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Assessment of environmental flow scenarios using state-and-transition models

Running title: state-and-transition modelling

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Abstract

1. Numerous methods have been developed to support the assessment of environmental flow requirements for rivers. Most methods are based around models of hydrologic time series rather than models of the ecological endpoints of interest. Important limitations that arise from this include 1) an inability to represent the state-dependency of response to future conditions (i.e. the effects of current ecosystem condition on future condition), 2) the inability to predict ecological states through time under alternative flow regimes, and 3) limited sensitivity to compare the differences between flow regimes with similar return intervals of ecologically important events, but different sequencing of those events.
2. Here we outline a simple state-and-transition modelling approach to assess differences in ecological responses to alternative sequences of floodplain inundation events in a lowland river system. Our approach explicitly incorporates the state-dependency of biotic response to flooding, thereby representing the influences of both antecedent conditions and current condition (in this case population state; good > medium > poor > critical).
3. Our approach thus captures the influence of the entire historical sequence of flow events via a first-order Markov chain process. We use prior data and expert opinion to determine state transitions for a broad suite of ecological indicators. Despite being implemented with deterministic transitions, and drawing heavily on expert opinion, this approach greatly improves on existing methods used in environmental flows planning, particularly when comparing scenarios with different sequencing of ecologically relevant flow events.
4. The outputs from these models are testable, and the approach is readily extensible to incorporate probabilistic state transitions and uncertainty, mechanistic links (via increased model complexity) and quantitative measures of population state (e.g. measures of abundance or tree condition). Most importantly, the adoption of such a framework represents a fundamental shift to modelling ecological endpoints rather than relying on quantifying just hydrologic surrogates to assess environmental flow scenarios.

1 Introduction

2 Consideration of the environmental impacts of flow regulation and water extraction is now a central
3 component of water planning in many parts of the world, and has led to rapid growth in modelling
4 methods to underpin the use of 'environmental flows', in an effort to determine the flow regime
5 required to sustain an agreed set of ecological targets (Arthington, 2012). This rapid growth has
6 resulted in a diversity of environmental flow assessment methods emerging over the last fifteen
7 years (Tharme, 2003; King, Brown & Sabet, 2003; Gippel *et al.*, 2009a; Poff *et al.*, 2010). Many of
8 these methods have been developed as a planning tools to help determine a hypothetical future flow
9 scenario (a set of flow 'rules') that describe the frequency, duration, timing and interval between
10 events of particular magnitudes, which, if delivered, will achieve the agreed environmental
11 objectives. These proposed flow rules are often the starting point for comparing the risks to
12 ecosystems under different water management scenarios (Gippel *et al.*, 2009b).

13 A feature common to most hydrological model-based approaches to environmental flow planning is
14 that they rely on summary metrics to describe aspects of the flow series believed to be ecologically
15 important, such as the average frequency or timing of high-flow or low-flow events. This includes
16 widely cited methods such as ELOHA (Poff *et al.*, 2010). A critical assumption of such models is
17 that the ecological values will be sustained at some agreed level over the long-term by the
18 prescribed hydrologic regime (Shenton *et al.*, 2012). Although this greatly simplifies the modelling
19 aspects of environmental flows planning, it limits the ability of these methods to represent
20 ecological feedbacks that affect ecosystem and population dynamics (Lancaster & Downes, 2010;
21 Shenton *et al.*, 2012). Important limitations that arise with these approaches include 1) an inability
22 to represent the state-dependency of response to future conditions (i.e. the effects of current
23 ecosystem condition), 2) arising from this, the inability to predict actual states through time under
24 some hypothesised future flow regime, and 3) limited sensitivity for comparing differences between
25 flow regimes with similar return intervals but different sequencing of ecologically important flow
26 events. A further limitation of many current environmental flow assessment methods is inability to
27 communicate, not just to authorities but to general public, the potential outcomes of different flow
28 scenarios and their variability through time.

29 These limitations have become increasingly problematic as planned environmental flow regimes are
30 being implemented, often in cases in which populations have already been depleted and annual
31 decisions are made about how best to deliver limited available water. A number of papers have
32 either advocated (Anderson *et al.*, 2006; Shenton *et al.*, 2012) or demonstrated (Sakaris & Irwin,
33 2010; Yen *et al.*, 2013) the application of dynamic population models based on modelling vital rates

1 (fecundity, survival etc.) that largely address these issues. Such modelling approaches are widely
2 used in other fields of ecological management, including closely related areas such as fisheries
3 management (Walters & Martell, 2004). A considerable drawback, however, is that such methods
4 require information on aspects of species life-history and population vital rates (fecundity, survival,
5 migration), which is frequently unavailable. This greatly limits the practical implementation of
6 these methods in addressing current management needs.

7 The aim of the current paper is to demonstrate the application of a simple modelling framework
8 based on a state-and-transition approach, which can be used to represent the dynamic responses of
9 plant and animal populations to different flow scenarios using readily obtainable information. State-
10 and-transition models have been widely used to model vegetation dynamics (Daniel *et al.*, 2016),
11 especially in rangeland management (Westoby, Walker & Noy-Meir, 1989; McIntyre & Lavorel,
12 2007; Briske, Fuhlendorf & Smeins, 2005), and have more recently been used to examine long-term
13 changes in floodplain vegetation communities in response to altered flood inundation frequency
14 (Bino, Sisson & Kingsford, 2015). However, these approaches have not been previously applied to
15 explore short-term ecological response dynamics in the context of environmental flows planning.

16 We use floodplain habitats along the lower River Murray in the southern Murray-Darling Basin
17 (MDB), Australia, as a case study to illustrate the approach. The MDB is a large inland catchment
18 of considerable agricultural importance and has recently been the focus of one of the world's largest
19 efforts to reallocate water to achieve desired environmental outcomes (totaling ~AU\$13 billion in
20 water buybacks and infrastructure programmes) under the Murray-Darling Basin Plan
21 (Commonwealth of Australia, 2007; Murray-Darling Basin Authority, 2012b). To date, this
22 reallocation process has been guided by definition of long-term flow regime requirements for a
23 broad suite of riverine and floodplain biota (floodplain and wetland vegetation, wetland birds and
24 fish assemblages), across a large number of MDB sites, using an umbrella environmental asset
25 approach (Swirepik *et al.*, 2016). Environmental outcomes have been inferred based on assessments
26 of how well the long-term environmental flow regime is met. The framework we present here
27 addresses the more specific need for more precise ecological modelling approaches to improve
28 understanding of the dynamic spatial and temporal ecological responses to different flow sequences.
29 This improved knowledge can support ongoing decisions regarding operational sequencing of
30 environmental watering events and monitoring and evaluation of ecological responses.

1 **Methods**

2 **Study system**

3 The Riverland-Chowilla floodplain is situated on the lower reaches of the Murray River in the
4 southern region of the Murray-Darling Basin, Australia (Figure 1). The area consists of a mosaic of
5 aquatic habitats including anabranching creeks, lakes, intermittent wetlands, and periodically
6 inundated floodplains. Vegetation dependent on flood water consists primarily of black box
7 (*Eucalyptus largiflorens* F.Muell.) woodlands, river red gum (*Eucalyptus camaldulensis* Dehnh.)
8 forests and woodlands, lignum shrublands (*Duma florulenta* (Meisn.) T.M.Schust.), tall emergent
9 macrophytes (actually a mix of tall grassland, sedgeland and rushland, and here abbreviated to tall
10 grassland), and submerged macrophytes (here referred to as benthic herblands) (Table 1) (Newall *et*
11 *al.*, 2009; Murray-Darling Basin Authority, 2012a). Floodplain wetlands are also critical for
12 waterbird breeding, feeding and refuge, and the Riverland is listed under the Ramsar convention
13 (Murray-Darling Basin Authority, 2012a). Both the main river channel and anabranch habitats
14 support significant populations of native fish such as Murray cod (*Maccullochella peelii* (Mitchell,
15 1838)) (Zampatti, Leigh & Nicol, 2011), and there are numerous terrestrial and aquatic fauna that
16 depend on the health of the floodplain vegetation for their survival (Murray-Darling Basin
17 Authority, 2012a).

18 Rainfall is low, with a long-term annual average of just 252.4 mm at Renmark, South Australia, at
19 the western end of the river reach (station 024003; Bureau of Meteorology). Hence floods derived
20 from wetter parts of the MDB upstream from the Riverland-Chowilla floodplain are an important
21 source of soil moisture. Inundation modelling based on flood mapping (Overton, 2005) provides a
22 good understanding of the inundation extent associated with different magnitude floods (Figure 1),
23 and variation in the frequency of different magnitude floods has created distinctive patterns of
24 vegetation distribution on the floodplain (Figure 2c). Flood frequency has been greatly reduced by
25 river regulation (Figure 2a,b), and this has had a significant negative effect on the condition and
26 likely persistence of some plant communities (Murray-Darling Basin Authority, 2012a).

27

28 **Modelling approach**

29 *Overview*

Our approach involved four key steps; (1) Conceptualisation and construction of state-and-transition models that reflect both the distinct states of the vegetation as well as transition pathways that occur under different environmental conditions, (2) development of alternative flow scenarios for comparison, (3) running the models combining flow sequences with the state transitions, and (4) interpreting the resultant time series. Each of these steps is described in more detail below.

Conceptualisation of the state-and-transition models

Our approach to conceptualising vegetation condition states and transitions builds on the conceptual model of Souter *et al.* (2010), which describes serial changes in the canopy of river red gum forests and woodlands in response to droughts and floods. The conceptual model recognizes that trajectories for canopy decline and canopy recovery are distinct, rather than a simple reversal, and do not proceed at the same rates (Figure 3).

This model, with its separation of decline and recovery trajectories and the flow events that drive these, was adapted to apply to each of the six major vegetation community types (see *study system* section for the names of each group). The response of each vegetation community to wet/dry cycles was assumed to reflect that of the dominant species in each group (Table 1), for which responses are relatively well known.

Vegetation condition (or 'health') was categorized on an ordinal scale (good > medium > poor > critical), with defined transitions between states. The four condition states are shaped by the overall goal for environmental watering which was "*to provide a flow regime which ensures the current extent of native vegetation of the riparian, floodplain and wetland communities is sustained in a healthy, dynamic and resilient condition*" (Murray-Darling Basin Authority, 2012a), thus placing an emphasis on maintaining current vegetation rather than expanding it. The dominant species differ in life-history, resistance and resilience, mode of recovery, and longevity of propagules (Table 1) and hence time between transitions in both decline and recovery (Table 3).

The general patterns of decline in vegetation condition in the absence of flooding (i.e. from good to medium, medium to poor, and poor to critical) are well established, with transitions occurring after a given number of years with no effective flooding (solid lines in Figure 3). These were derived from expert opinion and existing literature (Roberts & Marston, 2011; Rogers & Ralph, 2011), acknowledging that local conditions (e.g. access to groundwater) can lead to variability in the timing and occurrence of these transition sequences.

1 The recovery of floodplain trees was informed by the regeneration model of George (2004), with
2 transitions along the recovery trajectory occurring after a given number of floods in a specified time
3 (dotted lines in Figure 3). The recovery trajectory for forests and woodlands has an additional state
4 *intermediate* due to the length of time needed for trees to make a full recovery (i.e. to a good state)
5 from being in poor or critical condition. A description, the source of information and an explanation
6 for each transition for each vegetation type is given in Overton *et al.* (2014). All ecological
7 transitions were subject to extensive peer review and scrutiny by floodplain vegetation ecologists
8 within government agencies.

10 ***Development of alternative flow scenarios***

11 The development of alternative flow scenarios requires modelling potential rainfall and runoff
12 sequences and associated water availability in water storages over time, estimating downstream
13 water demands for consumptive use (primarily irrigation), including specific flows required to meet
14 environmental objectives (whether these be prescribed high flow events or some other component
15 of the flow regime). Here we focus on a comparison of three such flow scenarios: Pre-development
16 (with no anthropogenic water use), Development (with current anthropogenic demands but limited
17 additional environmental releases), and E-flow, which is indicative of the expected sequencing of
18 high flows in the River Murray if water recovery from consumptive users under the Basin Plan were
19 fully implemented. (Figure 2a, b). These scenarios were derived from hydrologic models developed
20 for the River Murray by the Murray-Darling Basin Authority (see Overton *et al.*, 2015 for details).
21 Hydrology was expressed as a time series of annual flood sequences (1 = flood criteria met, 0 =
22 flood criteria not met) spanning 114 years (1895-2009) for each flow scenario. For each scenario,
23 we further examined multiple flood events of different magnitude and duration (40k, 60k and 80k
24 ML/day; Table 2). These different flow bands each inundate increasingly large areas of the
25 floodplain, and like natural floods, tend to occur with declining duration as magnitude increases.
26 We assume that each vegetation type will show uniform trends through time within the incremental
27 area of the floodplain inundated by the increasing flood sizes we examined. As well as illustrating
28 the methodological approach, the three scenarios also illustrate the scale of potential benefits to
29 floodplain vegetation of additional environmental flows to the Riverland-Chowilla floodplain.

30 We did not consider the role of environmental engineering ‘*works and measures*’, such as the use of
31 regulators and levees to divert water onto floodplains at a lower river stage than required naturally,
32 which may provide higher inundation frequencies to some parts of the floodplain than are modelled
33 here (Bond, 2016). Such approaches are not without their risks (Stoffels *et al.*, 2014; Bond *et al.*,

2014; Pittock, Finlayson & Howitt, 2012), but are being examined and in some cases implemented at various sites within the southern MDB. The method is very amenable to including these additional ‘engineered’ floods.

Combining transition tables with hydrologic series

From the initial time series describing the sequence of flood/non-flood years, additional time series were derived that described the cumulative number of years n since the last flood, and the cumulative number of floods m in the previous x years, where x represents the window of interest in triggering transitions along the recovery trajectories (Table 3). These two series define the transitions between vegetation states that will occur in any given year by reference to a set of ‘if-then’ rules reflecting the state transitions (Table 3). These rules were coded in R and applied to the time series describing the inputs to derive a sequence of condition states for each vegetation type for each year under each flood magnitude and flow scenario. In the results presented here all vegetation types were initially (at t_0) in a ‘good’ state, noting that the time series shown here start at t_1 .

Summarising outputs

The resultant condition states were summarised graphically and through the calculation of summary statistics describing average condition scores and % time in different states under each flow scenario. For the purposes of summarizing time series, condition scores were converted to an ordinal scale ranging from good (0.9) through medium (0.6), poor (0.3) and critical (0.1). In the results presented we include individual time series for three of the vegetation types (river red gum woodland (hereafter RRG), lignum shrubland and benthic herbland), together with summary plots for all vegetation types. We also provide additional plots for four of the six vegetation types as supplementary material, however RRG forest and tall grasslands are excluded to keep plots readable, and because they are relatively rare at this site (Figure 2C). We emphasise that the raw time series are valuable as a communication tool in demonstrating the divergent dynamic cycles and differing resistance and resilience traits of different vegetation types to drought. However, a range of summary metrics may be useful, such as the percent of time in different states, average state (for continuous scales) etc.

The predictions arising from the models that we present have not yet been validated, although work on this logical next step has commenced. We therefore seek primarily to demonstrate the utility of a state-and-transition modelling approach in the context of environmental flows planning. At the

same time, the ability to generate explicit predictions of the expected system state at any given point in time, rather than just over the long-term, is a clear advantage of this modelling approach over those based on hydrologic summary metrics.

Results

Comparison of the three flow scenarios shows the marked effect of water resource development on the frequency of ecologically important high flow events that connect the river to adjacent anabranch, wetland and floodplain habitats (Figure 4). For example, events exceeding 40K ML/day for 90 days occurred on average more than 1 in every 2 years under the Pre-development scenario, but occur only 1 in every five years under the Development scenario. Similarly, large events (>80K ML/day for 30 days) occur approximately every 10 years under the Development scenario rather than every 1 in 3 years under the Pre-development scenario (Figure 4). The additional flows under the E-flow scenario lead to an approximate doubling of the frequency of 40K ML/day and 60K ML/day events (to ~2 in every 5 and 1 in every 3 years respectively), but result in a much smaller increase in the frequency of 80K ML/day events (Figure 4).

These differences in the average return interval of floods under each scenario are well reflected in the modelled flood sequences, and in the dynamics of vegetation condition states over time (Figure 5-7). Individual vegetation types showed distinct trajectories through time and in their response to the different flow scenarios. For example, the frequency of 40K ML/day events under the Pre-development scenario was sufficient to maintain RRG woodland in 'good' condition almost permanently, whereas RRG woodland condition fluctuates considerably under the Development scenario, with some periods in critical condition and lagged recovery from those periods (Figure 5). The E-flow scenario maintains RRG woodland in good condition for most of the time.

There were also marked differences between flow scenarios for other vegetation types such as lignum shrubland (Figure 6) and benthic herbland (Figure 7), although these groups also showed more dynamic responses to individual flood events, with benthic herblands in particular showing both very rapid declines and recovery in response to wet and dry periods respectively. Such dynamics closely mirror the rapid response of macrophytes to wet/dry cycles. The response of other vegetation types also varied in a manner consistent with the resistance and resilience patterns prescribed by their respective transition tables (Figures S1-S3).

Patterns of vegetation response higher on the floodplain (within areas reached by 60K and 80K ML/day flows) showed similar general trends, although most vegetation types would be predicted to

1 be in poorer condition due to the reduced flood frequency (Figure 8; Figures S2-S3). Notably, the
2 smaller relative increase in the frequency of 80K ML/day events from the Development to the E-
3 flow scenario was insufficient to restore black box woodland from critical condition within the 80K
4 ML/day flood zone, except toward the end of the series, when there was a sequence of 5 floods in
5 less than 10 years. A similar pattern is evident for RRG woodland and forest when compared to
6 areas influenced by the 40K and 60K ML/day events. Again, comparable trends and dynamics can
7 be seen for the other vegetation types, with smaller differences between the Development and E-
8 flow scenarios, consistent with the smaller change in average return interval. A number of
9 sequences clearly illustrate the minimal benefits of single isolated flood events in improving
10 vegetation condition (e.g. Figure 6-7).

11 The differences among the three flow scenarios (Pre-development, Development and E-flow) were
12 also summarised by examining the mean condition scores over the entire flow record (Figure 8).
13 Differences in average condition parallel expectations from examining the trajectories over time,
14 especially the reduced differences between the Development and E-flow scenarios for the larger
15 flow events (>80K ML/day), which are much less influenced by active water management. The
16 mean scores across each of the three floodplain inundation sequences reflect a clear gradient in each
17 vegetation type's water requirements. What is not revealed by these summary plots of each
18 vegetation type to different watering regimes, is how the spatial distribution of different vegetation
19 types across the floodplain influences the overall actual vegetation condition at a whole of
20 floodplain scale (Figure S3). Ultimately, at the whole of floodplain scale, despite the strong positive
21 response by some vegetation types to more frequent flooding (especially under the E-flow
22 scenario), relatively large areas of vegetation are predicted to remain in poor condition for much of
23 the time because only a small fraction of that communities =current distribution is predicted to
24 experience additional flows under the proposed E-flow scenario. From this perspective the
25 additional environmental flows predominantly seem to benefit benthic herblands close to the river
26 channel.

27

1 Discussion

2 Despite strong evidence for state-dependencies in the response of aquatic ecosystems to flow
3 variability (e.g. Souter *et al.*, 2014), most efforts to determine environmental flow requirements
4 focus on quantifying the water volumes associated with achieving a planned flow regime defined by
5 average return intervals of ecologically important flow components. In reality however, ecosystems
6 respond dynamically and differently to specific flow sequences. Methods reliant on average return
7 intervals ignore this state-dependency of ecological responses to flow variability, limiting their
8 ecological sensitivity as well as their utility in supporting operational decision making regarding the
9 outcomes of individual flow events. Here we have presented a simple framework based on state-
10 and-transition modelling that addresses these limitations. We have used the response of floodplain
11 vegetation to flow scenarios with different inundation sequences as a means of demonstrating the
12 approach.

13 Our modelling of state-condition over a 114-year time frame illustrates that vegetation condition at
14 Riverland-Chowilla is naturally dynamic and varies across the floodplain during droughts even in
15 the absence of river regulation. As well as allowing condition to be visualised over time, when
16 compared to approaches that rely on hydrologic summary metrics describing only the average
17 return interval of inundation, this approach greatly increases the sensitivity of models to represent
18 differences between scenarios. As predicted from expert opinion, our models demonstrated
19 significant differences between vegetation condition depending on the characteristics of the flow
20 scenario, and two flow scenarios with equivalent 'percentage of time inundated' can vary greatly in
21 their final condition state depending on the sequencing of flood events. For example, a vegetation
22 type inundated on average every 1 in 5 years will respond very differently if those events occur
23 every 1 in 5 years or 2 consecutive years in every 10.

24 As already mentioned, we have not had the opportunity to formally validate the predictions of our
25 model against empirical observations of changes in vegetation condition, but initial work has
26 recently commenced on this important next step. To this end, we regard the work described here as
27 preliminary and focused on method development. Nevertheless, anecdotally our results support the
28 observed widespread poor condition of water dependent vegetation in the region under a regulated
29 flow regime (i.e. the Development scenario; Cunningham *et al.*, 2018), as well as the limited
30 response to individual flow events by woody vegetation that is in poor condition (e.g. Souter *et al.*,
31 2014). The E-flow scenario supports expectations that additional water allocations will improve
32 average condition and reduce the periods of time of poor to critical condition. However, these
33 improvements were strongest for vegetation occurring on lower parts of the floodplain, with

1 vegetation types restricted to higher parts of the floodplain likely to benefit less from environmental
2 flows. This reflects that large volumes of water are required to restore flow to higher parts of the
3 landscape and the influence of constraints such as flooding of private land and bridges limiting the
4 ability to actively manage the restoration of large flood events. Even within low lying areas there
5 appear to be some drought cycles of a duration that may exceed the estimated longevity of seeds
6 (e.g. *Vallisneria australis*) and of rhizomes (e.g. *Phragmites australis*) in dry sediment (Carpenter
7 & Brock, 2011), which may greatly reduce the resilience of these species. Where establishment of
8 new individual plants does occur by reproduction from seed or vegetative propagules, germination
9 and recruitment often require hydrologic conditions that differ from those that maintain established
10 plants (van der Valk, 1981; Little *et al.*, 2011). These hydrologic conditions are not included in our
11 scenarios, and hence regeneration in the sense of recruitment of new individuals has not been
12 explicitly addressed. Modifying the models to include an ‘absorbing’ state, from which no recovery
13 transition occurs, would be a worthwhile extension to consider.

14 Over longer time scales, the loss of suitable conditions to maintain particular vegetation types
15 within an area will drive transitions not just in condition, but between different vegetation
16 community types (Bino, Sisson & Kingsford, 2015). A powerful extension of the work presented
17 here would be to combine models of vegetation condition such as we present, with models of
18 community change (such as those of Bino, Sisson & Kingsford, 2015), to simultaneously explore
19 spatio-temporal dynamics of condition and community structure. Such models are commonplace in
20 other areas of plant ecology, such as fire-ecology and forestry (Perry & Enright, 2006; Daniel *et al.*,
21 2016), and will be increasingly relevant in addressing the likely changes in floodplain vegetation
22 associated with longer-term climate change and altered hydrologic regimes.

23 The state-and-transition approach is flexible and well suited to incorporating climate change as well
24 as numerous other hydrologic and non-hydrologic drivers that may influence vegetation dynamics.
25 These include access to alternative water sources such as rainfall and groundwater, retention of
26 water in deeper wetlands, and influences that can modify responses, such as land management,
27 salinity, and acid sulfate soils. For example, Horner *et al.* (2016) show that the positive influences
28 of flooding on RRG seedling survival can be offset by grazing, salinity and sedimentation.
29 Validation of our model predictions with empirical observations would need to consider these
30 multiple interacting stressors. It is recommended that future model iterations incorporate the results
31 of long-term monitoring and targeted research undertaken to test and refine existing understanding
32 of state transitions. For example, Souter *et al.* (2014) demonstrate state dependency of changes in
33 crown extent of RRG following increased water levels in anabranches at Chowilla. Such data
34 collected across multiple years and sites would facilitate empirical calibration of state transitions,

1 including information on non-flow related influences. For vegetation, this approach could be
2 extended to examining changes in remotely-sensed data collected over much larger spatial scales
3 (e.g. Normalised Difference Vegetation Index [NDVI]). Similarly, time series of recruitment and
4 abundance data for animals (fish, waterbirds, amphibians, terrestrial grazers etc.) could be used to
5 derive semi-quantitative abundance-based classes and state transitions.

6 The modelling framework described here can also be applied to other taxa such as fish and
7 waterbirds using habitat preferences, longevity, and likely growth and survival under different flow
8 conditions to define states and transitions, but at present these exist only in the grey literature
9 (Overton *et al.*, 2015). It would be interesting to contrast the sensitivity/accuracy of simple state-
10 and-transition approaches with more sophisticated demographic models for taxa where both models
11 are available. Important components of modelling best practice also include consideration of the
12 influence of initial conditions, examination of model sensitivity to individual parameters, and
13 consideration of parameter uncertainty (Schmolke *et al.*, 2010). While not reported here, Overton *et*
14 *al.* (2014; 2015) undertook some of these evaluations, and readers are directed to these reports for
15 further insights.

16 As a technical aside, in the present study we adopted a rule based approach to modelling state
17 transitions, but it is also straightforward to implement a matrix based approach, which offers several
18 advantages, including the ability to include non-deterministic state transitions, and the use of matrix
19 multiplication to model output sequences. The inclusion of probabilistic state transitions can
20 represent both knowledge uncertainties and/or stochastic responses by vegetation to environmental
21 variability (Souter *et al.*, 2014), while matrix multiplication offers simplified coding. Non-
22 deterministic transitions are likely to be common, and this would offer a significant advance in
23 aligning the models with empirical data (Bino, Sisson & Kingsford, 2015). The principle difference
24 from a rules based approach, is in how the transition tables are presented, which would require
25 converting the transition tables as presented here (Table 3) to a set of matrices describing the
26 possible transitions in any given year, with distinct matrices being created for each class of year
27 (e.g. years 1-5 post flood, years 6-10 post flood etc.). For deterministic scenarios such as those
28 adopted here these matrices will be sparse with only a single transition possible in any given time
29 step (i.e. the matrices consist of only 0's and 1). Once these matrices have been transcribed,
30 multiplication of the matrix describing current vegetation states with the appropriate transition
31 matrix for each time step will produce a series of matrices describing vegetation condition through
32 time. This approach parallels matrix selection methods in population biology (Caswell, 2001). It is
33 worth noting that both the rule-based and matrix-based methods rely on vegetation condition being
34 described by a first-order Markov process (i.e. future vegetation states depend on the current state

only, rather than on past states). This is a distinct advantage of the state-and-transition framework over trying to describe complex hydrological sequences using lags or multi-year windows as might become tempting if examining this question through a lens more reliant on describing the sequence of flow events. Finally, there is also great opportunity to apply the modelling framework we have described to explore the impacts of a range of other factors influencing vegetation dynamics, such as salinity, fire, grazing and climate variability and climate change. The primary requirement is that environmental conditions through time can be described together with the state-dependent changes in vegetation that result under those different conditions.

Conclusions

The state-and-transition approach builds on the foundational hydrological models that have been widely used in environmental flow planning by providing a simple framework for translating hydrological regimes into an ecological outcome. One principal benefit of this approach is the ability to integrate the entire historical flow sequence and past ecological condition in determining ecological condition at any given point in time. The approach thus integrates both ‘individual event’ and ‘regime’ based perspectives on flow-ecology relationships – perspectives that are frequently seen as being at odds with one another when considering flow-ecology relationships. Other technical benefits include the increased ecological realism and greater consistency between the model predictions and the measurement of ecological ‘response’ that is possible within monitoring and adaptive management programs (Stoffels, Bond & Nicol, 2018). Finally, there is likely to be stronger alignment between dynamic ecological models and the emerging needs of water managers and decision makers who require guidance on how current ecological condition should influence operational planning (Horne *et al.*, 2017; Stoffels, Bond & Nicol, 2018). The relative simplicity of the approach is also likely to enhance its potential for adoption. Greater use of models that capture dynamic ecological responses to flow variability offers the potential for important advances within the field of environmental flows research, and we thus encourage others to explore the utility of this and other related simulation-modelling approaches.

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2 Table 1. Summary of the ecological characteristics for each of the vegetation types included in the
 3 modelling. Note river red gum woodland has a lower canopy density (Cunningham *et al.*, 2018) and
 4 require less frequent flooding than river red gum forest (Table 3).

Vegetation type	Ecological Characteristics
Black box woodland (<i>Eucalyptus largiflorens</i>)	Long-lived (centuries). Generally slow-growing and drought resistant. Recovers from minor stress by re-growth from leaf-tips; recovers from major stress by re-establishing canopy and branches from epicormics buds. Does not have a persistent seed bank.
River red gum woodland (<i>Eucalyptus camaldulensis</i> <i>var camaldulensis</i>)	Long-lived (centuries). Fast growing and drought sensitive. Recovers from minor stress by re-growth from leaf-tips; recovers from major stress by re-establishing canopy and branches from epicormics buds. Does not have a persistent seed bank.
River red gum forest (<i>Eucalyptus camaldulensis</i> <i>var camaldulensis</i>)	Long-lived (centuries). Fast-growing and drought sensitive. Recovers from minor stress by re-growth from leaf-tips; recovers from major stress by re-establishing canopy and branches from epicormics buds. Does not have a persistent seed bank. Flooded more regularly than red gum woodland.
Lignum shrubland (<i>Duma florulenta</i>)	Presumed to be long-lived. Drought resistant rootstock by dry-sensitive canopy. Characterised by slow decline and rapid recovery. Does not have a persistent seed bank.
Tall grassland (<i>Phragmites australis</i>)	Perennial. Canopy is seasonally renewed and sensitive to dry spells. Canopy re-establishes from underground rhizome which is key to persistence. Seed bank not important for on-site persistence.
Benthic herbland (<i>Vallisneria australis</i>)	Perennial. Canopy is sensitive to dry spells. Canopy re-establishes from root-stock and rhizome, or from seed bank. Root-stock and rhizome more sensitive to dry conditions than seed bank. Recovery from root-stock and rhizome is more rapid than from seed.

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Table 2. Summary of the floodplain inundation events used in the flood-sequences modelling.

Flow volume (ML/day)	Event duration (days)	Timing
40,000	90	Jun-Dec
60,000	60	Jun-Dec
80,000	30	Jun-May

Table 3. Number of years before transitions occurred between states for each vegetation type in the absence of, or following, flooding. Note the distinctive hysteresis in recovery of some vegetation types (see Figure 3). First-order modelling of these transitions required a running count of the number of flood events occurring within different multi-year time windows.

Condition States	Vegetation types					
	BB W	RRG W	RRG F	L S	TG	BH
Decline trajectory: number of consecutive years with no floods						
G ⇒ M	5	5	3	1	1	1
M ⇒ P	5	4	3	6	2	1
P ⇒ C	5	4	4	4	8	7
I ⇒ P	4	4	3	n.a	n.a	n.a
Recovery trajectory: number of floods in number of years						

M ⇒ G	1	1	1	1	1	1
P ⇒ M	n.a.	n.a.	n.a.	2	2	2
C ⇒ P	n.a.	n.a.	n.a.	2	n.a.	n.a.
P ⇒ I	3+ in 10 y	3+ in 9 y	3+ in 9 y	n.a.	n.a.	n.a.
C ⇒ I	5+ in 18 y	5+ in 15 y	5+ in 15 y	n.a.	n.a.	n.a.
I ⇒ G	2+ in 7 y	2+ in 7 y	2+ in 5 y	n.a.	n.a.	n.a.
C ⇒ M	n.a.	n.a.	n.a.	2	2	2

- 1 Key to Vegetation types: BB W = black box woodland, RRG W = river red gum woodland, RRG
- 2 F = river red gum forest, L S = lignum shrubland, TG = tall grassland, and BH = benthic herbland.
- 3 Key to Condition States: G = good, M = medium, P = poor, C = critical, I = intermediate.

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