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Ecological responses to flow regulation

Title

Understanding multiple ecological responses to anthropogenic disturbance: rivers and potential
flow regime change

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Abstract

Human-induced alteration of the natural flow regime is a major threat to freshwater ecosystems and biodiversity. The effects of hydrological alteration on the structural and functional attributes of riverine communities are expected to be multiple and complex, and may not be described easily by a single model. Based on existing knowledge of key hydrological and ecological attributes, we explored potential effects of a flow regulation scenario on macroinvertebrate assemblage composition and diversity in two river systems in Australia's relatively undeveloped wet-dry tropics. We used a single Bayesian Belief Network (BBN) to model potential changes in multiple assemblage attributes within each river type during dry and wet seasons given two flow scenarios: the current, near-natural flow condition; and flow regulation. We then used multidimensional scaling ordination to visually summarize and compare the most probable attributes of assemblages and their environment under the different scenarios. The flow regulation scenario provided less certainty in the ecological responses of one river type during the dry season, which reduced the ability to make predictions from the BBN outputs directly. However, visualizing the BBN results in an ordination highlighted similarities and differences between the scenarios that may have been otherwise difficult to ascertain. In particular, the MDS showed that flow regulation would reduce the seasonal differentiation in hydrology and assemblage characteristics that is expected under the current, low level of development. Our approach may have wider application in understanding ecosystem responses to different river management practices and should be transferred easily to other ecosystems or biotic assemblages to provide researchers, managers and decision makers an enhanced understanding of ecological responses to potential anthropogenic disturbance.

Key-words: Bayesian Belief Network; conceptual model; conservation, restoration and management; ecological modeling; flow regulation; macroinvertebrates; multiple response models; decision support

Introduction

Human-induced alteration of the natural flow regime is a major threat to freshwater ecosystems and biodiversity (Vörösmarty et al. 2010). Flow regulation and abstraction of water from river systems lead to changes in the ecologically relevant features of the flow regime: timing, duration, magnitude, frequency, variability and rate of change in river discharge (Poff et al. 1997; Puckridge et al. 1998). Such hydrological changes associated with water resource development have long been evidenced to affect adverse changes in the structural and functional composition of riverine biota (Nilsson and Berggren 2000; Bunn and Arthington 2002; Poff and Zimmerman 2010).

Despite the pervasiveness of water resource development throughout the world (Nilsson et al. 2005), river systems exist that are unregulated, have experienced relatively little structural modification or from which relatively little water is extracted, such that their flow regimes may be considered near-natural. However, water resource development options for these systems may be under investigation or planned for the future, e.g. in the wet-dry tropics of continental Australia (see Leigh and Sheldon 2008; Petheram et al. 2008). Conversely, there are also river systems to which a more natural flow regime may be restored, e.g. via dam removal (Bednarek 2001; Hart and Poff 2002). In both cases, multiple and complex effects of human-induced hydrological changes on the structural and functional attributes of riverine communities may be expected.

Bayesian Networks are emerging as tools to aid in the conservation, restoration and management of ecosystems and biodiversity (see McCann et al. 2006; Nyberg et al. 2006; Pollino et al. 2007; Shenton et al. 2011). They allow scientists to combine measured responses to environmental change with a conceptual understanding of the ecosystem in question within a quantitative and probabilistic framework. This enables biotic or ecosystem responses to potential, human-induced, change in the environmental drivers to be predicted. For example, Bayesian Networks were recently demonstrated to model the effects of multiple stressors on freshwater ecosystems and as a decision making tool in restoration and environmental flow management (Stewart-Koster et al. 2010). Their usefulness centers on their relative ease of construction and interpretation, and in particular, their ability to forecast changes, as well as the uncertainties around these changes, that result from different disturbance or management scenarios. Bayesian Networks can thus increase the transparency of decision making processes by incorporating any uncertainties into the model networks and propagating them through to model outputs (cf. Reckhow 1994; Borsuk et al. 2004, Bromley et al. 2005). As such, they have found wide use in mapping and predicting species distributions to support decisions on conservation priority habitats (e.g. Marcot et al. 2001; McCann et al. 2006; Smith et al. 2007). These same properties make Bayesian Networks a suitable choice for modeling expected responses of key ecological attributes of river systems to scenarios of hydrological disturbance or management. In the context of water resource development (whether it be potential, planned or even removed), modeling such responses would not only increase our understanding of the hydroecology of the river system in question, but likely aid in the conservation and/or restoration of river function and biodiversity.

In the ecological literature, Bayesian networks have been used to model unique attributes, or responses; e.g. change in one particular water quality parameter (e.g. Stewart-Koster et al. 2010) as well as multiple ecological responses (e.g. Borsuk et al. 2004; Langmead et al. 2009). Therefore, where knowledge on structural and functional attributes of biota within an ecosystem of interest exists, it would seem sensible to use this in a modeling context to predict likely changes in response to human-induced disturbance (cf. Olden 2003; Olden et al. 2006). However, increasing the complexity of a single Bayesian network to include multiple responses of biotic assemblages or other ecosystem attributes (i.e. multiple endpoints of interest) may reduce the interpretability of the network (Woolf et al. 2005). Standard visualization methods, such as ordination, that are commonly used to simplify and explore patterns of variation in multivariate data may provide a solution. Under this framework, we modeled expected responses of multiple ecological attributes in river systems of naturally contrasting flow regime types to potential hydrological modification within a single Bayesian Belief Network (BBN). We then used a multi-dimensional scaling (MDS) ordination to enhance interpretation of the potential effects of hydrological modification on river ecology. This approach is likely to have wider application in understanding ecosystem responses to different river management practices and may enhance our understanding of expected, multiple, and often complex, ecological responses to potential anthropogenic disturbance.

Methods

Model development and interpretation

We used existing knowledge of important hydrological and ecological attributes to explore potential effects of flow regulation on macroinvertebrate assemblage composition and diversity in two types of river systems in Australia's relatively undeveloped wet-dry tropics. A five-step

approach was used to develop a BBN model of multiple ecological responses in these river types to a potential flow regulation scenario and to interpret model outcomes. We began with the current understanding of the ecosystem and its biotic assemblages, as explained by a study on dry season macroinvertebrate diversity in the lower Gregory and Flinders river systems (Leigh and Sheldon 2009). Second, we used this understanding to develop a conceptual diagram of macroinvertebrate assemblage attributes in the two river types as directionally affected by environmental drivers. Third, the diagram was converted to a BBN by quantifying the directional links of influence, and their inter-relationships, via conditional probabilities. Fourth, two flow scenarios (current vs. future flow regulation) were imposed on the BBN to produce probabilities of environmental and assemblage attributes for the different river types with and without water resource development. Finally, the most probable outcomes of the two scenarios were used to construct theoretical states of the environmental and assemblage attributes that were then visually summarized and interpreted via MDS ordination.

Current understanding of ecosystem and taxa of interest (step 1)

The Gregory and Flinders river systems are located in the wet-dry tropics of north-eastern Australia. Riverine ecosystems here are characterized by monsoonal rains in the austral summer (c. November to April) followed by a dry season of little to no rainfall (c. May to October) and, under current conditions, flow regimes of the Gregory and Flinders river systems both display strong wet-dry seasonality. However, the Gregory River maintains surface flow throughout the year as a result of inputs from upland aquifers, whereas the lower Flinders River and channel network disconnect into waterholes each dry season. These two types of flow regime, typified by the lower Gregory and Flinders Rivers, are common throughout Australia's wet-dry tropics. The rivers have been described, respectively, as having 'tropical' and 'dryland' flow regimes (Leigh

and Sheldon 2008), and align with the stable baseflow and summer intermittent river types in the Australia-wide classification of Kennard et al. (2010).

Six sites were sampled in the Gregory and five in the Flinders river systems (approx. 17.8-18.9°S and 139.2-140.9°E) during the 2005 dry season and two sites within each river system were re-sampled the following year. Three samples of macroinvertebrates and accompanying environmental measures were collected at each site. Macroinvertebrates were later sorted in the laboratory and identified to lowest taxonomic resolution practicable using standard taxonomic keys (see Leigh and Sheldon 2009 for full details). The study showed that hydrological connectivity, as represented by flowing or non-flowing sites, had a strong effect on macroinvertebrate composition and diversity, a phenomenon also observed in tropical, arid-zone and temperate systems (e.g. Ezcurra De Drago et al. 2004; Marshall et al. 2006; Paillex et al. 2009). Sites with similar connection histories had the most comparable assemblages, and between-site ('beta') diversity was greatest between flowing and non-flowing sites. A key group of taxa were also associated with the difference between these site types, with the gastropod *Thiara (Plotiopsis)* sp. acting as an indicator species for flowing sites in the Gregory river system. Assemblages from flowing sites had greater taxonomic richness and, among taxa, abundances were more even in these assemblages compared with those from non-flowing sites, in which one taxon (not site-specific) tended to dominate.

In terms of functional composition of the assemblages, collector filterers and gatherers together had the greatest proportional abundance across the study region; shredders the least. Gatherers had greater proportional abundances in non-flowing sites and in the Flinders system; filterers and

grazers in flowing sites and in the Gregory system. Finally, multivariate variation in water physicochemistry (e.g. nutrient concentrations and conductivity) and biophysical habitat (e.g. presence/absence of macrophytes and snags) was associated with patterns of variation in assemblage composition.

Diagrammatic conceptual model (step 2)

Based on these findings, we created a simple diagram that included links among environmental drivers and an extended influence diagram that was linked to key attributes of macroinvertebrate assemblages in the study region (Fig. 1). We only included drivers that most strongly influenced macroinvertebrate composition and diversity in the ‘tropical’ Gregory and ‘dryland’ Flinders rivers, and only the direct links among these (as outlined in Leigh and Sheldon 2009). Including only the most relevant drivers, as opposed to indirect or unknown factors of influence, prevented the BBN structure from becoming overly complex as a result of unwieldy conditional probability tables (see Step 3; also McCann et al. 2006).

Probabilistic BBN model (step 3)

BBNs are based on conditional probabilities and Bayes theorem, which combines observed data and prior information, and incorporate uncertainty through Bayesian belief updating (Reckhow 1994; Korb and Nicholson 2004). Prior probabilities, based on existing data, expert opinion or both, are first assigned to all components and links within the network, via conditional probability tables (CPTs), in order to estimate the posterior probabilities of outcome events (McCann et al. 2006). As more data and knowledge becomes available, prior probabilities can be validated or updated accordingly (Spiegelhalter et al. 1993; Marcot et al. 2006).

We converted our influence diagram to a probabilistic BBN using the program Netica 4.09 (www.norsys.com/). The initial model contained three parent nodes (the unconditional *Season*, *Flow regime* and *Channel geomorphology* nodes) and 11 child (response) nodes (Fig. 2; a fourth parent node representing future anthropogenic disturbance was later added). Four of the response nodes represented the biophysical and chemical environment (*Site flow status*, *Hydrological connection history*, *Between-site flow status* and *Among- and within-site variation*), and these were linked to seven other response nodes that represented macroinvertebrate assemblage attributes (*Beta-diversity*, *Filterer and grazer abundance*, *Gatherer abundance*, *Richness and evenness*, *Dominance by one taxon*, *Thiara (Plotiopsis) sp. presence* and *Site specific variation in composition*). CPTs were populated for all states within all response nodes based on current hydrological conditions, empirical knowledge of the study region and results of previous studies on regional flow regimes and macroinvertebrate assemblages (Appendix A). For example, flow regime analyses and hydrographs presented in Leigh and Sheldon (2008, 2009) informed the CPTs for *Site flow status* and *Hydrological connection history*, such that: 1) the likelihood of being a flowing site within the *tropical* river type would be high in the *dry* season in a *deep* channel (0.90), higher still in the *wet* season (> 0.95), but lower in a *shallow* channel (0.70); and 2) the likelihood of sites becoming disconnected each dry season was greater in the *dryland* than the *tropical* river type, but was also dependent on channel depth (*dryland d* = 0.99, *dryland deep* = 0.95, *tropical shallow* = 0.50, *tropical deep* = 0.01).

Studies on macroinvertebrate assemblages during the wet season and, in particular, across both dry and wet seasons in Australia's wet-dry tropics are rare. However, we were able to use one study on macroinvertebrates in a lowland river system (Outridge 1988) to inform the CPTs influenced by the *wet* state within the *Season* node of our BBN. Magela Creek is a seasonally

flowing tributary of East Alligator River, Northern Territory, in a largely undeveloped region of Australia's wet-dry tropics. Surface flow is permanent in its upstream, sandstone escarpment reaches, but generally ceases in the lowlands during the dry season. Thus, the flow regime of lower Magela Creek may be more similar to the lower Flinders River ('dryland') than the lower Gregory River ('tropical') (see also Kennard et al. 2010); however, there is one perennially flowing channel within the system's network that was included in Outridge's (1988) study, along with seasonally connected waterbodies on both the main channel and floodplain. Outridge (1988) described monthly changes across a 12-month dry-wet season cycle and found a general decline in taxonomic richness and abundance during the dry season compared with a general increase during the wet season, particularly around its onset. Between-site beta-diversity, particularly between the flowing and non-flowing sites, was high in the dry season compared with the wet season. In addition, dry season differences in assemblages between flowing and non-flowing sites were similar to those found by Leigh and Sheldon (2009) in the Gregory and Flinders river systems. In lower Magela Creek, flowing-channel fauna had greater diversity than that of any non-flowing site during the dry season and, by late dry season, assemblages from flowing and non-flowing sites had distinctly different taxonomic compositions (Outridge 1988).

The BBN was compiled once the CPTs were fully specified, which allowed the uncertainty of each state (its probability of occurrence) within each node to propagate through the links in the model. We then assessed the relative and expected importance of each influencing node (e.g. *Flow regime*) on the response nodes (e.g. *Between-site flow status*) using an entropy reduction sensitivity analysis, which is used for BBNs with discrete levels within nodes (see Marcot 2006). This assesses the BBN structure and its outcomes by ranking the effect that each linked node's state and associated probability has on the response node of interest. The greater a node's entropy

reduction value, the greater is its influence on the response node (Marcot 2006). This helped validate the model and CPTs by highlighting the degree of correspondence between factors that had the greatest effect on environmental and assemblage characteristics according to previous wet and dry season studies in Australia's wet-dry tropics (Outridge 1988; Leigh and Sheldon 2009) and those according to the BBN (e.g. Table 1).

The accuracy of the BBN was tested (via belief updating; see Step 4 for more detail) using field data collected from the Gregory and Flinders river systems during the dry seasons of 2005 and 2006 (45 cases; Leigh and Sheldon 2009) (Appendix B). Each case (representing each sample collected during the two dry seasons) was described by the observed states within each node of the BBN, except for *Between-site flow status* and *Beta-diversity*, which did not apply to individual samples. For the macroinvertebrate response nodes, the BBN's mean error (misclassification) rate was 21% with a spherical payoff of 0.79 (Table 2). Spherical payoff gives an indication of model performance and ranges between 0 and 1 (1 being the best fit) (Marcot et al. 2006). Results suggested that the BBN was satisfactorily accurate so we did not use the test cases to permanently update, and potentially over-fit, the model.

Next, we explored the potential effects of a flow regulation scenario that (a) encapsulated a similar level of hydrological change that has occurred in Australia's highly modified Murray-Darling Basin, and (b) was based on regulation resulting from the kind of water resource development investigated, proposed or planned for rivers and catchments in Australia's wet-dry tropics (e.g. DNRW 2007), i.e. physical barriers that impound water (such as dams, weirs and levees) for water storage, distribution or flood control purposes. We incorporated a *Flow regulation* node that was directly linked to three environmental response nodes (*Site flow status*,

Hydrological connection history and *Among- and within-site variation*) via conditional probability tables (e.g. Fig. 2b). Under current conditions (represented by the *current* state within the node), the BBN functioned as detailed above, but conditional probabilities within the three environmental response nodes changed under the flow regulation scenario (represented by the *future* state) (Table 3). Specifically, the likelihood of sites being disconnected, hydrological connection history being seasonal, and among- and within-site variation being present (through the loss of wet-dry cycles) was decreased by 60% upon activation of the *future* scenario. For example, the likelihood that a site with a *shallow* channel in the *dryland* river type had a *seasonal* connection history was 99% under the *current* scenario (current hydrological conditions); however, this changed to 40% under the *future* scenario. The percentage change imposed was based on previous research (Thoms and Sheldon 2000) and all potential effects of the scenario on macroinvertebrate composition and diversity (the posterior probabilities, see Step 4) were considered worst-case, given no management or rehabilitation.

Model outcomes (step 4)

Posterior probabilities were first generated under current hydrological conditions (the *current* scenario) for all combinations of states within the unconditional nodes *Season* (dry or wet) and *Flow regime* (dryland or tropical) (e.g. Fig. 2a). States within the only other unconditional node (*Channel geomorphology*) followed a uniform distribution (deep and shallow channels equally likely) as this was considered the best choice given the diverse topology of channels and floodplains in Australia's north (Erskine et al. 2005). Posterior probabilities were estimated in the BBN using the belief updating method based on Bayes theorem of conditional probability, assuming that conditional probabilities were independent and that prior distributions were Dirichlet functions (Spiegelhalter et al. 1993; Marcot et al. 2001; Ellison 2004). These values

served as the benchmark from which we assessed the effects of the flow regulation scenario on macroinvertebrate composition and diversity (cf. Sheldon et al. 2000; Davis and Brock 2008), which were generated by activating the *future* scenario for each of the four river type and season combinations (e.g. Fig. 2b).

Visualization of model outcomes (step 5)

Lastly, we constructed theoretical states for the environmental and assemblage response nodes for each combination of flow regime type, season and flow regulation scenario: 1) ‘dryland’ river, dry season, current conditions, 2) ‘dryland’ river, dry season, future regulation, 3) ‘dryland’ river, wet season, current conditions, 4) ‘dryland’ river, wet season, future regulation, 5) ‘tropical’ river, dry season, current conditions, 6) ‘tropical’ river, dry season, future regulation, 7) ‘tropical’ river, wet season, current conditions, and 8) ‘tropical’ river, wet season, future regulation. States were selected based on the most probable outcomes from the model, which we defined as posterior probabilities between 70 and 100% (state likely to occur) or between 0 and 30% (state unlikely to occur). For example, if the posterior probabilities for the ‘high’ and ‘low’ states within the *Filterer and grazer abundance* node for a particular scenario combination were 85.2 and 14.8% respectively, then the node was assigned the theoretical state of ‘high’ (Table 4). When posterior probabilities were greater than 30 but less than 70% (i.e. close to 50%), the outcome was considered ‘uncertain’.

Thus, for each scenario combination, we defined the probabilities of each state of each of the 11 response nodes of the BBN to use as inputs in ordinations to visualize the probable patterns of change under modeled flow regulation. States of the environmental and assemblage response nodes were defined as either ‘uncertain’ or as one of their defined states: ‘flowing’ or ‘non-

flowing' for *Site flow status*; 'flowing–flowing', 'flowing–non-flowing' or 'non-flowing–non-flowing' for *Between-site flow status*; 'seasonal' or 'permanent' for *Hydrological connection history*; 'high' or 'low' for *Among- and within-site variation*, *Site-specific variation in composition*, *Filterer and grazer abundance*, *Gatherer abundance*, *Richness and evenness*, *Dominance by one taxon* and *Beta-diversity*; 'present' or 'absent' for *Thiara (Plotiopsis) sp.* (e.g. Table 4). When the state of a response node was 'uncertain' for more than one scenario combination, that state's uncertainty was defined differently for each such combination. For example, if gatherer abundance was uncertain in the *future, dryland* river type during both the *dry* and *wet* seasons, then its state for the dry season was defined as 'uncertain(a)' and for the wet season as 'uncertain(b)'. This was because the uncertainty surrounding the expected state of the response node was likely to be due to different ecological processes related to the seasonal differences in hydrology. Also, and more generally, gatherer abundance in the dry season could actually be in a different state (e.g. high) to the wet season (e.g. low), or it could be in the same state (high in both seasons, or low in both seasons) – however, at this stage the BBN cannot quantify this with any certainty. This meant the nodes where the states were not 'uncertain' (i.e. probabilities $\leq 30\%$ or $\geq 70\%$) had relatively more weight in the ordinations than would have been the case if all 'uncertain' outcomes were defined identically. Treating the 'uncertain' states in this manner firstly ensured that scenario combinations were close together in the ordinations because they had similar *probable* outcomes, rather than being similarly uncertain. Second, it ensured that differences such as seasonal hydrologic variation in future scenarios were not masked in the ordinations by the inherent model uncertainty in the BBN.

To visualize the model outcomes we used multidimensional scaling (MDS) based on Gower's similarity index of the defined states to produce the ordinations (in R, www.r-project.org/).

Gower's index can be used to calculate ecological similarity among objects based on quantitative, semi-quantitative, or qualitative data (such as the most probable ecological outcomes that we defined from the BBN results) (Gower 1971; Laliberté and Legendre 2010). We created MDS plots based on (i) both environmental and assemblage attributes, (ii) environmental attributes only, and (iii) assemblage attributes only.

Results

In all but one combination of *Flow regime* and *Season*, the flow regulation scenario resulted in greater certainty that waterbodies in our model had surface flow and/or were permanently connected; for the 'dryland' river type during the dry season there was less certainty that waterbodies would be non-flowing and seasonally connected. In turn, the greatest changes in posterior probabilities for macroinvertebrate composition and diversity attributes between *current* and *future* flow scenarios occurred for the 'dryland' river during the dry season with increased uncertainty surrounding model expectations (Table 5). For example, the probability that *Filterer* and *grazer abundance* was low changed from 94.7% under current conditions (i.e. very likely) to 49.9% under the flow regulation scenario (i.e. highly uncertain). The exception was the presence or absence of *Thiara (Plotiopsis)* sp., for which the posterior probabilities did not change for the 'dryland' river, dry season combination. Excluding this node, the probability of each state within each of the assemblage response nodes for the 'dryland' river type during the dry season was less certain under the *future* scenario: the *future* posterior probabilities were closer to 50% than to either 0 or 100%. For the three other combinations of *Flow regime* and *Season*, there was either the same or greater certainty in the posterior probabilities of assemblage response nodes between current and future scenarios. The only exception was for *Site specific variation in composition* in

the ‘tropical’ river type during the dry season, for which certainty in the *future* state was lower (the outcome was less certain).

Based on our definitions of most probable outcomes, the environmental and assemblage responses for two scenario combinations (current conditions, ‘dryland’ river type, dry season; and future flow regulation, ‘tropical’ river, wet season) were all certain (no outcome was defined as uncertain). The overall outcomes for these two scenarios were among the most distinct from each other in terms of their (most probable) environmental and assemblage attributes, being two of the most distant of any pair of points on the MDS plots (Fig. 3). In addition, the outcome for the current ‘dryland’ river, dry season scenario was more distinct from the outcomes of other scenario combinations than was the outcome of the future ‘tropical’ river, wet season scenario. The future ‘dryland’ river, dry season scenario had the greatest number of uncertain responses (only two out of the 11 environmental and assemblage responses were defined as certain). As a result, its overall outcome in ordination space was well separated from the outcomes of all other scenarios (Fig. 3).

For all other scenario combinations, there were between one and three uncertain responses of the environmental and assemblage attributes. In general, the most probable outcomes of the future scenarios were distinct from the current scenarios, except when only the assemblage responses were considered. In this case, the separation in ordination space between current and future outcomes of any one flow regime-season combination (except the ‘dryland’ river in the dry season) was short. However, the separation between seasons (dry versus wet) in the overall outcomes of the ‘tropical’ river type (for environmental or assemblage attributes) was always

shorter in ordination space for the future flow regulation scenarios than the current condition scenarios (Fig. 3).

Discussion

Riverine flow regimes in much of Australia's wet-dry tropics are relatively undisturbed; however, anthropogenic impacts on riverine landscapes, including those resulting from water resource development, are predicted to increase (Kennard et al. 2010). In other parts of Australia and across the world, flow regulation has been associated with adverse ecological impacts, including changes to the composition and diversity of biota (Kingsford 2000; Sheldon et al. 2000; Aarts et al. 2004). In accord with this, the results of our combined BBN and ordination approach indicated that intense flow regulation may reduce the differentiation between the wet and dry seasons in the environmental and macroinvertebrate assemblage attributes of river systems with 'tropical' flow regimes in Australia's north. These findings link readily with predictions based on historical and modeled flow data from large rivers across the Gulf of Carpentaria (in the wet-dry tropics, see Leigh and Sheldon 2008), whereby loss of variation in hydrological connectivity, including temporal variation between wet and dry seasons, is expected to lead to habitat homogenization and, in turn, to lower biodiversity in both space and time (Pringle 2001; Rahel 2002; Sheldon et al. 2002; Olden et al. 2004). In addition, our findings suggest that, during the dry season, the environmental and assemblage attributes of rivers in this region that have intermittent to ephemeral flow regimes ('dryland' river types) may be particularly distinct from those in the wet season and from those of rivers with more regular, 'tropical' flow regimes.

The Bayesian statistical approach to model development provides a framework to make use of disparate sources of information (Korb and Nicholson 2004; Pollino et al. 2007). We successfully

combined information from multiple sources via a BBN to provide ecological forecasts of biotic response to potential anthropogenic environmental change. We used results from previous studies at our study locations to parameterize some nodes of the BBN while integrating information from studies in similar catchments to fully populate the network. This is both a strength of our approach and a potential caveat to it. For example the wet season component of our BBN was based on a study of macroinvertebrate assemblages across a dry-wet season cycle in Magela Creek (Outridge 1988), a river in Australia's wet-dry tropics approximately 1000km northwest of the rivers on which we based the dry season component of our model (Leigh and Sheldon 2009). Both studies had consistent findings regarding patterns of variation within dry season assemblages (see Methods), which increased our confidence in the validity of using the Magela Creek study to inform our wet season conditional probability tables. In addition, the diversity and abundance of macroinvertebrate assemblages in Magela Creek and its floodplain have recently been found similar to that of other floodplain systems in the world's tropics, including Australia's (Pettit et al. 2011). Nonetheless, our knowledge on macroinvertebrate assemblages during the wet season in Australia's north is limited (mainly due to practical constraints on sampling during the wet season in this region) and, for modeling purposes, this may in turn limit our ability to draw conclusions about seasonal differences under both current conditions and future development scenarios. This could be improved with further research at a finer temporal resolution to examine biotic response to flow variation both within and between seasons, including the possibility of short-term declines or booms in diversity, a response often associated with sudden and/or severe flooding (Bunn et al. 2006; Chiu et al. 2008).

The expected changes in environmental and macroinvertebrate assemblage attributes in our model were based on hydrological changes in Australia's Murray-Darling Basin following

widespread flow alteration including dams, weirs, diversions and surface water abstraction. Kingsford (2000) suggests that over 50% of Australian floodplains associated with developed rivers (mainly situated in the southeast) may no longer receive inflow from overbank flood events. Since the advent of damming and flow regulation in the Barwon-Darling River in the Murray-Darling Basin, for example, small overbank flows have been reduced in magnitude by 35-70% (Thoms and Sheldon 2000). This level of hydrological change and flow modification is extreme, and as such, should the rivers of Northern Australia undergo less extreme development, we would likely see different ecological outcomes from those predicted by the BBN. In addition, our model summarized the broad-scale and likely changes to flow characteristics and hydrological connectivity resulting from such a scenario, and the particulars of flow regulation within any one river system will likely result in particular ecological responses. For example, an upstream dam operated to reduce flows during the wet season is likely to affect different responses in the macroinvertebrate assemblages of a floodplain waterbody (which now receives little overland flow in the wet season) from the responses due to conversion of a seasonally inundated floodplain to a permanent channel for the conveyance of water for irrigated agriculture (eliminating cease to flow events). Changes to the flow regime are also likely to elicit changes in water quality, as evidenced in the Murray-Darling Basin (Sheldon et al. 2000), particularly if flow modification affects flow permanence or is associated with groundwater disturbance. In turn, macroinvertebrate assemblages are likely to respond to these changes, and although the effect of spatial variation in water physicochemistry on variation in assemblage composition was accounted for in our model, direct responses to potential decline in water quality were not. Studies have shown, however, that flow modification combined with a decline in water quality is likely to intensify the effects of flow modification on macroinvertebrate assemblages (e.g. Lind et al. 2006). Quantifying relationships between macroinvertebrates assemblages and water quality

in these relatively undisturbed systems is thus an avenue for further research that may enhance the utility of the BBN. Finally, our model was exclusive of climate change-related impacts on or interactions with the current and future flow regulation scenarios. However, given the current understanding of flow regimes and assemblage characteristics in lowland rivers of Australia's wet-dry tropics and the broad-scale changes to hydrological connectivity witnessed in southeast Australia due to flow modification, our results suggest that unmitigated water resource development in the wet-dry tropics is likely to lead to tangible shifts in aquatic biodiversity and biotic composition.

A key finding of our BBN model was the uncertainty in many of the posterior probabilities for assemblage attributes under the flow regulation scenario, particularly for the 'dryland' river type in the dry season. Under this scenario, 'dryland' rivers in the dry season had an increased probability of displaying flow characteristics typical of 'tropical' rivers (e.g. greater flow regularity and permanence). However, rather than resulting in an increased certainty of a more 'tropical' assemblage in the 'dryland' river sites under the flow regulation scenario, the posterior probabilities of the assemblage attributes were closer to 50% than to 0% or 100%. This was due to uncertainties surrounding expected hydrologic changes (e.g. *Hydrological connection history*, Fig. 2) under the flow regulation scenario that propagated through the BBN. However, one of the benefits of using a scenario-driven BBN is that it can be validated and updated with results of further study, the integration of expert knowledge or both (Pollino et al 2007). This can change conceptually-based BBN scenarios from basic belief systems to more rigorous and effective modeling and management tools (McCarthy and Masters 2005; Marcot 2006; Smith et al. 2007); they can be made as complex as desired, given the data or knowledge available (e.g. Batchelor and Cain 1999; Nyberg et al. 2006; Stewart-Koster et al. 2010). For our study, the uncertainty in

model outcomes, and therefore in our interpretation, may reduce as a result of such model updating. This adaptive capability is particularly beneficial when modeling ecosystems that are targets for management intervention, and those of high integrity that are faced with increasing pressure from anthropogenic development (e.g. like those in Australia's wet-dry tropics; Finlayson et al. 2005), particularly when understanding of their current ecosystem function and attributes is limited.

The BBN allowed us to acknowledge the uncertainties in our model, while the ordination of the most probable outcomes provided a deeper understanding of the potential effects of the future development scenario. The uncertainties within BBNs must remain transparent, however, and we do not recommend presentation of ordinations based on the BBN outputs alone, as it is important to take uncertainties into account when devising management goals to direct conservation or rehabilitation effort (Reckhow 1994). Further, the results of the ordination are very much contingent on the somewhat arbitrary cut-off of probabilities between 30% and 70% to define states as 'uncertain'. A cut-off of 20% and 80%, for example, could result in slightly different ordination patterns. That stated, the scenario that resulted in the largest number of 'uncertain' outcomes in the responses of ecological attributes to the flow regulation scenario, in accord with our BBN results, was for the 'dryland' river type during the dry season. Despite the uncertainty in the modeled responses to the flow regulation scenario, the ordinations indicated that the environmental and assemblage attributes under current conditions in the dry season, 'dryland' river type were distinct from those of other seasons and river types. As such, this 'dryland' river, dry season ecosystem type may be vulnerable to anthropogenic disturbance in that it is potentially less replaceable, from a conservation perspective (cf. Linke et al. 2008), than other riverine ecosystem types in the wet-dry tropics. Coupled with the uncertainty surrounding the expected

ecological outcomes in the BBN, the vulnerability of this ecosystem type highlights the need for further research into the effects of flow regulation in the region.

With increasing regulation of the world's rivers, aquatic ecologists and hydrologists have been focused on understanding the impacts and changes associated with current regulation practices or trying to predict the impact of future regulation practices (Bunn and Arthington 2002; Poff and Zimmerman 2010). With an increasing number of dams and weirs aging in many parts of the world we are now also challenged with predicting the outcome of removing regulation structures (Bednarek 2001). The approach we have outlined here is not only useful for predicting potential future changes associated with flow regulation but also changes associated with returning rivers to their free-flowing state. The approach should also transfer easily to other ecosystems or biotic assemblages of interest to provide researchers, managers and decision makers an enhanced understanding of expected, multiple, and often complex, ecological responses to potential anthropogenic disturbance. From a broader planning and management perspective, visually explaining patterns of change in model outputs (e.g. via ordination) may help identify communities or ecosystems in need of further research or those most susceptible to unacceptable change as a result of human impact, and provide additional decision support regarding management investment and effort.

Acknowledgements

Research funding was provided by Land & Water Australia (Project code GRU35) with additional support from the Griffith School of Environment and Australian Rivers Institute. We thank local indigenous communities, pastoral leaseholders and station managers for granting permission and access to field sites for macroinvertebrate sampling, and volunteers for assistance

in the field. Ethical clearance was granted by Griffith University's Animal Ethics Committee and research was conducted in accordance with the requirements of this committee. We thank the reviewers for their comments on our manuscript, in particular for the helpful critique of the ordination analysis.

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666

667 **Ecological Archives material**

668 Appendix A: Conditional probability tables for response nodes in the BBN.

669 Appendix B: Case file used to test BBN.

670

Tables

Table 1: Sensitivity of an environmental response node (*Between-site flow status*) to states and values of nodes that directly influence it (*Site flow status*, *Season* and *Flow regime*)^a.

Between-site flow status	Entropy reduction
Site flow status ^b	0.7541
Season	0.3567
Flow regime	0.2735

^a *Season* and *Flow regime* nodes in unselected states.

^b Expected to have the strongest influence on states within *Between-site flow status* given patterns found in the study region (Leigh and Sheldon 2009).

Table 2: BBN classification test results for assemblage response nodes, based on field data collected from the Gregory and Flinders river systems during the dry seasons of 2005 and 2006 (45 cases; Leigh and Sheldon 2009).

Response node	True positive classification rate (%)	Error (misclassification) rate (%)	Spherical payoff
Site specific variation in composition	87	13	0.87
<i>Thiara (Plotiopsis)</i> sp.	100	0	1.00
Filterer and grazer abundance	64	36	0.66
Gatherer abundance	67	33	0.68
Richness and evenness	87	13	0.87
Dominance by one taxon	67	33	0.68
Mean	79	21	0.79
Standard error	6	6	0.06

Note: Case file input data are given in Appendix B.

682 Table 3: Conditional probability tables for the three response nodes directly linked to the *Flow regulation* scenario node in the BBN
 683 (see Fig. 2), based on combinations of relevant influence nodes.

Response node	States in nodes of influence				States in response nodes	
<i>Site flow status</i>	<i>Season^a</i>	<i>Flow regime^a</i>	<i>Channel geomorphology^b</i>	<i>Flow regulation^a</i>	<i>Flowing</i>	<i>Non-flowing</i>
	Dry	Tropical	Deep	Current	0.90	0.10
				Future	0.96	0.04
			Shallow	Current	0.70	0.30
				Future	0.88	0.12
		Dryland	Deep	Current	0.10	0.90
				Future	0.64	0.36
			Shallow	Current	0.01	0.99
				Future	0.60	0.40
	Wet	Tropical	Deep	Current	0.99	0.01
				Future	1.00	0.00
			Shallow	Current	0.95	0.05

				Leigh et al.	
<i>Hydrological connection history</i>	Dryland	Deep	Future	0.98	0.02
			Current	0.99	0.01
		Shallow	Future	1.00	0.00
			Current	0.90	0.10
			Future	0.96	0.04
				<i>Seasonal</i>	<i>Permanent</i>
	Tropical	Deep	Current	0.01	0.99
			Future	0.00	1.00
		Shallow	Current	0.50	0.50
			Future	0.20	0.80
Dryland			Deep	Current	0.95
	Future	0.38		0.62	
	Shallow	Current	0.99	0.01	
		Future	0.40	0.60	
		<i>Among- & within-site variation^c</i>			<i>High</i>

Dry	Current	0.75	0.25
	Future	0.30	0.70
Wet	Current	0.45	0.55
	Future	0.18	0.82

^a States within *Season*, *Flow regime* and *Flow regulation* were either one or the other only.

^b States within *Channel geomorphology* were described by a uniform distribution (states within node are equally likely) as the probability of each state was uncertain.

^c Among- and within-site variation in biophysical and chemical characteristics of waterbodies is affected directly and indirectly by many factors and natural variation in these characteristics may be high; however, among- and within-site variation was considered more likely to be high in the dry season than in the wet season when there is widespread flooding.

691 Table 4: Theoretical states of environmental and macroinvertebrate assemblage response nodes constructed for a particular scenario
692 combination ('tropical' river type during the dry season under current conditions), based on posterior probabilities of the BBN.

Response node	State	Posterior probability	Theoretical state (most probable)
Site flow status	Flowing	80.0	Flowing
	Non-flowing	20.0	
Between-site flow status	Flowing–Flowing	64.0	Flowing–Uncertain
	Flowing–Non-flowing	35.0	
	Non-flowing–Non-flowing	1.0	
Hydrological connection history	Seasonal	25.5	Permanent
	Permanent	74.5	
Among & within-site variation (environmental)	High	75.0	High
	Low	25.0	
<i>Thiara (Plotiopsis)</i> sp.	Present	76.2	Present

	Absent	23.8	
Filterer and grazer abundance	High	85.2	High
	Low	14.8	
Gatherer abundance	High	16.8	Low
	Low	83.2	
Richness and evenness	High	84.2	High
	Low	15.8	
Dominance by one taxon	High	23.0	Low
	Low	77.0	
Site-specific variation in composition	Present	74.5	Present
	Absent	25.5	
Beta diversity	High	38.7	Uncertain
	Low	61.3	

693 *Note:* Rules used to determine most probable states from the posterior probabilities are given in the methods.

694

695 Table 5: Posterior probabilities for states within response nodes of the BBN modeled on the conceptual diagram in Fig. 1 of
696 macroinvertebrate assemblages (composition and diversity) for a *dryland* or *tropical* flow regime in the *dry* or *wet* season, given the
697 *current* or *future* flow regulation scenario.

		‘Dryland’ regime, dry season		‘Dryland’ regime, wet season		‘Tropical’ regime, dry season		‘Tropical’ regime, wet season	
Response node	State	Current	Future	Current	Future	Current	Future	Current	Future
<i>Environmental attributes</i>									
Site flow status	Flowing (F)	5.5	<u>62.2</u>	94.5	97.8	80.0	92.0	97.0	98.8
	Non-flowing(NF)	94.5	<u>37.8</u>	5.5	2.2	20.0	8.0	3.0	1.2
Between-site flow status	F-F	< 0.1	0.6	89.8	92.9	64.0	73.6	96.0	97.8
	F-NF	6.4	<u>62.0</u>	9.1	6.6	35.0	26.0	3.9	2.2
	NF-NF	93.6	<u>37.4</u>	1.1	0.4	1.0	0.4	0.1	0.0
Hydrological connection history	Seasonal	97.0	<u>38.8</u>	97.0	<u>38.8</u>	25.5	10.2	25.5	10.2

	Permanent	3.0	<u>61.2</u>	3.0	<u>61.2</u>	74.5	89.8	74.5	89.8
Among- & within-site variation	High	75.0	<u>30.0</u>	45.0	18.0	75.0	<u>30.0</u>	45.0	18.0
	Low	25.0	<u>70.0</u>	55.0	82.0	25.0	<u>70.0</u>	55.0	82.0
<i>Macroinvertebrate assemblages</i>									
<i>Thiara (Plotiopsis)</i> sp.	Present	1.0	1.0	1.0	1.0	76.2	87.5	92.2	93.1
	Absent	99.0	99.0	99.0	99.0	23.8	12.5	7.8	6.1
Filterer and grazer abundance	High	5.3	<u>50.1</u>	75.7	78.3	85.2	93.5	96.9	98.2
	Low	94.7	<u>49.9</u>	24.3	21.7	14.8	6.5	3.1	1.8
Gatherer abundance	High	95.2	<u>56.1</u>	33.8	31.5	16.8	7.3	3.4	1.9
	Low	4.8	<u>43.9</u>	66.2	68.5	83.2	92.7	96.6	98.1
Richness and evenness	High	23.3	<u>57.3</u>	76.7	78.7	84.2	93.1	96.8	98.1
	Low	76.7	<u>42.7</u>	23.3	21.3	15.8	6.9	3.2	1.9

Dominance by one taxon	High	90.0	<u>39.0</u>	10.0	7.0	23.0	12.2	7.7	6.1
	Low	10.0	<u>61.0</u>	90.0	93.0	77.0	87.8	92.3	93.9
Site-specific variation in composition	Present	74.5	<u>30.4</u>	45.1	18.6	74.5	<u>30.4</u>	45.1	18.6
	Absent	25.5	<u>69.6</u>	54.9	81.4	25.5	<u>69.6</u>	54.9	81.4
Beta-diversity	High	15.6	<u>64.2</u>	18.1	13.1	38.7	29.8	9.9	7.5
	Low	84.4	<u>35.8</u>	81.9	86.9	61.3	70.2	90.1	92.5

Notes: Boldface type indicates when the posterior probability for a state was greater than 30% but less than 70% (i.e. close to 50%).

Underlined text indicates when certainty in the state was lower in the *future* compared with the *current* scenario.

Figure legends

Figure 1: Diagram of directional links among the major environmental factors of influence on macroinvertebrate composition and diversity in the lower Gregory and Flinders river systems (top); with directional links from these factors extended to specific assemblage attributes (bottom), based on a dry season study by Leigh and Sheldon (2009).

Figure 2: Example BBN showing the expected effect (represented by posterior probabilities) of a ‘dryland’ river type (e.g. the lower Flinders river system) during the dry season on the composition and diversity of macroinvertebrate assemblages: (a) under current conditions, as based on Fig. 1; and (b) under a future flow regulation scenario.

Figure 3: MDS ordinations of environmental and macroinvertebrate assemblage attributes in ‘dryland’ and ‘tropical’ river types during the dry and wet seasons under current and flow-regulated conditions, based on BBN posterior probabilities of response nodes (Table 5) converted to most probable outcomes (see Methods for detail).

Figure 1

Figure 2

Figure 3