species compositions, eventually removing those species with the life-history  
345 traits that do not confer an advantage from the regional pool (Sternberg & Kennard, 2013b). It  
346 follows that river basins with a diversity of life-history traits will have a higher capacity to withstand  
347 this selection pressure ultimately conferring greater assemblage stability in response to future  
348 environmental change. In Australian river basins, low levels of functional dispersion were observed  
349 in inland river basins, particularly through Australia's arid centre. This suggests that a relatively  
350 narrow range of life-history traits confer an advantage for species responding to the inherent

351 environmental variability typical of these systems (Balcombe & Arthington, 2009) and that fish  
352 communities may have a reduced potential to resist long term changes to this variability as a result  
353 of future environmental change.

354           Functional evenness measures the regularity of the distribution of species in functional  
355 space for a given community (Villegger *et al.*, 2010; Mouilott *et al.*, 2003). Low values of functional  
356 evenness are associated with under-utilisation of available niches, a decreased capacity to withstand  
357 non-native species invasions and a decreased resilience to disturbance (Dukes, 2001; Mouilott *et al.*  
358 2013). Low functional evenness of life-history traits was observed in inland river basins as well as a  
359 number of smaller coastal river basins across the tropical north and was associated with smaller  
360 basins with lower inter-annual flow variability, relatively warmer temperatures and higher NPP. In  
361 inland river basins, reduced niche realisation may be the product of irregular disturbance events that  
362 typically take the form of unpredictable high discharge events and floodplain inundation of short to  
363 medium duration (days to weeks) coupled with long durations (months to years) of severe dry  
364 periods (Bunn *et al.*, 2006). These natural but unpredictable cycles of wetting and drying may act to  
365 exclude many of those species with combinations of life-history traits that are disadvantageous in  
366 this environmental setting, such that, fish communities in these areas may resemble a cluster of  
367 functionally redundant species that share similar life-history characteristics and relatively few  
368 species with functionally unique life-history strategies (Buisson *et al.*, 2013). The loss of one or more  
369 of these unique species may have important consequences for broader ecosystem process (i.e. key-  
370 stone species) and patterns of regional biodiversity. Further, these areas may be at greater risk from  
371 non-native species invasion by virtue of under-utilised niche spaces in the fish assemblages. Indeed,  
372 many studies have highlighted the potential for alien species invasion in arid systems such as the  
373 Lake Eyre Basin and portions of the Murray-Darling Basin (Lintermans, 2007; Olden *et al.*, 2008;  
374 Kerezszy & Fensham, 2013).

375           Life-history strategy composition of river basins varied markedly between the three end-  
376 point strategies along gradients of environmental variation across the study area. Our results



377 showed that habitat availability, temperature, net primary production and runoff were important for  
378 explaining variation in the frequency and distribution of life-history strategies in Australian river  
379 basins. These life-history strategy-environment relationships highlight the importance of  
380 environmental selective forces for structuring fish communities across the landscape and provide  
381 insight into the potential mechanisms responsible for shaping broad-scale fish biodiversity in  
382 Australia. The proportion of opportunistic strategists was highest in larger, more productive river  
383 basins with higher temperatures, lower runoff and inter-annual variability in flows such as those  
384 located throughout inland Australia and some smaller coastal basins along much of the north-east  
385 coast. This result confirms the expectation that 'opportunistic' strategists occur more frequently in  
386 unpredictable environments where high temperature and productivity, but reduced runoff and  
387 inter-annual flow variability may facilitate the rapid colonisation and population growth that is  
388 typical of these strategists in temporally variable systems (Winemiller, 2005; Balcombe & Arthington,  
389 2009). We also found a high proportion of 'equilibrium' strategists in smaller, wetter, northern  
390 coastal river basins draining into the Gulf of Carpentaria that were associated with a decrease in  
391 stream-density and net primary production. These river basins are typically low gradient, where a  
392 reduction in stream density likely results in reduced floodplain drainage and an increase in floodplain  
393 wetland habitats. An increase in the proportion of 'equilibrium' species is expected in these habitats  
394 given that these strategists maximise fitness in hydrologically stable environments by increasing  
395 their investment in juvenile survivorship in response to low food resource availability and increased  
396 predator-prey interactions (Winemiller, 2005). 'Periodic' species richness was highest in smaller,  
397 cooler, and more hydrologically variable river basins which may reflect spatial (patchiness) and  
398 temporal (seasonality) heterogeneity across the study area. These species maximise fitness by  
399 allocating reproductive effort across multiple generations where some individuals achieve  
400 reproductive success despite long intervals where environmental conditions are unfavourable for  
401 juvenile survival (Winemiller, 2005).

402           Quantifying the environmental determinants of biogeographic patterns in life-history  
403 functional diversity and basin scale life-history strategy composition across Australian rivers is a key  
404 step toward identifying species extrinsic threats and potential extirpations in response to future  
405 environmental change. Our analyses showed that including spatial and phylogenetic eigenvectors in  
406 the modelling procedure was an effective means of reducing both residual autocorrelation and  
407 identifying the most parsimonious candidate models. However, we recognise that there are a  
408 number of alternative analytical frameworks for linking environmental filtering and community  
409 assembly (e.g. Pillar & Duarte 2010; Pavoine et al. 2011; Peres-Neto *et al.*, 2012). Our approach  
410 recognises the importance of considering both spatial and phylogenetic determinants of the  
411 distribution of ecological communities (Sternberg & Kennard, 2012b). As such, our results provide a  
412 prospective, yet exciting, investigation into a number theoretically founded life-history trait-  
413 environment relationships with generalizable key findings to inform species conservation in light of  
414 future environmental change.

415           Our analytical framework has allowed us to show that habitat availability, climate,  
416 productivity and hydrological stability, unpredictability and seasonality are important determinants  
417 of basin scale biogeographic patterns in life-history indices that warrant further consideration.  
418 However, the contribution of biogeographic factors such as historical patterns of connectivity and  
419 dispersal, and vicariance processes to the functional composition of river basins should not be  
420 overlooked. Australia has a long history of isolation from other continents, which, when coupled  
421 with increasing aridity and flow unpredictability, has contributed to a high rate of endemism among  
422 major geographic provinces and relative to other continental fish faunas (Unmack 2013). As a result,  
423 the functional composition of fish communities and the unique associations of life-history traits  
424 (particularly in the endemic species) typical of the Australian fish fauna are likely evolved to  
425 maximise ecosystem function and species fitness in relation to natural variation in environmental  
426 predictability, stability and seasonality (Winemiller and Rose 1992). Quantifying key life-history trait-  
427 environment relationships and any potential intrinsic threats to endangered species will ultimately

428 help identify potential changes to community composition in response to future changes in these  
429 environmental conditions.

430 This study is the first to quantify multivariate life-history indices in relation to environmental  
431 variation within a spatio-phylogenetic framework and has advanced our understanding of the  
432 relationship between patterns of fish assemblage composition and broad-scale environmental  
433 variation. Our results show that the diversity and evenness of life-history traits in fish communities is  
434 related to temperature, productivity and hydrological variation and may confer greater resistance  
435 and/or resilience to future environmental change in some fish assemblages. We have also shown  
436 that the composition of life-history strategies across Australian river basins differs in relation to  
437 environmental variability, stability and seasonality and that these patterns highlight both the  
438 importance of environmentally driven community assembly processes and the potential changes to  
439 freshwater fish biodiversity in response to climate change.

440

441

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582



583 **BIOSKETCH**

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588 [institute/members/hdr-students/mr-david-sternberg](http://www.griffith.edu.au/environment-planning-architecture/australian-rivers-institute/members/hdr-students/mr-david-sternberg)

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595 **Stephen Balcombe** is a research fellow at the Australian Rivers Institute, Griffith University,  
596 Brisbane, Australia. His main research interests are associated with the persistence of freshwater  
597 fish in arid and semi-arid regions and the influence of trophic relationships, body condition, juvenile  
598 recruitment and floodplain/river interactions on their spatial and temporal dynamics.

600 **Table 1.** Ten Life-history traits quantified for 194 Australian native freshwater fish species.

<b>Trait</b>	<b>Description</b>	<b>Abbreviation</b>
Longevity	Maximum potential life span (years)	Long
Age at maturation	Mean age at maturation (years)	AgeMat
Length at maturation	Mean total length at maturation (cm)	LenMat
Spawning substrate	Mineral (e.g. gravel, rocks)	SPSUB1
	Organic (e.g. plants, wood)	SPSUB2
	Various (mineral and organic)	SPSUB3
	Pelagic	SPSUB4
	Other (e.g. buccal)	SPSUB5
Spawning frequency	Single spawning per season	SPFRQ1
	Batch/repeat/protracted spawner per season	SPFRQ2
	Single spawner per lifetime	SPFRQ3
Reproductive guild	Nonguarders (open substratum spawners)	REPG1
	Nonguarders (brood hiders)	REPG2
	Guarders (substratum choosers)	REPG3
	Guarders (nest spawners)	REPG4
	Bearers (internal)	REPG5
	Bearers (external)	REPG6
Total Fecundity	Total number of eggs or offspring per breeding season	TFec
Egg size	Mean diameter of mature (fully yolked) ovarian oocytes (mm)	EggS
Parental care	Metric representing the total energetic contribution of parents to their offspring <i>sensu</i> Winemiller (1989)	PC
Maximum body length	Maximum total body length (cm)	MaxL

602 **Table 2.** Description and summary statistics (mean  $\pm$  standard error [SE] and range) for five  
 603 environmental variables characterised for 123 Australian river basins.

<b>Catchment Scale Variables</b>	<b>Abbreviation</b>	<b>Description</b>	<b>Mean <math>\pm</math> SE</b>	<b>Range</b>
<b>Habitat Availability</b>				
Stream density	STREAM_DENS	Total length of the stream network / catchment area (km/km <sup>2</sup> )	0.74 $\pm$ 0.2	0.11 - 1.29
<b>Climate</b>				
Temperature	TEMP	Mean annual catchment temperature ( $^{\circ}$ C)	21.6 $\pm$ 0.4	10.4 - 27.5
<b>Productivity</b>				
Net primary production	NPP	Mean catchment net primary production (pre-1788) (tC ha <sup>-1</sup> )	3.99 $\pm$ 0.23	0.24 - 9.76
<b>Hydrology</b>				
Runoff	RUNOFF	Discharge/catchment area (ML/km <sup>2</sup> )	265.9 $\pm$ 23.1	0.3 - 1660.4
Coefficient of variation	CV	Coefficient of variation of the discharge	1.0 $\pm$ 0.1	0.3 - 4.1

604

605 **Table 3.** Best supporting models of the relationships between life-history indices and environmental  
606 predictor variables modelled within a spatio-phylogenetic framework (See Fig. 1) and standard  
607 analytical framework. Life-history indices are functional dispersion (FDis), functional evenness (FEve)  
608 and the proportion of opportunistic (%Opp), periodic (%Per) and equilibrium (%Equ) strategists,  
609 respectively. “-“ indicates coefficient was not selected in model with the best subset of predictor  
610 variables based on the Bayesian Information Criterion. Also shown are the number of spatio-  
611 phylogenetic covariates (filters) in the modelling procedure, model  $R^2$  and residual Moran’s I for  
612 each model (\* indicates significant at  $p < 0.05$ ).

	<b>Spatio-phylogenetic framework</b>		<b>Life history index</b>		
	FDis	FEve	%Opp	%Per	%Equ
<b>Coefficient</b>					
Intercept	0.222	0.731	0.510	0.368	0.122
Area	-0.007	0.018	0.048	-0.031	-0.013
Stream Density	-	-	-	-	-0.013
Temperature	-0.004	-0.034	0.034	-0.033	-
NPP	0.008	-0.017	0.035	-	-0.020
Runoff	0.005	-	-0.018	-	0.012
CV	0.006	0.006	-0.019	0.021	-
# Filters	11	16	10	11	9
$R^2$	0.591	0.800	0.564	0.786	0.684
Residual Moran's I	0.007	-0.060	-0.058	0.001	0.014
<b>Standard framework</b>					
	FDis	FEve	%Opp	%Per	%Equ
<b>Coefficient</b>					
Intercept	0.222	0.731	0.510	0.368	0.122
Area	-0.007	-0.019	0.033	-0.032	-0.019
Stream Density	-	-	-	-	-
Temperature	-	-0.038	0.037	-0.040	-
NPP	0.009	-0.019	0.041	-	-0.037
Runoff	0.005	-	-	-	0.020
CV	0.007	-0.007	-	0.023	-
$R^2$	0.411	0.557	0.238	0.333	0.397
Residual Moran's I	0.264*	0.323*	0.365*	0.602*	0.218*

613

614

615 **Table 4.** Best supporting models derived from the exhaustive model selection procedure, with and  
616 without spatio-phylogenetic filters, of the relationship between life-history indices (FDis: functional  
617 dispersion; FEve: functional evenness; %Opp, %Per, %Equ: the proportion of opportunistic, periodic  
618 and equilibrium strategists, respectively) and environmental predictors (See Table 2 for  
619 abbreviations) across Australian river basins. ‘filters’ refers to the forced inclusion of spatio-  
620 phylogenetic filters in the variable subset selection procedure. \* indicates significant at  $p < 0.05$ .

<b>Best supporting model (BIC)</b>					
<b>Response</b>	<b>Predictors</b>	<b>R<sup>2</sup></b>	<b>Residual Moran's I</b>	<b>BIC</b>	<b>ΔBIC</b>
<b>FDis</b>	AREA, NPP, RUNOFF, CV, TEMP, filters	0.618	0.001	-53.9	-
	AREA, NPP, RUNOFF, CV, filters	0.599	0.030	-52.2	1.7
	AREA, NPP, RUNOFF, CV	0.411	0.264*	-45.2	8.8
	AREA, NPP, RUNOFF, CV, TEMP	0.425	0.273*	-44.3	9.6
<b>FEve</b>	AREA, TEMP, NPP, CV, filters	0.800	-0.060	-119.2	-
	AREA, TEMP, NPP, STREAM_DENS, CV, filters	0.806	-0.066	-118.9	0.3
	AREA, TEMP, NPP, RUNOFF, CV, filters	0.805	-0.046	-118.5	0.7
	AREA, TEMP, NPP, STREAM_DENS, RUNOFF, CV, filters	0.810	-0.052	-117.9	1.3
	AREA, TEMP, NPP, CV	0.557	0.323*	-80.2	38.9
	AREA, TEMP, NPP	0.540	0.399*	-79.4	39.7
	AREA, TEMP, NPP, RUNOFF, CV, filters	0.564	-0.058	-41.2	-
<b>%OPP</b>	AREA, TEMP, NPP	0.238	0.365*	-17.3	24.0
	AREA, TEMP, NPP, RUNOFF, CV, filters	0.564	-0.058	-41.2	-
<b>%PER</b>	AREA, TEMP, CV, filters	0.786	0.001	-132.5	-
	AREA, TEMP, CV	0.333	0.602*	-33.7	98.8
<b>%EQU</b>	AREA, NPP, RUNOFF, STREAM_DENS, filters	0.684	0.014	-88.2	-
	AREA, NPP, RUNOFF	0.397	0.218*	-46.1	42.1
	AREA, NPP, RUNOFF, TEMP,	0.410	0.194*	-45.0	43.3
	AREA, NPP, RUNOFF, STREAM_DENS, TEMP	0.425	0.163*	-44.4	43.8

621

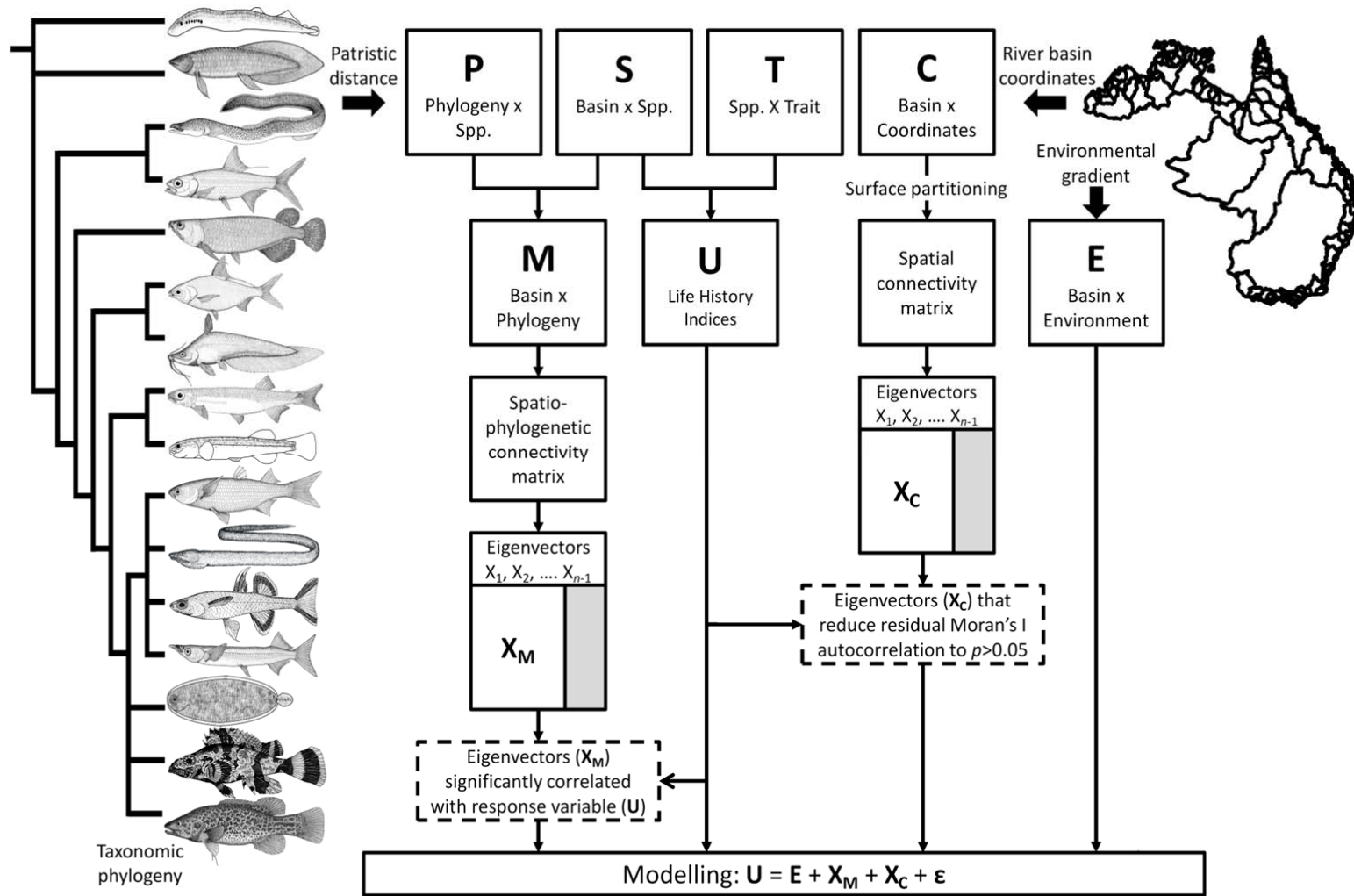
622

623 **LIST OF FIGURES**

624 **Figure 1.** General overview on the eigenvector filtering method used in the multiple linear regression  
625 approach to relate environmental predictor variables to life-history index response variables (U)  
626 while accounting for spatial and phylogenetic autocorrelation in the ecological data. First,  
627 phylogenetic (P), species distribution (S), species trait (T) and river basin coordinates (C) matrices are  
628 introduced from which spatio-phylogenetic and spatial triangular connectivity matrices are derived  
629 and eigenvectors ( $X_M$  &  $X_C$ ) extracted that reduce the residual spatial and phylogenetic  
630 autocorrelation in the final modelling procedure ( $U = E + X_M + X_C + \epsilon$ ). See text for detailed  
631 description of methods. Fish illustrations by B.J Pusey used with permission.

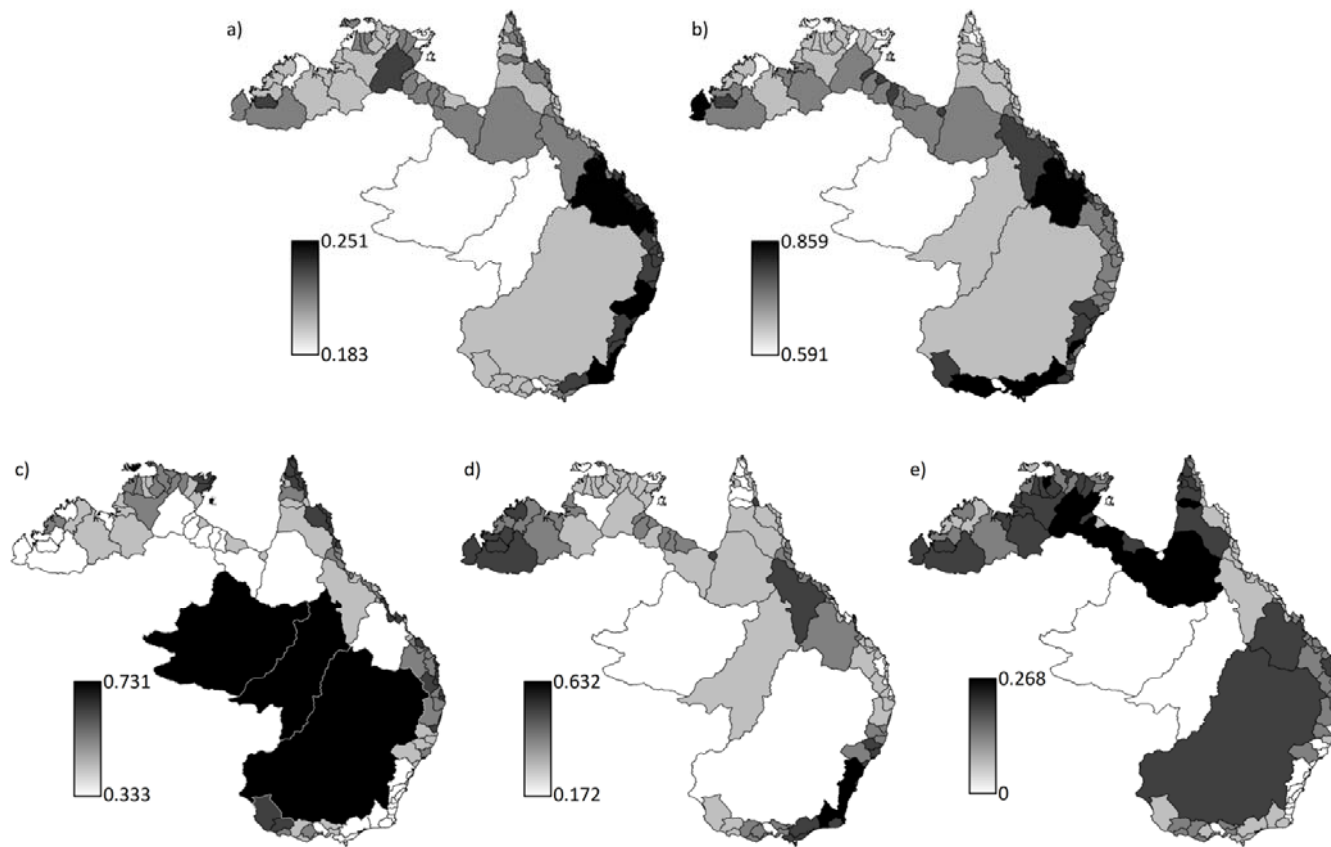
632

633 **Figure 2.** Spatial variation in a) functional dispersion (FDis); b) functional evenness (FEve); and the  
634 proportion of c) 'opportunistic'; d) 'periodic'; and e) 'equilibrium' species, respectively, in each of the  
635 123 Australian river basins. Light colours indicate low values, while dark colours indicate high values.



636

637 Figure 1



638

639 Figure 2