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Author/s:
Webb, JA;de Little, SC;Miller, KA;Stewardson, MJ

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DR. ANGUS WEBB (Orcid ID : 0000-0003-0857-7878)

DR. MICHAEL J. STEWARDSON (Orcid ID : 0000-0003-1356-0472)

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

J. Angus Webb[*], Siobhan C. de Little[1], Kimberly A. Miller[2], Michael J. Stewardson

Department of Infrastructure Engineering, The University of Melbourne, Parkville, 3010, Victoria, Australia

[1] Present address: Cesar Australia, Parkville, 3052, Victoria, Australia

[2] Present address: Zoos Victoria, Healesville Sanctuary, Healesville, 3777, Victoria, Australia

[*] Corresponding: angus.webb@unimelb.edu.au, +61 3 8344 9347, +61 3 9344 6215

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

Keywords

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

Introduction

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

In Australia, some 2750 gigalitres – (2.75×10^9 m^3) are being returned annually to the Murray and Darling river systems as environmental flows under the Commonwealth Governments 'Basin Plan'

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

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

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

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

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

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

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

Methods

Study area and data

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

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

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

Statistical model structure

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

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

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

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 (xs) below (eq. 3), with a mean effect of 0 across all levels,

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

$$\gamma_{xs} \sim N\left(0, \sigma^2_{xs}\right) \qquad \sigma^2_{xs} \sim U\left(0,10\right) \qquad \text{(eq. 3)}$$

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

$$\varepsilon_{c_i} \sim U\left(lb_{c_i}, ub_{c_i}\right) \qquad \text{(eq. 4)}$$

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

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

$$\sqrt{c_i} \sim N\left(\mu_i, \sigma^2\right)$$

$$\mu_i = v_0 \cdot e^{\left(-m\sum_{j=0}^{4} e^{\frac{-j\cdot d}{n}} \cdot \frac{T_{ij}}{f_{ij}}\right)} + \alpha \sum_{j=0}^{4} e^{\frac{-j\cdot d}{n}} \cdot Se_i + \beta \cdot Sl_i + \kappa \cdot St + \gamma_{xs} + \delta_{yr} \qquad \text{(eq. 5)}$$

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

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

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

$$m_k \sim N\left(r.m_p, \sigma^2_{r.m}\right)$$
$$r.m_p \sim N\left(g.m, \sigma^2_{g.m}\right)$$

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

We used minimally-informative prior distributions for many of the parameters. Prior estimates of standard deviation parameters were assigned minimally-informative uniform priors: *U*(0,0.1) for $\sigma_{r.m}$, $\sigma_{g.m}$; *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 for different parameters were adopted to improve model convergence; however all posterior distributions for the parameters were unimodal, and distributed over substantially less than the 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, 1.9]. For the mean $g.\beta$., we used a minimally-informative normal distribution *N*(0,10). For other means, we were able to use informative prior distributions. These were derived from an expert-derived Bayesian belief network (BBN), the creation of which is described in de Little *et al.* (2018). Briefly, however, we used structured expert elicitation processes to quantify the conditional probability relationships within a BBN that linked terrestrial vegetation cover to the duration, frequency and season of inundation, and also to the effects of grazing on the river bank. To produce informative prior distributions, the BBN was used to create new data sets that corresponded to different states of the parent nodes, and their consequent distributions of vegetation cover. Most of

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

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

Model fitting and validation

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

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

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

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

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

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

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

Results

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

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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-

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

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

Discussion

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

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

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

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

Coordinated data collection over large scales

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

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

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

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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

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

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

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

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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

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

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

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

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

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

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

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

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

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

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

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

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

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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

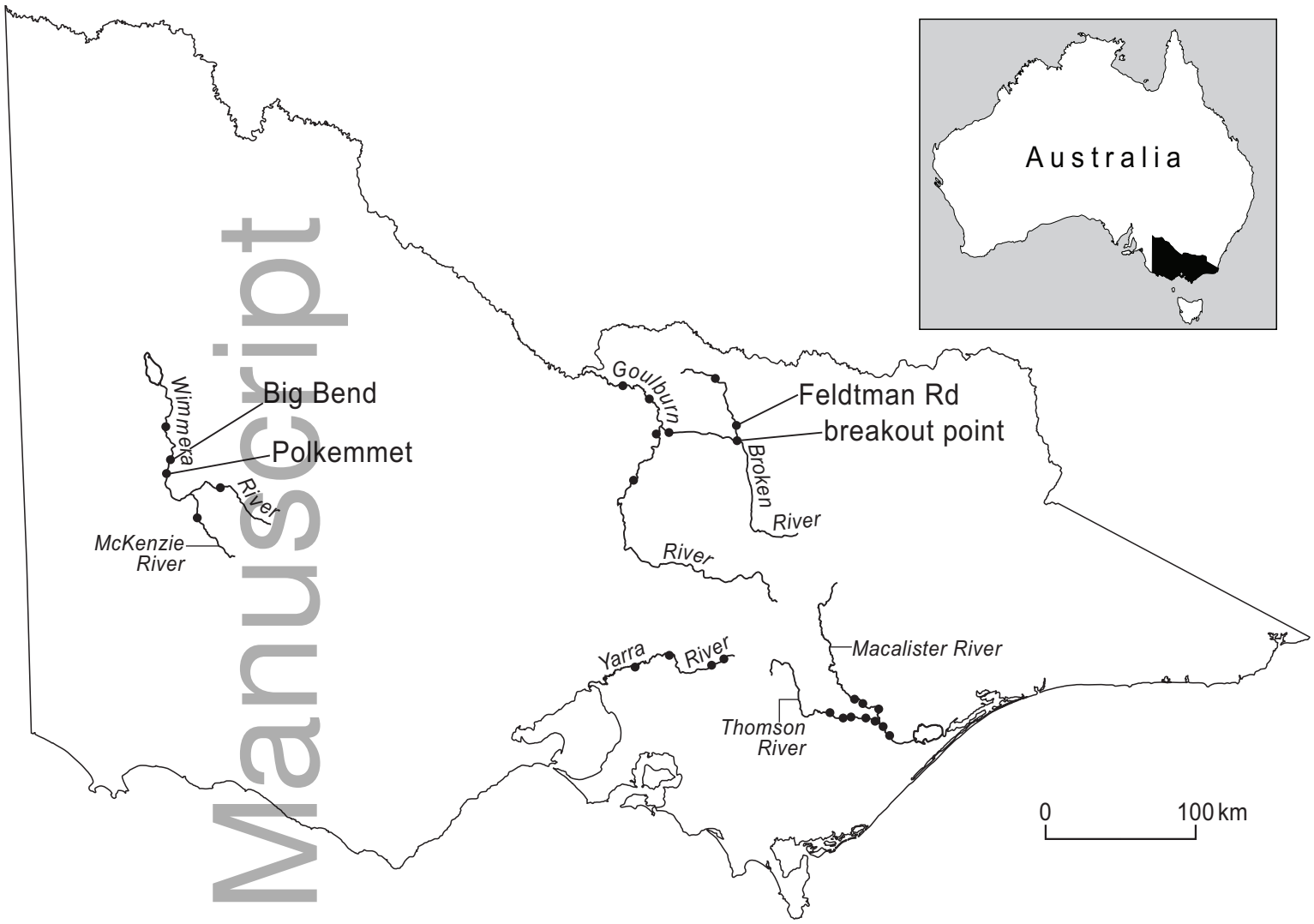
704 ## Supporting information

705 A separate file has been submitted for an online appendix

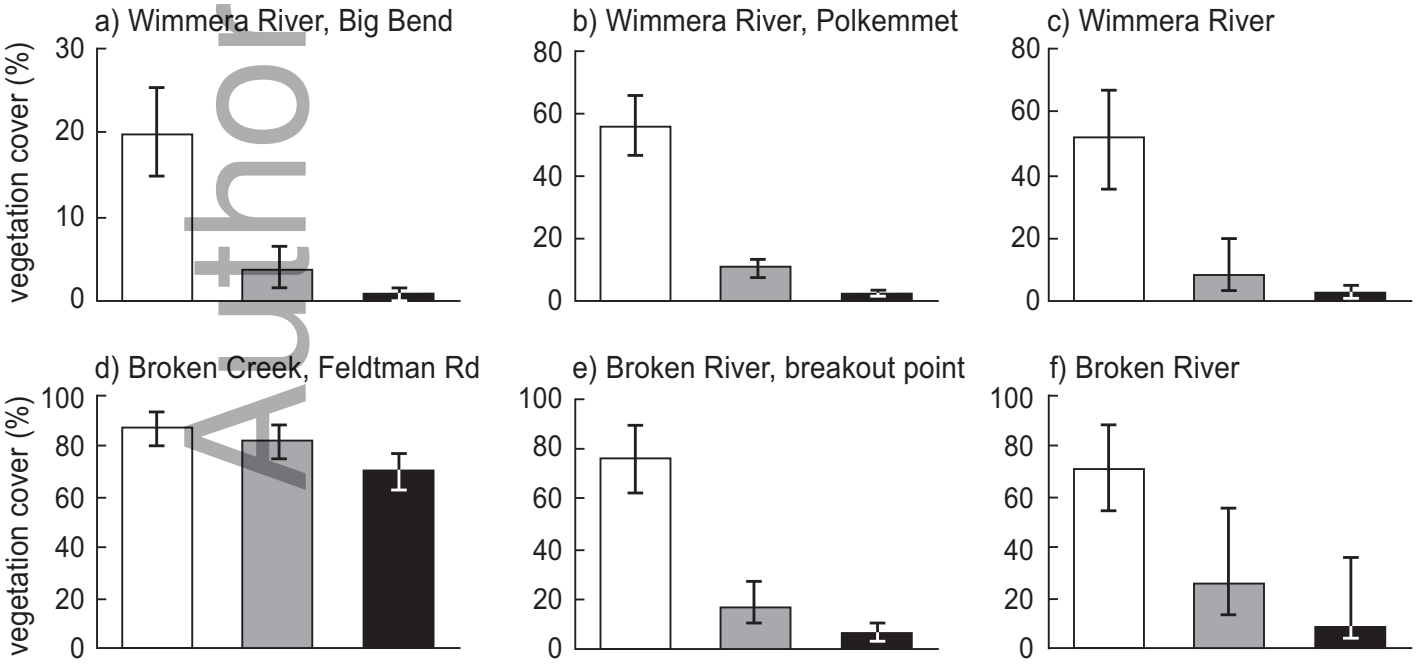
706 Appendix S1: Full OpenBUGS model code, including interpretive commenting.

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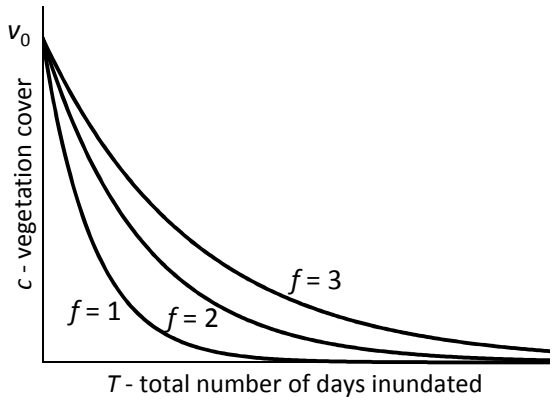
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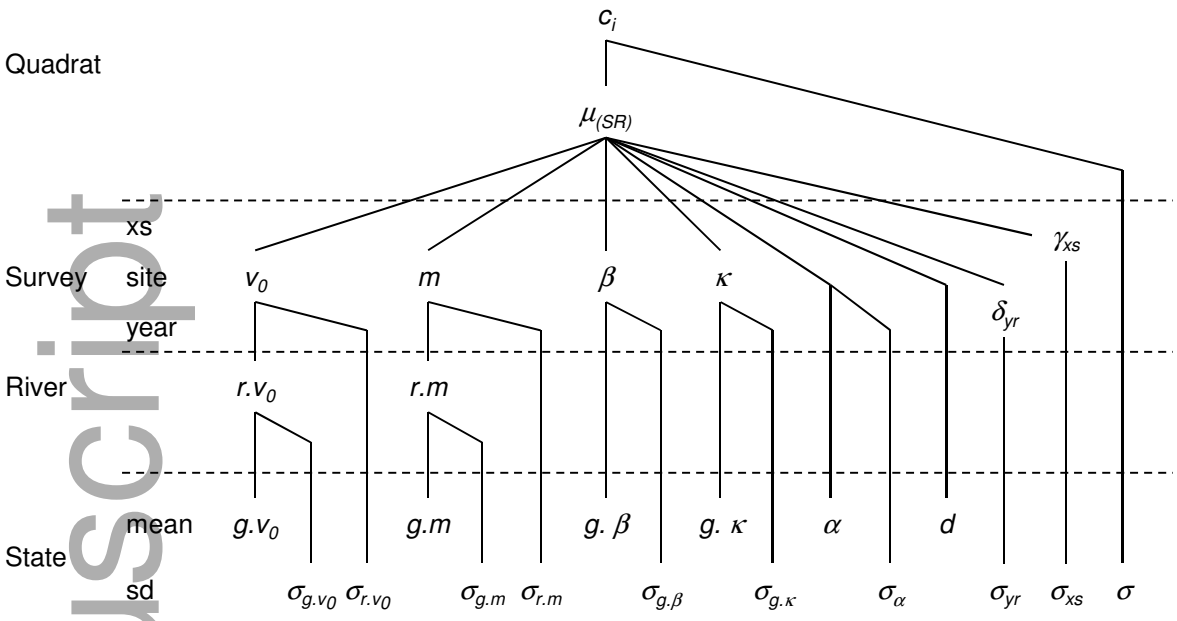


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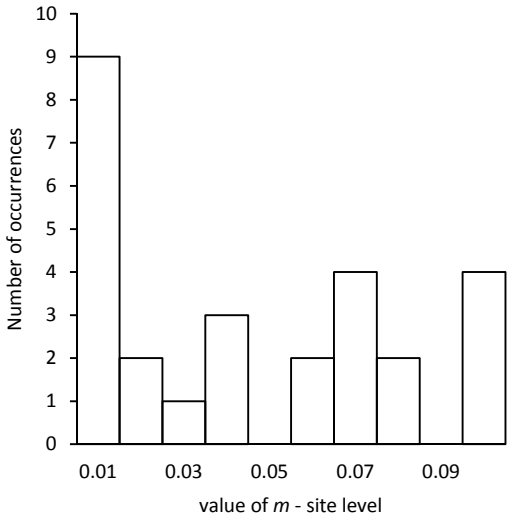
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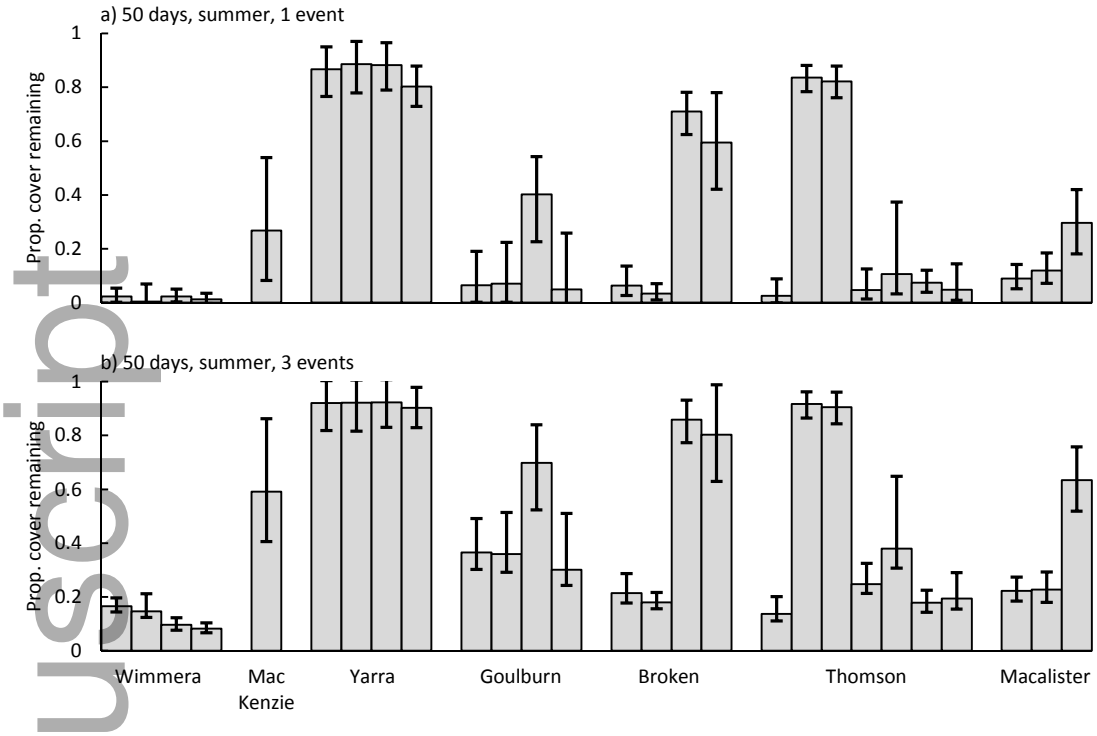
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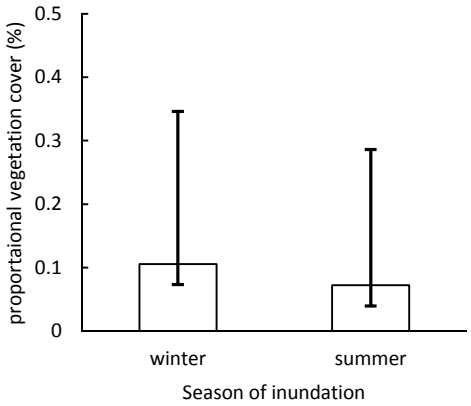


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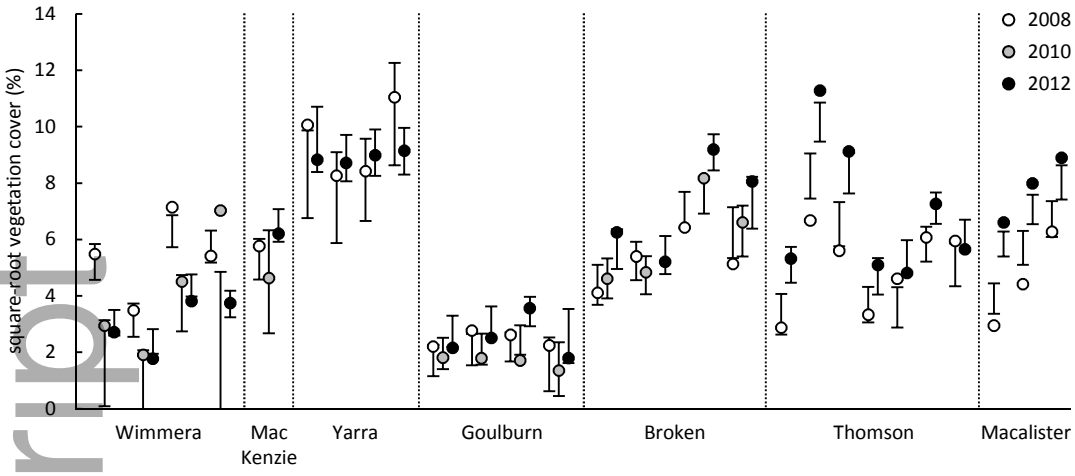
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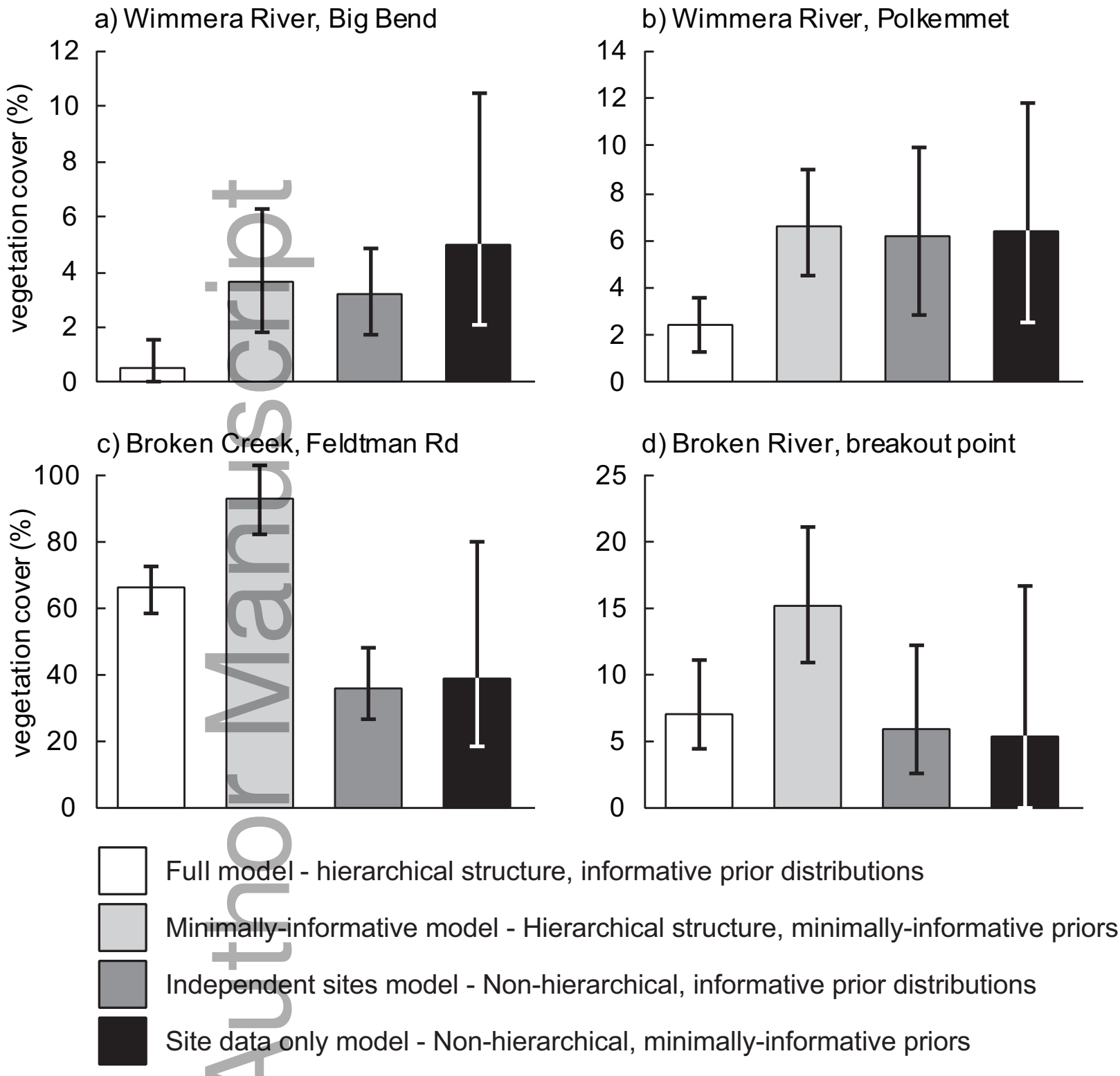
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