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Quantifying and predicting the benefits of environmental flows: combining large-scale monitoring data and expert knowledge within hierarchical Bayesian models

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Running Head

Bayesian models for predicting effects of environmental flows

Summary

1. Despite large investments of public funds into environmental flows programs, we have little ability to make quantitative predictions of the ecological benefits of restored flow regimes. Rather, ecological predictions in environmental flow assessments typically have been qualitative and based largely upon expert opinion. Widely-applicable, quantitative models would help to justify existing flows programs and to inform future planning.

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- 25 2. Here, we used a hierarchical Bayesian analysis of monitoring data coupled with expert-
26 derived prior distributions, to develop such a model. We quantified the relationship
27 between the duration and frequency of inundation, and encroachment of terrestrial
28 vegetation into regulated river channels. The analysis was informed by data from 27 sites on
29 7 rivers.
- 30 3. We found that longer inundation durations reduce terrestrial vegetation encroachment. For
31 example, a 50 day continuous inundation during winter reduced predicted vegetation cover
32 to a median of 11% (95% C.I.: 7-35%) of cover predicted under non-inundated conditions.
33 This effect varied among sites and rivers, and was moderated by the frequency of inundation
34 events.
- 35 4. The hierarchical structure improved precision of model predictions relative to simpler
36 analysis structures. Informative prior distributions also improved precision relative to
37 minimally-informative priors.
- 38 5. The hierarchical Bayesian analysis allows us to make quantitative predictions of ecological
39 response under the full range of flow conditions, allowing us to assess the benefits of
40 planned or delivered environmental flows. It can be used to make estimates of ecological
41 effects at sites that have not been sampled, and also to scale up site-level results to
42 catchment and regional scales. Quantitative predictions of ecological effects provide a more
43 objective risk-based approach, allowing improved planning of environmental flows and
44 building public confidence in these major investments of public funds.

45 **Keywords**

46 environmental flows; predictive model; Bayesian hierarchical; terrestrial vegetation; monitoring and
47 evaluation

48 **Introduction**

49 Human-induced alteration of flow regimes impacts the ecological integrity of rivers around the world
50 (Dudgeon *et al.*, 2006; Vorosmarty *et al.*, 2010). In response, many countries have adopted policies
51 to partially restore natural flow regimes through the delivery of environmental flows. Large-scale
52 implementation of environmental flows has lagged behind policy positions (Le Quesne, Kendy &
53 Weston, 2010), but these programs are now being established across the world.

54 In Australia, some 2750 gigalitres – ($2.75 \times 10^9 \text{ m}^3$) are being returned annually to the Murray and
55 Darling river systems as environmental flows under the Commonwealth Governments 'Basin Plan'

56 initiative (<https://www.mdba.gov.au/basin-plan-roll-out>). This is approximately 20% of the volume
57 of water previously used for irrigated agriculture. The program is expensive, with some \$15B (AUD)
58 of public money to be spent on environmental flows and associated works through to 2019-20
59 (Skinner & Langford, 2013). Apart from the cost, the programs are controversial because they
60 remove large amounts of water from traditionally productive uses (primarily irrigated agriculture) in
61 return for uncertain ecological benefits.

62 The ecological effects of flow restoration have been poorly monitored historically (Souchon *et al.*,
63 2008). Attempts to combine disparate sets of studies to achieve general quantitative understanding
64 of the effects of flow alteration on riverine organisms have been unsuccessful (Poff & Zimmerman,
65 2010). Thus, although we have good *qualitative* understanding of how changes in flow regime will
66 affect aquatic organisms (Webb *et al.*, 2013), we have had little ability to make *quantitative*
67 predictions of the likely benefits of environmental flows programs (Souchon *et al.*, 2008). This makes
68 it more difficult to justify public investment in current environmental flows programs, and reduces
69 capacity to improve planning of future flows programs.

70 The Victorian Environmental Flows Monitoring and Assessment Program (VEFMAP) was established
71 in the Australian state of Victoria in 2005 in a deliberate attempt to address the shortcomings of
72 previous environmental flows monitoring programs (Webb *et al.*, 2010a). It is a state government-
73 funded initiative that established compatible monitoring of fish assemblages, vegetation, water
74 quality, and channel form across 10 rivers that receive environmental flows (Fig. 1). Inference of
75 ecological effects relies upon an analytical framework that is designed to make best possible use of
76 all the information available (Stewardson & Webb, 2010; Webb *et al.*, 2015). The final phase in this
77 framework is the synthesis of data collected from the large-scale monitoring program using
78 hierarchical Bayesian statistical analyses.

79 Hierarchical Bayesian approaches are employed increasingly in ecological settings because of their
80 flexibility to accommodate the complex data structures that arise in natural systems (Borsuk *et al.*,
81 2001; Wikle, 2003; Clark, 2005; Cressie *et al.*, 2009). This flexibility can reduce impacts of the 'poor
82 experimental design' commonly associated with ecological data, for example, the lack of before-
83 after or control-impact treatments, presence of confounding environmental variables, and spatial
84 and temporal autocorrelation among samples. They can also be improved by the incorporation of
85 prior information on the relationships being studied (McCarthy & Masters, 2005). A hierarchical
86 model combines information from multiple 'exchangeable units'. These can be broadly thought of as
87 replicates, in that exchangeable units need to be able to be considered as being drawn from a larger
88 distribution of potential sampling units (Gelman *et al.*, 2004). This has the practical effect of reducing

89 uncertainty in unit-level parameter estimates, and drawing all estimates towards a global mean,
90 processes known as borrowing strength and shrinkage respectively (Gelman *et al.*, 2004). The
91 hierarchical structure also allows one to test hypotheses and report results at multiple scales
92 (Gelman & Hill, 2007).

93 In previous work, we argued that hierarchical Bayesian approaches are well suited to identifying
94 flow-response relationships (Webb, Stewardson & Koster, 2010b). In these models, sites within
95 rivers, and rivers within basins, formed the exchangeable units. We demonstrated the efficacy of
96 Bayesian models using limited data sets for stream salinity and for the abundance of the fish,
97 Australian smelt (*Retropinna semeoni*). We argued that by using Bayesian approaches to describe
98 continuous relationships between changes in flow regime and ecological response, we can develop
99 the ability to predict the benefits of environmental flows.

100 Here, we extend the application of hierarchical Bayesian models to the scale envisaged in Webb et
101 al. (2010a; 2014). We use a large-scale data set across multiple rivers and years, and also incorporate
102 expert knowledge in the form of elicited prior distributions for model parameters. The case study
103 chosen is whether flow management can be used to reduce or prevent encroachment of terrestrial
104 vegetation into river channels. This response was selected by the management stakeholders in
105 VEFMAP (Webb *et al.*, 2015) because, by the end of the 'millennium drought' in south-eastern
106 Australia (September 2010), many river channels had been colonised by terrestrial species.
107 Environmental flow recommendations for several of the rivers suggested that high flows could be
108 used to manage terrestrial vegetation, but these recommendations were based upon expert opinion
109 and experience rather than on empirical data. The resulting Bayesian models of the VEFMAP data
110 provide the ability to predict ecological responses to different flow regimes (including with and
111 without environmental flows) that has previously been lacking. They also can report results at
112 multiple scales and potentially make predictions for sites that have not been monitored.

113 **Methods**

114 ***Study area and data***

115 The data analysed in this paper were collected from 27 sites on 7 of the 10 VEFMAP rivers (Fig. 1).
116 *Eucalyptus camaldulensis* – river red gum – is the dominant overstorey species for most sites, with
117 the mid-storey being dominated by species such as the native silver wattle (*Accacia dealbata*), and
118 the understorey by exotic grasses and forbs (Greet, Cousens & Webb, 2013). A small proportion (6
119 out of 27) of the sites is grazed by stock (sheep and cattle).

120 The VEFMAP vegetation data were collected from multiple (usually 10) cross-sectional transects at
121 each site, spread over approximately 500 m of the river. They were collected as Braun-Blanquet
122 cover class scores (Meuller-Dombois & Ellenberg, 1974). This is an ordinal scale that divides
123 percentage cover into one of 6 classes: + = present (which we treated as < 1%), 1 = 1-5%, 2 = 5-25%,
124 3 = 25-50%, 4 = 50-75%, 5 = 75-100%, and is used to reduce sampling error issues associated with
125 precisely estimating percentages. Cover scores were recorded for each species present in 1 x 1 m
126 quadrats along that part of each transect that would be regularly inundated under natural flow
127 regimes (up to half way up the bank - 'zones A and B'; Christie & Clarke, 1999). This process was
128 repeated up to 3 times (2008, 2010, 2012), but there was no systematic attempt to survey the same
129 quadrats each time. Species were classified into functional groups according to Casanova and Brock
130 (2000), and the mid-points of the Braun-Blanquet cover classes (0.5%, 3%, 15%, 37.5%, 62.5%, 87.5%)
131 of all the terrestrial species (Terrestrial Dry and Terrestrial Damp; Casanova & Brock, 2000) were
132 summed together to give a total terrestrial vegetation cover for each quadrat. Overall, the analysis
133 incorporated data from 9465 quadrats.

134 The elevation of each quadrat relative to the river channel and water surface was determined from
135 channel cross-section surveys conducted from 2005-2008. These surveys were also used to develop
136 1-dimensional hydraulic models of the sites using the HEC-RAS software (Version 4.1, US Army Corps
137 of Engineers). Both of these steps occurred as part of establishing the VEFMAP monitoring programs
138 (e.g. SKM, 2007), and followed industry standard practice for hydraulic model calibration and
139 validation. These models were combined with daily measured discharge data from nearby sites
140 (Victorian Water Measurement Information System: <http://data.water.vic.gov.au/monitoring.htm>)
141 to determine the inundation regime (number of days inundated and number of separate inundation
142 events) for each quadrat.

143 ***Statistical model structure***

144 The hierarchical Bayesian analysis modelled the interacting effects of the duration and frequency of
145 inundation upon terrestrial vegetation cover, along with several other covariates and random effects
146 to reduce unexplained variation. Results of a systematic synthesis of evidence from the literature
147 (Miller *et al.*, 2013) and an expert-based Bayesian network (de Little *et al.*, 2018) predicted that
148 terrestrial vegetation cover within river channels will be highest with little or no inundation, and will
149 decrease with increasing total annual duration of inundation (Fig. 2). Also, for a given total annual
150 duration of inundation, longer and fewer inundation events are expected to reduce terrestrial
151 vegetation cover by a greater amount. This conceptual relationship can be represented
152 mathematically as:

153
$$c_i = v_0 \cdot e^{-m \left(\frac{T_i}{f_i} \right)}$$
 (eq. 1)

154 where c_i is the % terrestrial vegetation cover expected for a quadrat (i), v_0 is a fitted parameter
 155 specifying the maximum cover seen when inundation is zero, and m is a fitted parameter that
 156 determines how the steepness of the relationship between c_i and inundation duration (T_i) changes
 157 with the number of distinct inundation events (f_i) for that quadrat.

158 Generalising this equation to consider inundation histories over extended periods, we included
 159 hydrological data for 5 years prior to the vegetation sampling, calculating T_i and f_i separately for
 160 each 12-month period, starting with the 12 months immediately preceding vegetation sampling. We
 161 assessed the importance of inundation in more recent years relative to older events, and indeed the
 162 choice of the inclusion of 5 years of data, by fitting a parameter $-d$ – that weighted the inundation
 163 data according to their age. Thus, the simple exponent $-m(T_i/f_i)$ in Eq. 1 above, becomes:

164
$$-m \sum_{j=0}^4 e^{-j \cdot d} \cdot \frac{T_{ij}}{f_{ij}}; \quad n = \sum_{j=0}^4 e^{-j \cdot d}$$
 (eq. 2)

165 where j denotes the number of years prior to vegetation sampling for those values of T_i and f_i . The
 166 summation terms weight the inundation data by the effect of their age, with the decay in relative
 167 importance of years specified by d , and n normalizes the sum of weights over five years to 1.

168 The analysis also included several variables previously identified by our literature analysis and/or
 169 expert elicitation process as relevant for explaining terrestrial vegetation cover. The effect of season
 170 of inundation was included as a continuous additive effect, with season of inundation quantified as
 171 the ratio of days of inundation in the ‘water year’ austral winter/spring (May-November) to days of
 172 inundation in summer/autumn (December-April), centred on zero. We weighted the effect of more
 173 recent years using summation terms similar to eq. 2, above. We included the angle of the bank for
 174 each quadrat as a continuous additive effect, determining the angle from the previously-described
 175 channel cross-section surveys. The effect of livestock access was included as an additive categorical
 176 factor, with the data coded in the analysis as recent presence or absence of stock.

177 To account for any pseudo-replication in our sampling design, we included random effects for
 178 transects and sample years in the analysis. Both random effects are calculated in the same way as
 179 demonstrated for the effect of transect (x_s) below (eq. 3), with a mean effect of 0 across all levels,

180 and a minimally-informative uniform (U) prior distribution for the standard deviation among the
 181 levels of the random effect.

$$182 \quad \gamma_{xs} \sim N(0, \sigma_{xs}^2) \quad \sigma_{xs}^2 \sim U(0, 10) \quad (\text{eq. 3})$$

183 We also included a factor to take account of the sampling imprecision inherent in Braun-Blanquet
 184 cover scores. We assumed that a single Braun-Blanquet cover score for any one species could be
 185 considered as a uniformly-distributed random variable drawn from the range of the cover class. For
 186 example, a cover class score of 2 has a mid-point of 15%, but can be anywhere between 5% and
 187 25%. These bounds were summed across the different terrestrial species in a single quadrat to
 188 provide a lower (lb) and upper (ub) cover for that quadrat, with the imprecision ε_{ci} being drawn from
 189 that interval.

$$190 \quad \varepsilon_{ci} \sim U(lb_{ci}, ub_{ci}) \quad (\text{eq. 4})$$

191 However, initial versions of the model containing ε_{ci} produced near-identical results to versions that
 192 did not contain this variable. Some more complex versions of the model containing this variable
 193 would not run, and those that did ran much slower. Accordingly, we dropped this variable for the
 194 remainder of analyses.

195 Finally, we square-root transformed the cover data prior to analysis in order to achieve a better
 196 spread of points around the fitted function, and to allow us to assume Gaussian-distributed
 197 residuals. The transform was effective for the data, despite the cover estimates being nominally
 198 bounded at 0 and 100%; the data were skewed towards lower coverages, and there were relatively
 199 fewer high cover values. The full statistical model at the site scale (i.e. we have not included a
 200 subscript for site) is thus:

$$201 \quad \begin{aligned} \sqrt{c_i} &\sim N(\mu_i, \sigma^2) \\ \mu_i &= v_0 \cdot e^{\left(-m \sum_{j=0}^4 e^{\frac{-j \cdot d}{n}} \cdot \frac{T_{ij}}{f_{ij}} \right)} + \alpha \sum_{j=0}^4 e^{\frac{-j \cdot d}{n}} \cdot Se_i + \beta \cdot Sl_i + \kappa \cdot St + \gamma_{xs} + \delta_{yr} \end{aligned} \quad (\text{eq. 5})$$

202 where μ_i is the modelled vegetation cover data for each quadrat (i), and is assumed to be normally
 203 distributed (N) with overall variance σ^2 . The summation terms weight the effect of inundation (T_{ij}, f_{ij})

204 and seasonal ratio of inundation (Se_i). α and β are fitted parameters describing the continuous
 205 effects of season of inundation (Se_i) and bank slope (Sl_i), respectively. κ is the fitted effect of
 206 stocking (St) at that site. γ_{xs} and δ_{yr} are the above-described random effects of cross sectional
 207 transect (xs), and sampling year (yr).

208 A number of parameters in the analysis were estimated hierarchically (Fig. 3). With the focus of the
 209 analysis being the effect of inundation, v_0 and m at the site level (k) were assumed to be drawn from
 210 fitted river-level ‘hyperparameter’ (sensu Gelman *et al.*, 2004) distributions (leading letter r) of the
 211 parameter values for the exchangeable units (sites). The means of each river (p) were then drawn
 212 from a state-level hyperparameter distribution (leading letter g).

$$m_k \sim N(r.m_p, \sigma_{r.m}^2)$$

$$r.m_p \sim N(g.m, \sigma_{g.m}^2)$$

214 The construction for v_0 was identical to this. For these parameters, the standard deviation among
 215 sites within rivers, and among rivers were both fitted at the state level; there were insufficient
 216 replicate sites within rivers to reliably estimate between-site variation within each river separately
 217 (Gelman, 2006). The effect of bank slope (β) and of stocking (κ) were also fitted at the site level, but
 218 with site-level means drawn from a state-level normal distribution. All other parameters were fitted
 219 directly at the state level (Fig 3).

220 We used minimally-informative prior distributions for many of the parameters. Prior estimates of
 221 standard deviation parameters were assigned minimally-informative uniform priors: $U(0,0.1)$ for
 222 $\sigma_{r.m}$, $\sigma_{g.m}$; $U(0,10)$ for d ; $U(0,100)$ for σ , $\sigma_{r.v0}$, $\sigma_{g.v0}$, $\sigma_{g,\beta}$, $\sigma_{g,\kappa}$, σ_{xs} , σ_{yr} . The different uniform priors
 223 for different parameters were adopted to improve model convergence; however all posterior
 224 distributions for the parameters were unimodal, and distributed over substantially less than the
 225 prior ranges (e.g. 95% CIs: $\sigma_{r.m} = [0.022, 0.045]$, $\sigma_{g.m} = [0.0030, 0.062]$, $d = [0.40, 0.64]$ $\sigma_{r.v0} = [0.9,$
 226 $1.9]$). For the mean $g.\beta$, we used a minimally-informative normal distribution $N(0,10)$. For other
 227 means, we were able to use informative prior distributions. These were derived from an expert-
 228 derived Bayesian belief network (BBN), the creation of which is described in de Little *et al.* (2018).
 229 Briefly, however, we used structured expert elicitation processes to quantify the conditional
 230 probability relationships within a BBN that linked terrestrial vegetation cover to the duration,
 231 frequency and season of inundation, and also to the effects of grazing on the river bank. To produce
 232 informative prior distributions, the BBN was used to create new data sets that corresponded to
 233 different states of the parent nodes, and their consequent distributions of vegetation cover. Most of

234 the data are continuous, and the Bayesian network used discretized states. To produce continuous
235 data from the Bayesian network, we fitted continuous beta distributions to the discretized
236 distributions, and then sampled from these fitted distributions. We varied the state of a single node
237 at a time, sampling 100 data points for each level of the state, with all other nodes held even.
238 Overall, this resulted in a data set of 900 cases. These data were then run through the hierarchical
239 Bayesian model described here, with minimally-informative priors for all parameters. The fitted
240 distributions used as informative prior distributions for the final hierarchical model were: $g.v_0 \sim 100 \cdot$
241 $B(0.83, 1.30)$; $g.m \sim 0.1 \cdot B(0.88, 1.25)$; $g.\kappa \sim N(-0.28, 0.044)$; and $g.\beta \sim N(-0.30, 0.042)$, where B is the
242 beta distribution.

243 The inclusion of variables with minimal explanatory power in a Bayesian model will reduce overall
244 posterior precision (Cheeseman & Stutz, 1996), and hence predictive power. Having included the
245 effects of inundation as the main explanatory variables for vegetation cover, we assessed the
246 additional importance of the covariate effects of season, bank slope and stocking using Bayesian
247 model averaging methods (Congdon, 2005). In the model statement above (eq. 5), each of these
248 effects was multiplied by a Bernoulli-distributed parameter ($\phi_\alpha, \phi_\beta, \phi_\kappa$), which had a prior probability
249 of 0.5. The inclusion of these variables meant that each variable was either included ($\phi=1$) or
250 excluded ($\phi=0$) from the model at each iteration during model fitting. The posterior probability for
251 each ϕ parameter is the proportion of iterations in which its corresponding covariate was included in
252 the model, giving a measure of its importance. Moreover, the combination of values for the three ϕ
253 parameters at each iteration tells us which model structures were more common (and therefore did
254 a better job of fitting the data). By using the model averaging approach, the predicted value of
255 vegetation covers presented below are weighted averages of the different possible model
256 structures, and thus take into account the explanatory power of the different covariates.

257 ***Model fitting and validation***

258 All model fitting was done using OpenBUGS Ver. 3.2.2 (Lunn *et al.*, 2009). We used 2 parallel Markov
259 chains for model estimation. Each chain was burned in for 10,000 iterations, with a further 20,000
260 iterations for parameter estimation, resulting in total sample size for parameter estimation of
261 40,000. Visual checks of the chain histories, as well as the Brooks-Gelman-Rubin diagnostic (Brooks
262 & Gelman, 1998) were used to confirm convergence of the chains by the end of the burn-in. Full
263 model code is included in Appendix S1.

264 We used fake data simulation (Gelman & Hill, 2007) to assess model fit to the data. Fake data
265 simulation tests the appropriateness of the model structure by assessing whether the model can

266 reproduce the data to which it has been fitted. It works by using the fitted model to produce
267 modelled data points, which are then compared to the observed data.

268 Here, the fitted values of μ_i and σ^2 were used to generate fake data, reversing the process used to fit
269 those parameters to the observed data. In a Markov chain Monte-Carlo simulation, different values
270 of α , β , and σ^2 will be computed for every iteration of the chain. Thus μ_i is also different for every
271 iteration. These differences, together with the inherent uncertainty introduced by σ^2 , mean that a
272 distribution of potential fake values will be created over the thousands of iterations of the Markov
273 chain. This distribution will reflect the assumptions made in the model statement (i.e. eq. 5).

274 If the model is a reasonable reflection of the physical/chemical/ecological processes used to
275 generate the data, then the observed data point will lie within the distribution of fake data values
276 with acceptable probability. With a substantial data set (e.g. 100 points), we fully expect some
277 observed data points to be at the tails of the distribution of fake data (i.e. we expect 5% of observed
278 data points to lie outside the middle 95% of the probability mass for the corresponding fake data
279 point). However, if substantial numbers of points lie outside the fake data distributions, it suggests
280 an inadequacy of model structure.

281 For the study of terrestrial vegetation encroachment, the model statements relate to mean
282 expected cover vegetation cover; there is no expectation of being able to reproduce the quadrat
283 level data. We assessed model fit by simulating fake data at the level of 'survey' (site \times year
284 combinations), and compared these distributions to the mean cover observed for each survey.

285 Following validation, we explored the effect of the different independent variables (duration of
286 inundation, number of inundation events, season of inundation) on vegetation cover by using the
287 model to predict cover under different combinations of these variables at multiple scales. To assess
288 the effect of using other information in the analysis, we ran non-hierarchical versions of the analysis.
289 This was done by removing the higher-level hyperparameters from the model, and instead assigning
290 the prior distributions to the parameters at the site level. We also ran a version of the analysis
291 without the informative prior distributions.

292 **Results**

293 The analysis allowed us to make predictions of vegetation cover under different hypothetical flow
294 regimes. For the example results below, we concentrate on two inundation periods (20 days and 50
295 days), which are consistent with total recommended durations of inundation from environmental

296 flow assessments on the target rivers for removing encroached vegetation (e.g. SKM, 2002). We
297 explore results only for a sub-set of the 27 sites included in the analysis, indicative of the ranges of
298 results observed; full results are available in Miller *et al.* (2015). We describe overall patterns of
299 consistency among the full set of sites, plus effects of the other variables in the model.

300 There were variable effects of inundation on vegetation cover among the 27 sites, with median
301 values of the m parameter ranging from just over 0 (small effect) to near 0.1 (larger effect) (Fig. 4). In
302 general, the analysis predicted substantial reductions in vegetation encroachment with relatively
303 short periods of continuous inundation (Fig. 1). For most sites, 20 days inundation in winter should
304 be sufficient to substantially reduce vegetation encroachment, with 50 days continuous inundation
305 having a greater effect (Fig. 1). However, effectiveness varied among sites (Fig. 5), and 8 of the 27
306 sites had little predicted effect of inundation (Fig. 1.d, Fig. 5).

307 The river-level predictions of vegetation encroachment under 20 and 50 days inundation in winter
308 were similar to the site level results (Fig. 1.c, f), except that reductions in cover were predicted for all
309 rivers. Similarly, the state-level predictions showed substantial reductions in terrestrial vegetation
310 encroachment relative to non-inundated conditions (Fig. 1.g). Breaking the same period of
311 inundation into several distinct events reduced the effect on encroachment (Fig. 5).

312 The covariates differed in their explanatory power. Season of inundation appeared in 91% of models.
313 Bank slope was less important, appearing in 50% of models. Presence of stock was unimportant,
314 appearing in <1% of models. Overall, the great majority of models either only contained the Season
315 covariate, or included Season in combination with Slope (Table 1). However, the overall effect of
316 season of inundation was small (Fig. 6), with the median predicted cover following inundation in
317 summer being only slightly smaller than for inundation in winter, and well within the 95% credible
318 interval for the prediction.

319 The temporal decay parameter, d , showed that inundation in recent years had greater explanatory
320 power than inundation in earlier years, and that the inclusion of 5 years of data was reasonable. The
321 median parameter value of 0.52 (95% credible interval: 0.40 to 0.64) means that each year's
322 inundation data has ~1.7 times the explanatory power of the year preceding it. When the five years
323 of inundation data were weighted to sum to one, the effect of inundation in each year for explaining
324 terrestrial vegetation encroachment was 43%, 26%, 15%, 9%, and 5% for years 0 to 4 prior to
325 vegetation sampling, respectively.

326 The fake data simulation showed that the analysis did a reasonable, although not outstanding, job of
327 reproducing the data to which it had been fitted (Fig. 7). Twenty-one of the 67 measured survey-

328 level (i.e. combination of site and year) values fell outside of the 95% credible interval for mean
329 predicted cover. However, nearly all of these 21 were only marginally outside the 95% credible
330 interval, and only the prediction for one site on the Wimmera River (Gross Bridge, second from the
331 left for that river; Fig. 7) in 2010 was markedly different to the measured cover. The poorer
332 predictions were clustered upon specific rivers and sites. Five out of 6 measured covers for the
333 Macalister River, and 6 out of 14 measured covers for the Thomson River, were outside the 95%
334 credible intervals for mean predicted cover. For the Thomson River, this figure included all data
335 points for two sites (flow gauge 225212, and Reedy Creek Rd). For these rivers, observed covers
336 were higher than expected by the model for 2012 and lower than expected for 2008. Overall, given
337 the complexity of the model used here, the wide range of vegetation covers observed, and the
338 identified deficiencies with data collection (see Discussion), the fit of the model to the data is
339 satisfactory.

340 There was a noticeable effect on results of both the expert-based priors and the use of the
341 hierarchical model structure (Fig. 8). Uncertainties around predicted vegetation covers were higher
342 both for models that employed minimally-informative priors, and for models that did not employ a
343 hierarchical structure. This effect was exacerbated in the 'site data only model' that employed
344 neither informative priors, nor a hierarchical structure. Median predicted covers were also different
345 in these alternate model structures, but not consistently compared to the full model (Fig. 8).

346 **Discussion**

347 Environmental flows science has suffered from an inability to describe general quantitative
348 relationships between changes in flow regime and ecological response (Poff & Zimmerman, 2010;
349 Konrad *et al.*, 2011; Olden *et al.*, 2014). This has reduced our ability to make quantitative predictions
350 of the ecological benefits of environmental flow programs (Souchon *et al.*, 2008). With water being a
351 heavily-contested resource around the world (Poff *et al.*, 2003), such predictions are necessary to
352 justify environmental flows, and to improve future planning.

353 Here, we have demonstrated one approach that can provide this type of predictive capacity. The
354 case study goes well beyond the scale of work previously reported in Webb *et al.* (2010b),
355 demonstrating that the approach is viable with more complex statistical models, much larger data
356 sets, and with the incorporation of expert-based informative prior distributions. By quantifying
357 continuous relationships between flow regime and ecological response, we have the capacity to
358 predict ecological response to any given flow regime, including both with and without environmental
359 flows. The two components of the analysis are of equal importance. We do not believe that either

360 hierarchical Bayesian analysis or a large-scale monitoring program could provide this quality of
361 outputs alone. Rather, they complement each other to produce strong inference and predictive
362 capacity.

363 Our analysis shows that relatively short periods of inundation will be sufficient to largely prevent
364 terrestrial vegetation encroachment. This supports the qualitative conclusions of a recent literature
365 evidence synthesis (Miller *et al.*, 2013), but the quantitative predictions go well beyond these earlier
366 results, and can be used to fine-tune flow-based terrestrial vegetation management into the future.

367 *Coordinated data collection over large scales*

368 Poff and Zimmerman (2010) ably demonstrated that we cannot achieve quantitative understanding
369 of ecological responses to altered flow regimes by combining results from multiple studies that use
370 different methods, endpoints, and quantification of flow regimes. The benefits of a hierarchical data
371 analysis are best realised when it employs a large-scale data set collected using compatible methods.
372 Thus, at least some of the inferential strength of the analyses presented here stems from the sheer
373 volume of data included in the analysis (~10,000 points).

374 Coordinated monitoring over such scales requires substantial investment of public funds. However,
375 these costs are several orders of magnitude lower than the public investment in the actual
376 environmental flows delivery programs. For data analysis of such programs, the greatest difficulty is
377 the lack of control over data collection. In VEFMAP, data were collected by contractors engaged by
378 the local river managers. Monitoring providers vary among rivers, and can change over time (Webb
379 *et al.*, 2014). There was thus considerable opportunity for reduced data quality and there were
380 occasional serious divergences of exact approaches used throughout the data set.

381 Potential problems with parts of the data set analysed here are evident with the results from those
382 sites that predicted very little effect of inundation on terrestrial vegetation encroachment (i.e. sites
383 on the Yarra River, and two sites each on the Broken and Thomson rivers; Fig. 5). While we
384 presented results only for up to 50 days inundation, for these sites there was little predicted
385 reduction for much longer inundation periods (e.g. up to 200 days); a result that is clearly
386 ecologically implausible. We believe that these incongruous results arise from a mismatch between
387 the vegetation data and the cross-section surveys that were used to compute the inundation of the
388 quadrats, rather than any particular failure to include important ecological variables in the model
389 structure. These two data sets were collected by different contractors, and it appears that on
390 occasions the vegetation surveyors did not appreciate the need to follow the cross-sections

391 precisely. In the worst case, an entire season's worth of vegetation data had to be discarded for one
392 river, as they bore no relation to the surveyed cross sections. Elsewhere, we invested considerable
393 time correcting these effects, but for several sites it appears we were unable to fully resolve the
394 discrepancies. This is an inherent challenge associated with the analysis of data from any large-scale
395 monitoring program.

396 *Bayesian analysis of flow-ecology responses*

397 The flexibility of the Bayesian statistical analysis allowed us to construct a model that better
398 captured the ecological processes, rather than simply testing for associations between flow
399 components and ecological responses (sensu Clark, 2005). By fitting continuous relationships
400 between flow and ecological response, we gain the capacity to make predictions of the effects of the
401 full range of flow scenarios experienced, which could subsequently be used to inform management
402 decisions.

403 The fake data simulation is an intuitive way of assessing model fit – checking to see whether the
404 model can generate the data to which it has been fitted (Gelman *et al.*, 2004). Here, we found a
405 considerable number of observed data points falling outside of the modelled distributions. However,
406 for two reasons, this is not surprising. First, we had employed expert-derived prior probability
407 distributions, which reduce the uncertainty of model parameters, and hence the uncertainty of the
408 fake data distributions. Second, the hierarchical analysis brings together data from different rivers
409 across a wide range of physical and climatic conditions. With the relationships from one river
410 affecting those quantified for another, we expect to see some discrepancy. Also, the hierarchical
411 structure further reduces the uncertainty of modelled data points, highlighting a lack of fit with any
412 outlying data points. We also noted some consistent departures from fit (e.g. high estimates some
413 years and low estimates other years for individual rivers; Thomson and Macalister rivers, Fig. 7). This
414 indicates that our model was not capturing some process/es driving terrestrial vegetation cover, and
415 could have been caused by a lack of detail in model specification and/or the non-inclusion of a non-
416 monitored environmental variable. The fact that fit varied among years suggest that the model may
417 be missing an important climatic variable in these locations. However, because the differences were
418 relatively minor, and the overall fit of the model was acceptable, we did not explore these further.

419 We used model averaging approaches to assess the importance of season of inundation, bank slope,
420 and stock access. Model averaging is widely practiced across different types of statistical analysis,
421 but is not usually a simple process. Within the Markov Chain-Monte Carlo based Bayesian analysis
422 the use of the Bernoulli-distributed d parameters within the regression model provides an elegant

423 way to undertake model averaging with almost no extra effort. Variance component partitioning
424 would have been another way that we could have assessed co-variate importance, and is readily
425 undertaken within a Bayesian analysis (Gelman, 2005).

426 The hierarchical analysis allowed us to incorporate data from multiple exchangeable units in the
427 same analysis – here sites within rivers and rivers within the state. This reduces uncertainty through
428 ‘borrowing strength’ – the use of information from other units to strengthen results within individual
429 units (Gelman *et al.*, 2004). Another potential benefit made possible by the hierarchical approach is
430 that the model could be used to make predictions at sites for which monitoring data have not been
431 collected. For example, given basic knowledge (covariate states and channel form) for a new site on
432 one of the rivers included in this analyses, we could sample from the river-level distributions (e.g.
433 variables $r.m$, $r.v_0$) to produce estimates of terrestrial vegetation cover under current or future flow
434 regimes at the new site. Such predictions could only be made for sites that are sufficiently similar to
435 those already in the analysis that they could be assumed to come from the same population. The
436 predictions also will have greater uncertainties than those at sites for which vegetation data have
437 been collected, but this is a far more robust extrapolation than the current practice of assuming
438 results at non-monitored sites will be the same as the small number of monitored sites. The
439 hierarchical approach also allows us to report results at multiple scales. Here we were able to make
440 predictions of the effects of inundation on terrestrial vegetation encroachment at the site, river, and
441 state scales.

442 The Bayesian approach also provides a formal framework for the incorporation of prior knowledge in
443 analyses (McCarthy & Masters, 2005). Bayesian theoreticians have debated whether a prior
444 distribution is best conceived of as a distribution of data sets from similar (i.e. exchangeable)
445 experimental units, or as the opinion of experts prior to collecting data (Efron & Morris, 1977; Webb
446 *et al.*, 2017b). Here, we employ both conceptions. A prior distribution at a site is a function of data
447 from the other sites through the hierarchical structure (for example, for site-level m , these are $r.m$
448 and $g.m$). However, we go further than this, using prior distributions for global hyperparameters
449 (e.g. $g.m$) derived from formal expert elicitation (de Little *et al.*, 2018). The combination of the two
450 steps implies that we believe the expert opinion to be a sound estimate of the among-site variation
451 in the parameter value. Although the incorporation of prior information in Bayesian models is
452 discussed extensively in the literature, with both supporters and detractors (McCarthy, 2007), many
453 Bayesian analyses in ecological research fall back on the use of minimally-informative prior
454 distributions. Expert knowledge is widely used in environmental flows science and management
455 (Stewardson & Webb, 2010; Webb, Arthington & Olden, 2017a). However, it is generally elicited and

456 employed using informal and ad-hoc methods that are non-transparent and susceptible to bias. The
457 Bayesian approach to data analysis can retain the benefits of expert knowledge to improve
458 predictions, while at the same time ensuring rigour in its use. Any discipline where data are scarce
459 would benefit from this greater use of prior information.

460 Together, the hierarchical framework and the incorporation of prior knowledge greatly improves the
461 precision of site-level estimates of predicted responses to different flow regimes relative to
462 estimates based solely upon the data collected at that site. It should be noted that the
463 exchangeability assumption in the hierarchical model is not testable; departure of a site's data from
464 the predictions of a hierarchical model (as described for the fake data simulation) may be because of
465 data imprecision, because of departure from the assumption of exchangeability, or often both.
466 However, we believe that the risk of assuming exchangeability is outweighed by the benefits of
467 doing so. Most 'standard' statistical analyses would be restricted to the least-informative scenario
468 illustrated here – i.e. considering data only from the site. More precise predictions allow for greater
469 certainty in planning, which is especially important when uncertainty in ecological responses may be
470 used as an argument against providing environmental flows.

471 ***Managing environmental flows***

472 We have demonstrated the utility of the combination of hierarchical Bayesian analysis, expert-based
473 prior information, and large-scale environmental flow monitoring programs. The inevitable tradeoff
474 is the effort and expense of establishing the large-scale programs, and that the analysis methods
475 require a much greater level of training and experience. Hence, the approach is not immediately
476 available to managers. Development of these models is likely to remain the domain of academic
477 researchers or the research branches of management agencies. Even running novel scenarios
478 through these models requires the input of new data sets generated from hydraulic models and
479 simulated flow regimes. This is not a trivial operation. At the moment, we believe that the best
480 model for the use of Bayesian analysis for informing environmental flow management is one of
481 partnership between researchers and managers, with researchers adopting the role of 'ecological
482 modelling specialist', and undertaking the analyses and scenario tests required to inform the
483 development and assessment of management plans (Webb *et al.*, 2017a).

484 The analyses described here are consistent with application as part of an ELOHA (Poff *et al.*, 2010)-
485 based environmental flow assessment. The authors of that framework express the desire that fully
486 quantitative relationships be used in formulating flow alteration-response relationships, but
487 acknowledge that categorical or trajectory-based relationships often will need to be used because of

488 a lack of data. The hierarchical approach also has the potential to inform such relationships for the
489 different classifications of rivers in an ELOHA assessment (i.e. to treat each type as an exchangeable
490 unit in a hierarchical analysis). This would allow users to estimate relationships for the different river
491 types, without fully separating the analyses and therefore losing the capacity for data from one type
492 of river to reduce uncertainty in the predictions for another type.

493 The potential capacity to make predictions for areas that have not been monitored is particularly
494 important for management applications, and provides an elegant solution to the well-known
495 ecological problem of scaling-up site-based results to landscapes. Site-based monitoring programs
496 are normally required to be able to reach conclusions at larger scales and for non-monitored areas.
497 In the past, this has often been accomplished using the problematic concept of the 'representative'
498 monitoring site – one that shares characteristics with non-monitored sites, and by assuming that
499 patterns observed at the monitored site will also be occurring at non-monitored sites (Downes,
500 2010). The hierarchical approach allows for mathematically-robust predictions, using variation
501 among the monitored sites to inform the range of plausible outcomes at non-monitored sites.

502 Similarly, the ability to report results at multiple scales (e.g. Fig. 1) is very important for
503 management. These different scales will be primarily relevant to different stakeholders. Site-level
504 results will be most relevant to fine-scale planning, and understanding how different complementary
505 management actions at a site might interact with flow management. In communicating to a land
506 owner or community group, site-scale results will provide information on what environmental flows
507 mean for 'their' part of the river. River-level results will be most relevant for a regional river
508 manager seeking to communicate outcomes to a more general group of stakeholders. They
509 effectively summarise the multiple site-level results for that river, providing simplicity and clarity of
510 findings. State-level results will be most relevant for the state management agency that reports to
511 the politicians who ultimately decide whether to continue investing in environmental flows. By
512 providing a generalised understanding of how rivers respond to environmental flows at the scale
513 relevant to governance, such results are less likely to be bogged down in the detail that can derail
514 communication of scientific results.

515 Finally, the Bayesian approach to data analysis fits naturally into an adaptive management program
516 for environmental flows (Webb *et al.*, 2017b). The expert-based priors employed here provide a
517 robust starting point to improve the analysis of early data sets. Over time however, the posterior
518 distributions of parameters should become the prior distributions for new analyses. This will lead to
519 improved understanding of the factors driving regional and site-specific patterns of ecological
520 responses, and better-informed decision making for environmental flows delivery. Collecting

521 coordinated data over large spatial scales and long time frames, and then analysing those data using
522 hierarchical Bayesian analysis, require considerable commitment from management agencies and
523 funders, and long-term partnerships between researchers and managers (Webb *et al.*, 2014).
524 However, the potential gains are enormous. Through this approach, environmental flows science can
525 move from a discipline that describes responses to changes in flow regimes, to one that is able to
526 make robust predictions of what will happen under future flow regimes. This type of capacity will be
527 important contributor to a shift from experienced-based to evidence-based management of
528 environmental flows.

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661

662 Table 1. Importance of the different covariates. Table shows the different combinations of covariates
 663 included in models, and the proportion of models for each combination.

Covariates included in model	Proportion of models
Season	0.455
Season, Slope	0.453
Slope	0.047
NA	0.044
Season, Stock	<0.001
All other models including stock	0

664

665 **Figure captions**

666 Fig. 1. Map of the location of study sites on 7 rivers within the south-eastern Australian state of
 667 Victoria. There are 3 other rivers in VEFMAP not shown here: the Glenelg, the Loddon and the
 668 Campaspe. Also shown are the example results, showing the range of response types. Inset graphs

669 (a, b, d, e) are for two sites on each of two river systems (Wimmera River and Broken River/Broken
670 Creek). Bars show median predicted vegetation cover (%) with the error bars encompassing the 95%
671 credible interval for the estimate under 3 inundation scenarios: 0 days, 20 days in winter, 50 days in
672 winter, as shown in the key. River-level predictions for the two rivers are also shown (c, f), along with
673 the overall state-level prediction (g).

674 Fig. 2. Diagrammatic representation of the relationship between vegetation cover and the duration
675 and frequency of inundation. c = vegetation cover, T = total duration of inundation, v_0 = vegetation
676 cover for zero days inundation, f = number of inundation events that T is broken into. Reproduced
677 from Webb *et al.* (2015).

678 Fig. 3. Hierarchical structure of the terrestrial vegetation encroachment model. The diagram shows
679 the level of the hierarchy at which different parameters are estimated, and how they link together
680 among levels. Definitions of individual terms are described in the Methods.

681 Fig. 4. Histogram of median values of the m parameter that describes the steepness of the slope
682 with which vegetation cover decreases with increasing durations of inundation. Higher values
683 indicate a greater reduction in cover for a given duration of inundation.

684 Fig. 5. Effects of frequency and between-site variation. Bars show median proportion of vegetation
685 expected at each of the 27 sites under two inundation scenarios relative to zero days inundation.
686 The scenarios are for 50 days continuous inundation in summer, and 50 days inundation in summer
687 divided into 3 separate events. Error bars illustrate the 95% credible interval for the estimate. Sites
688 from each river are grouped together with the most upstream site at the left hand side of the group
689 of bars.

690 Fig. 6. Effect of season of inundation. Bars show the state-level prediction for proportion of
691 vegetation cover (compared to zero days inundation) for 50 days inundation in winter and summer
692 respectively. Error bars encompass the 95% credible interval for the estimate.

693 Fig. 7. Posterior predictive performance of the model. Circles are the average of square-root
694 transformed covers observed across all quadrats for each of 67 surveys (site by year combinations).
695 Superimposed whiskers show the 95% credible interval for the fake data estimate of cover for each
696 survey. Different surveys for each site are grouped together with circle fill denoting survey year as
697 shown in the key. Dotted vertical lines separate sites from different rivers. Y-axis is in square-root
698 transformed units, as this was the scale used for the analysis.

699 Fig. 8. Effects of expert-derived prior distributions and hierarchical model structure. Bars show
700 median predicted vegetation cover under 50 days continuous inundation in winter for the same four
701 sites as shown in Fig. 1 using four different model structures, as described in the key. Error bars
702 encompass the 95% credible interval for the estimate.

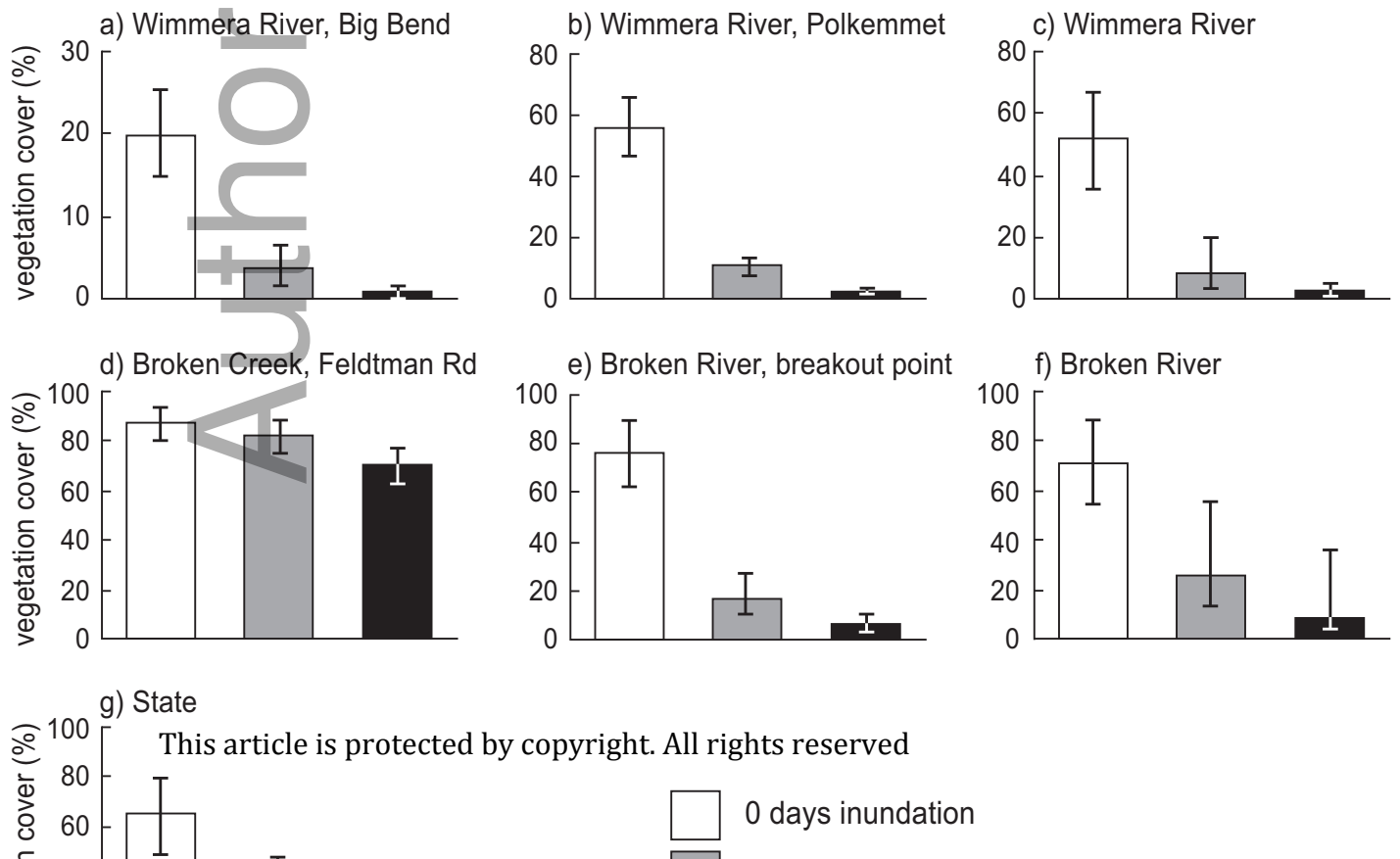
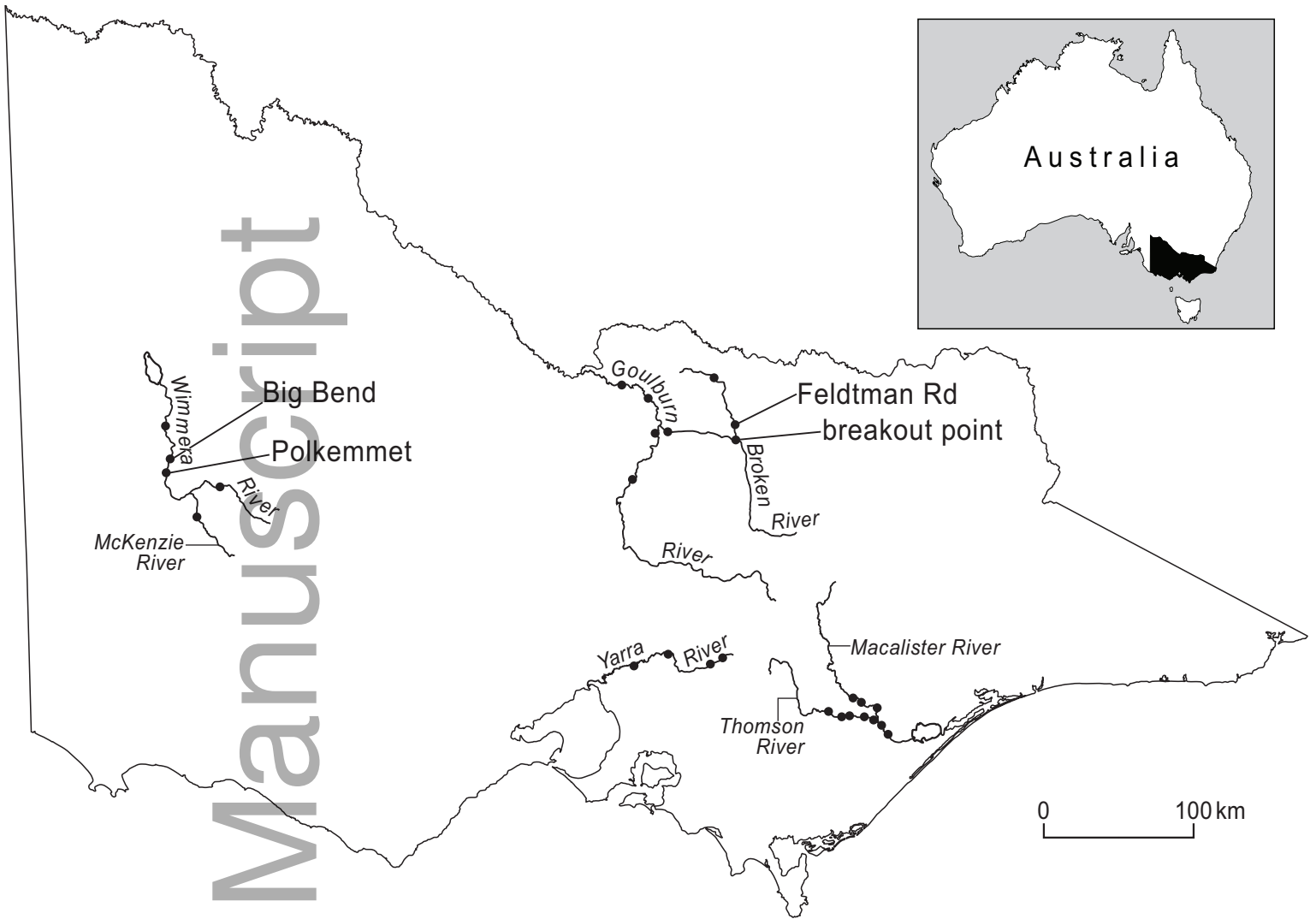
703

704 **Supporting information**

705 A separate file has been submitted for an online appendix

706 Appendix S1: Full OpenBUGS model code, including interpretive commenting.

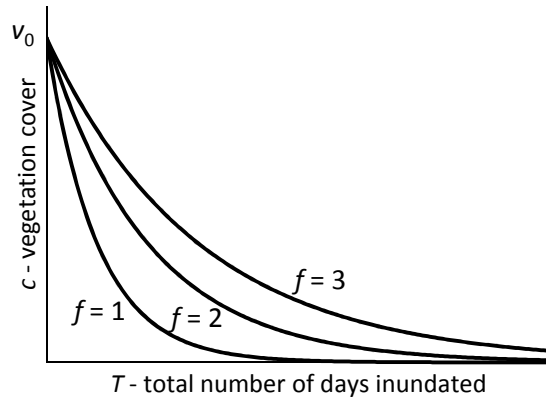
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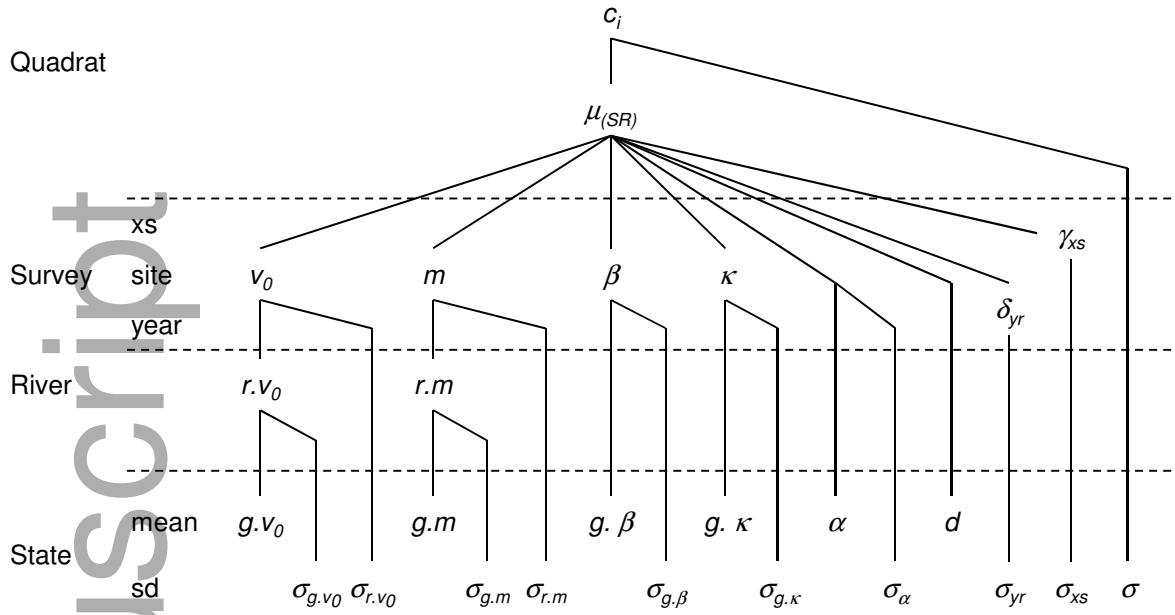
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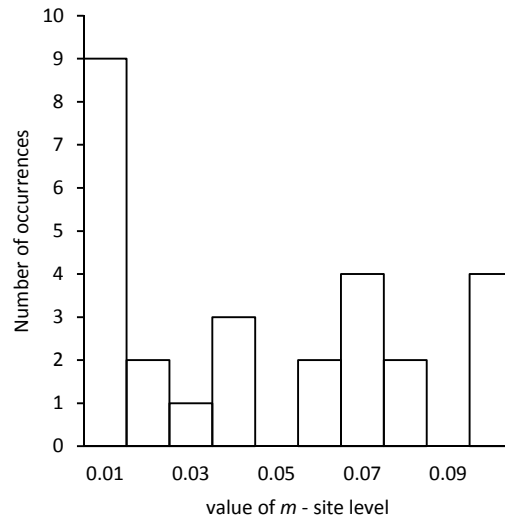


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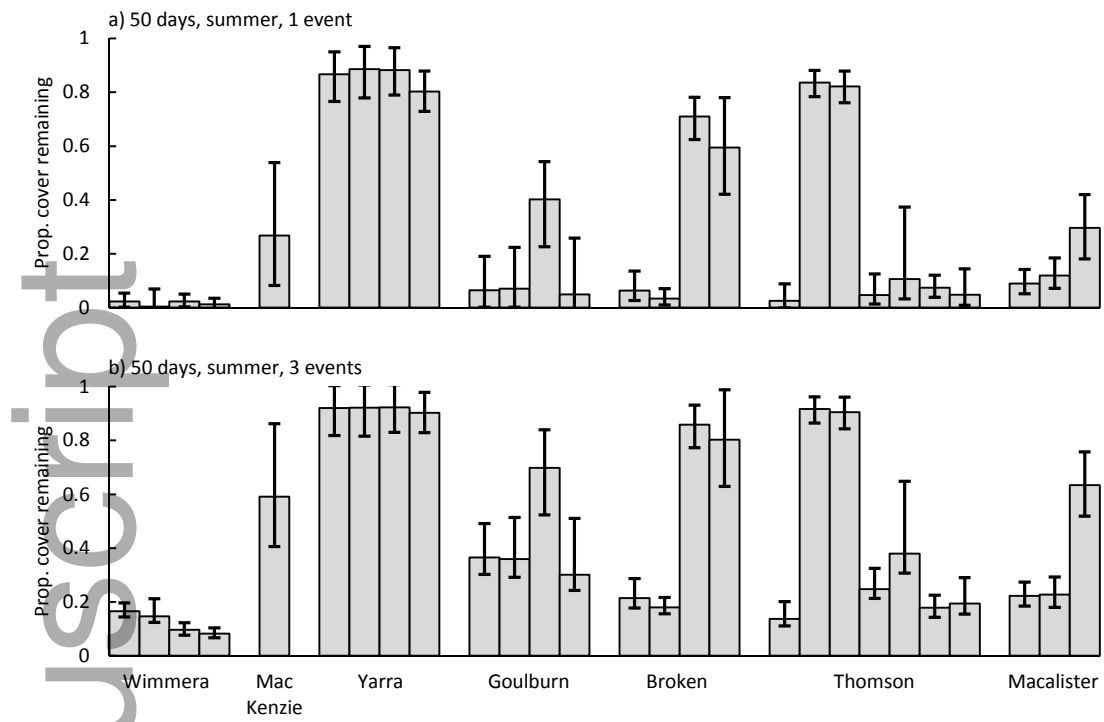
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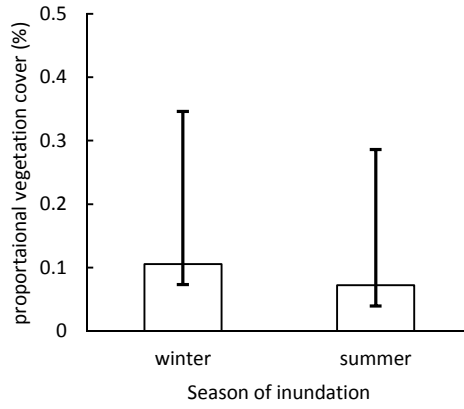
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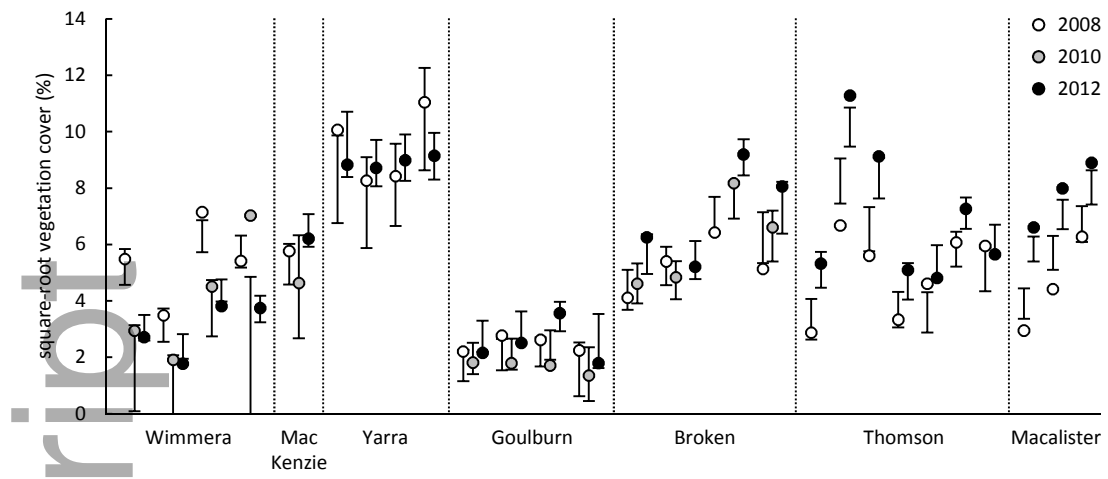
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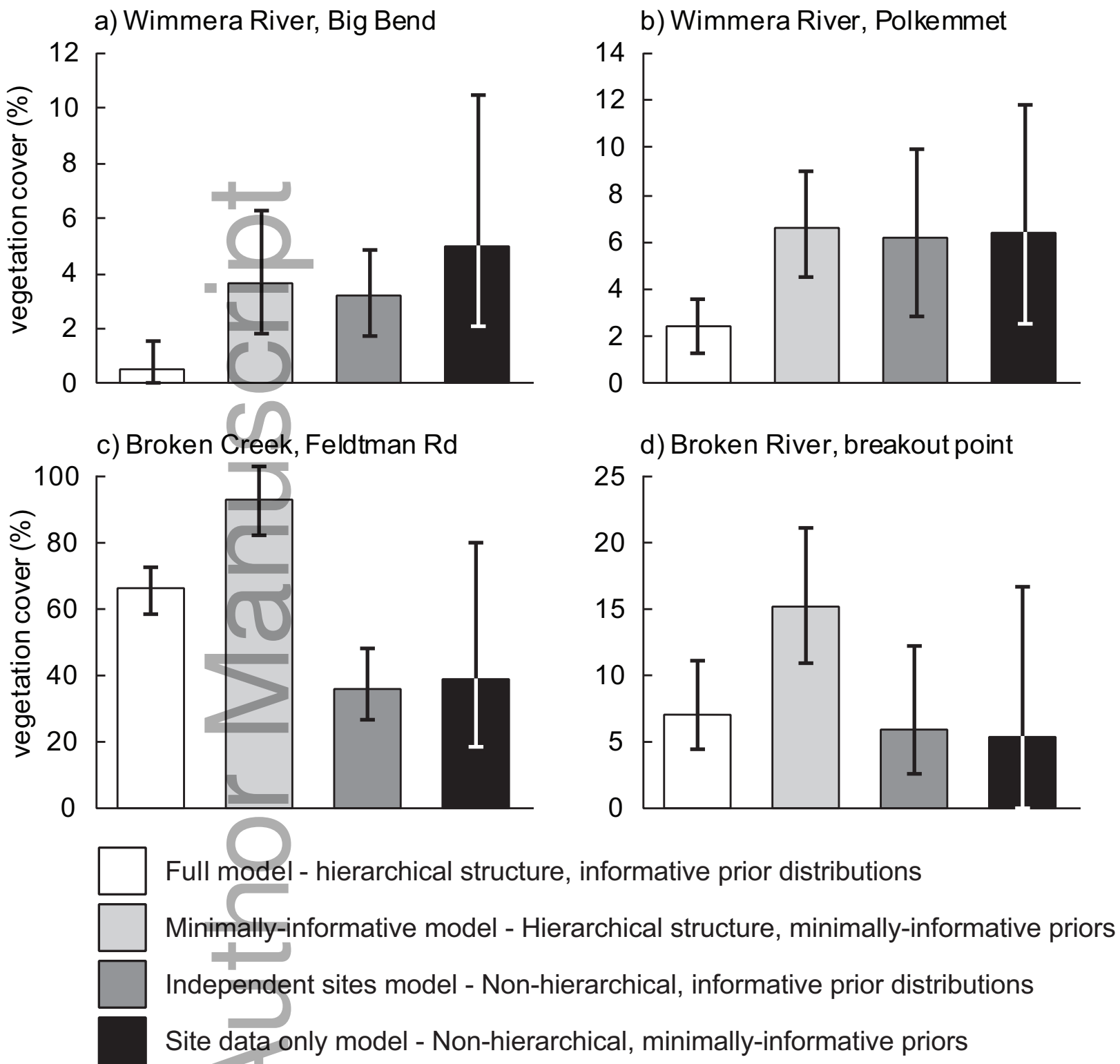
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