

# Identifying habitats at risk: simple models can reveal complex ecosystem dynamics

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**Abstract.** The relationship between ecological impact and ecosystem structure is often strongly nonlinear, so that small increases in impact levels can cause a disproportionately large response in ecosystem structure. Nonlinear ecosystem responses can be difficult to predict because locally relevant data sets can be difficult or impossible to obtain. Bayesian networks (BN) are an emerging tool that can help managers to define ecosystem relationships using a range of data types from comprehensive quantitative data sets to expert opinion. We show how a simple BN can reveal nonlinear dynamics in seagrass ecosystems using ecological relationships sourced from the literature. We first developed a conceptual diagram by cataloguing the ecological responses of seagrasses to a range of drivers and impacts. We used the conceptual diagram to develop a BN populated with values sourced from published studies. We then applied the BN to show that the amount of initial seagrass biomass has a mitigating effect on the level of impact a meadow can withstand without loss, and that meadow recovery can often require disproportionately large improvements in impact levels. This mitigating effect resulted in the middle ranges of impact levels having a wide likelihood of seagrass presence, a situation known as bistability. Finally, we applied the model in a case study to identify the risk of loss and the likelihood of recovery for the conservation and management of seagrass meadows in Moreton Bay, Queensland, Australia. We used the model to predict the likelihood of bistability in 23 locations in the Bay. The model predicted bistability in seven locations, most of which have experienced seagrass loss at some stage in the past 25 years providing essential information for potential future restoration efforts. Our results demonstrate the capacity of simple, flexible modeling tools to facilitate collation and synthesis of disparate information. This approach can be adopted in the initial stages of conservation programs as a low-cost and relatively straightforward way to provide preliminary assessments of nonlinear dynamics in ecosystems.

**Key words:** Bayesian networks; bistability; feedbacks; Moreton Bay, Queensland, Australia; nonlinear ecosystem dynamics; seagrass; *Zostera muelleri*.

## INTRODUCTION

Understanding how habitats resist or recover from impact is of central importance to the management and conservation of resilient and functioning ecosystems (Thrush et al. 2009). Environmental managers consider habitat (e.g., Harborne et al. 2008) and species (e.g., Beger et al. 2007) as conservation targets, but collating information relevant to a local context can be difficult (e.g., Grech and Coles 2010), so planning decisions are often required in the absence of important ecological information (e.g., Foley et al. 2010). This lack of local information can reduce the effectiveness of conservation and management activities (e.g., Sypard et al. 2011). Therefore, the development of tools to collate informa-

tion on the processes that promote resistance or recovery in impacted and degraded ecosystems has become key to improving management efficacy (Suding et al. 2004).

In coastal habitats, conservation and restoration efforts have traditionally focused on reestablishing the abiotic conditions that existed prior to ecosystem degradation (e.g., Young 2000). These successional-based approaches rely on the natural return of habitats and species once the pre-degradation conditions have been reestablished (e.g., Young et al. 2001). In ecosystems that rely on habitat-forming species, however, successional restoration is often ineffective due to the presence of strong controlling processes that link biotic and abiotic components (Koch et al. 2009). The presence of these controlling processes (feedbacks) in ecosystems results in a strongly nonlinear relationship between abiotic conditions and the structure of the ecosystem, such that small increases in impact levels can cause a disproportionately large response in

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ecosystem structure (e.g., Beisner et al. 2003). Non-linearities in the response of ecosystems to impacts suggest that, in the middle ranges of impact levels, ecosystems can theoretically exist in one or more regimes, a situation known as bistability (Andersen et al. 2009, Carr et al. 2010).

In shallow coastal zones, seagrass is a dominant habitat-forming organism (Larkum et al. 2006) providing critical services such as habitat provision (Heck et al. 2003), nutrient recycling (McGlathery et al. 2007), coastline stabilization (de Boer 2007), and carbon sequestration (Duarte et al. 2005). Seagrass ecosystems are declining globally, along with the significant services and productivity that they provide (Waycott et al. 2009). Threats include global issues such as increasing sea surface temperature and storm frequency, as well as local impacts such as declining water quality from increased sediment and nutrient loading (Duarte 2002). When combined with cascading effects from the loss of top-down controlling processes such as grazing, it can be difficult to understand the effects of multiple impacts and thus difficult to protect seagrass ecosystems against them (Orth et al. 2006).

The extent to which managers can characterize bistability in ecosystems such as those dominated by seagrasses is determined by the tools available to them (e.g., Suding and Hobbs 2009). Characterizing the feedback processes that enable ecosystems to resist impacts, and those feedback processes that prevent recovery, is essential for predicting how ecosystems will respond to increasing impacts (e.g., Nyström et al. 2012). Models that incorporate feedback processes and alternate regimes can help managers to determine how ecosystems might react to changing levels of impact. Predicting complex nonlinear dynamics from models, however, can be done without specialized modeling skills. Bayesian networks (BN) are an emerging tool that can assist in the management of ecosystems (Ticehurst et al. 2007, Leigh et al. 2012). BNs allow for the combination of responses of an ecosystem to changes in impact levels and environmental conditions within a quantitative and probabilistic framework (e.g., Aguilera et al. 2011). They are flexible, enabling the practitioner to define relationships between components (or nodes) of the BN using a range of data types, including quantitative data sets and expert opinion. Accordingly, BNs enable the use of literature-based data in the initial stages of a conservation project without the explicit need for local data sets. When additional, more relevant, data sets are collected, these BNs can be updated easily to reflect the change in knowledge. Additionally, if certain parameters are shown to be important determinants of model output, new or additional data can be collected.

Here, we show how a simple probabilistic BN can reveal nonlinear dynamics in seagrass ecosystems by using relationships between the important ecosystem components elucidated from data sourced from the

literature. We then use the BN in a case study to show how understanding bistability can help to prioritize the risk of loss, and the likelihood of recovery, for the conservation and management of seagrass. We also show how, through the development of the BN, practitioners can identify components of the ecosystem that require better quantification, effectively providing a prioritizing tool to focus subsequent research.

## MATERIALS AND METHODS

### *Model development*

A five-step approach was used to develop a BN to test ecological responses across gradients of the multiple impacts in seagrass ecosystems.

- 1) Cataloguing the current understanding of ecological responses in seagrass ecosystems to a range of drivers and impacts.
- 2) Using the catalogue to develop a conceptual diagram of the ecological processes that respond to selected impacts and that influence seagrass.
- 3) Converting the conceptual diagram to a BN by quantifying the effects of selected drivers and impacts on the various nodes via conditional probabilities.
- 4) Using the BN to predict the likelihood of starting seagrass biomass under different combinations of impact levels.
- 5) Determining the effect that different levels of starting seagrass biomass have on the likelihood of more seagrass biomass.

Using the model outputs, we investigated the utility of the model using a case study of a subtropical coastal embayment dominated by seagrass meadows to predict areas at risk of seagrass loss and areas that may resist recovery once impact levels are reduced.

### *Step 1: cataloguing the seagrass meadow response to environmental impacts*

Based on an extensive literature review, we created a table of relationships between environmental impacts and the response of seagrass to those impacts (Table 1). We included impacts, processes, and responses that were most likely to strongly influence the growth of *Zostera muelleri*, the focus species in the case study. Each impact and its corresponding response originated from a published study. We then applied a “relevance” category, from 1–4, to each of the studies, based on the applicability to *Zostera muelleri*. Where possible, studies that focused on *Zostera muelleri* (category 1), were used in preference to seagrass species uncommon or absent from Moreton Bay. If those criteria were unable to be met, studies that focused on other *Zostera* species (category 2) and then other subtropical species were used (category 3). When these were not available, we accepted studies from non-subtropical seagrass species (category 4). Assigning a simple relevance category to

each of the components of the model allowed us to assess the limitations of the model and determine where further research efforts might be directed.

*Step 2: development of the conceptual diagram*

Based on the relationships listed in Table 1, we built a conceptual diagram composed of individual nodes (Fig. 1). Each node represents a key environmental impact or an expected ecological response with directional links between nodes. Following the initial literature review, we kept the network as simple as possible by combining the published examples of impacts and ecological responses together. An impact or response was only included as a node in the network if there were three or more published examples, or they described relationships specific to *Zostera muelleri* (category 1). We validated our network by reviewing it with local seagrass experts and marine park managers.

*Step 3: building the Bayesian network*

The conceptual diagram was used to develop a BN. BNs are based on conditional probabilities that combine observed data and prior information (Reckhow 1994, Korb and Nicholson 2004). Construction of the BN allowed the common relationships between nodes of the conceptual diagram to be integrated within a single statistical framework. Links between nodes in the conceptual diagram were assigned conditional probabilities based on the findings of the original studies. This then allowed for the estimation of the probabilities of outcomes (e.g., McCann et al. 2006); see Table 1.

The BN was developed using the program Netica 4.16 (Norsys 2012). The network contains five input nodes (Fig. 1): two nodes based on anthropogenic impacts (i.e., fishing effort and nutrient availability) and three based on the physical characteristics of the seagrass meadow (i.e., starting seagrass biomass, water movement, and sediment grain size). Each input node is linked, and therefore affects the outcome of nodes representing either the ecological responses to environmental inputs, or ecological processes that in turn link to ecological response nodes. Ultimately, the model ends in a solitary “finding” or output node that predicts the state of the system (in this case, the “likelihood of increased seagrass biomass”).

Each node contains only two states, high and low, except the starting seagrass biomass node, which also contains “absent” as an additional state (each state is defined in Table 1). Although many of the nodes could be presented as continuous variables, we have kept them as discrete nodes in order to show that even the simplest probabilistic models can be used to identify bistability. Conditional probability tables (CPTs) were populated for all states for all nodes using the relationships outlined in Table 1. To show how the relationships between nodes were used to populate the CPTs, the following example outlines how the nodes

“nutrient availability” and “starting seagrass biomass” ultimately affect the outcome node, increased seagrass biomass. When nutrient concentrations were high, Stapel et al. (1996) found that “nutrient uptake” was 25% higher than when nutrient availability was low. Additionally, Boon et al. (1986) found that nutrient uptake was 90% higher when seagrass was present than absent. Both findings are used to populate the CPT for the nutrient uptake node. In turn, Thursby and Harlin (1984) showed that there was 41% increased seagrass biomass when nutrient uptake was high. This finding, along with the findings from the nodes “light availability” and “algal biomass,” are used to populate the CPT for the increased seagrass biomass node.

The design of the BN was modified to accommodate the presence of seagrass-facilitating feedback loops. The nodes of the BN include the key processes that make up feedback loops. Each loop starts and ends with seagrass biomass, which is represented in the BN by two nodes, starting seagrass biomass and likelihood of increased biomass.

The BN was compiled following the completion of the CPTs, which allowed the uncertainty of each state (its probability of occurrence) within each node to propagate through the links of the model. An example CPT is presented in Table 2. Once compiled, we assessed the relative and expected importance of each node on the output node (likelihood of increased seagrass biomass) using an entropy reduction sensitivity analysis (e.g., Marcot et al. 2006). This assesses the outcomes of the BN by ranking the effect that each node has on the output node. Nodes with greater entropy reduction values have a greater influence on the output node (Marcot et al. 2006).

*Step 4: determining the effect of different impact levels on starting seagrass biomass*

We first used the model to predict the likelihood of starting seagrass biomass (by summing the probability of high or low biomass) under different combinations of input conditions. We manipulated four of the data input nodes (e.g., “fishing effort,” “sediment grain size,” “water movement,” and “nutrient availability”) by starting with each node at a likelihood of 0% of the “high” state (i.e., the best-case scenario). We then increased the likelihood of the “high” state for each input node by increments of 25% in different combinations until 100% high state for all input nodes (i.e., worst-case scenario) was reached (Appendix A: Table A1). In total, 45 input combinations were used. For each input combination, we recorded the percentage likelihood of starting seagrass biomass by adding the percentage likelihood of the high and low states in the starting seagrass biomass node. We then fitted linear and nonlinear models to the results to describe the nature of the relationship between impact levels and the likelihood of seagrass biomass.

TABLE 1. Relationships between nodes based on the conceptual diagram (Fig. 1); parent nodes are those that determine the outcome of the child node.

Child node, nested under parent node	Child node value	
	High child state	Low child state
Fishing effort		
Large predatory fish biomass, WM	10 kg·2 ha <sup>-1</sup> ·night <sup>-1</sup>	2 kg·2 ha <sup>-1</sup> ·night <sup>-1</sup>
Piscine grazer abundance	600 ind/25 m <sup>2</sup>	75 ind/25 m <sup>2</sup>
Large predatory fish		
Small predatory fish biomass, WM	55 g/m <sup>2</sup>	5.5 g/m <sup>2</sup>
Small predatory fish		
Invertebrate grazer abundance	150 grazers/g leaf DM	36 grazers/g leaf DM
Piscine grazer biomass		
Algal grazing pressure†	0.8	0.28
Invertebrate grazer biomass		
Algal grazing pressure†	0.8	0.28
Algal grazing pressure		
Epiphytic algae biomass	3 mg AFDM/cm <sup>2</sup>	0.5 mg AFDM/cm <sup>2</sup>
Algal biomass		
More seagrass biomass	15.3 g·m <sup>-2</sup> ·d <sup>-1</sup>	6.3 g·m <sup>-2</sup> ·d <sup>-1</sup>
Starting seagrass biomass		
Piscine grazer abundance	600 ind/25 m <sup>2</sup>	75 ind/25 m <sup>2</sup>
Invertebrate grazer abundance	5.76 ind/m <sup>2</sup>	2.46 ind/m <sup>2</sup>
Nutrient uptake	75 g N·m <sup>-2</sup> ·yr <sup>-1</sup>	25 g N·m <sup>-2</sup> ·yr <sup>-1</sup>
Small predatory fish biomass	55 g/m <sup>2</sup> , WM	5.5 g/m <sup>2</sup> , WM
Sediment resuspension		
Light availability	15 mol photons·m <sup>-2</sup> ·d <sup>-1</sup>	2 mol photons·m <sup>-2</sup> ·d <sup>-1</sup>
Light availability		
Epiphytic algae biomass	3 mg AFDM/cm <sup>2</sup>	0.5 mg AFDM/cm <sup>2</sup>
More seagrass biomass	15 mol photons·m <sup>-2</sup> ·d <sup>-1</sup>	2 mol photons·m <sup>-2</sup> ·d <sup>-1</sup>
Nutrient uptake		
More seagrass biomass	15.3 g·m <sup>-2</sup> ·d <sup>-1</sup>	6.3 g·m <sup>-2</sup> ·d <sup>-1</sup>
Nutrient availability		
Phytoplankton biomass	3.0 mg Chl <i>a</i> /L	0.9 mg Chl <i>a</i> /L
Nutrient uptake	75 g N·m <sup>-2</sup> ·yr <sup>-1</sup>	25 g N·m <sup>-2</sup> ·yr <sup>-1</sup>
Macroalgal biomass	150 g/m <sup>2</sup>	50 g/m <sup>2</sup>
Epiphytic algae biomass	3 mg AFDM/cm <sup>2</sup>	0.5 mg AFDM/cm <sup>2</sup>
Sediment grain size		
Sediment resuspension	80 mg/L	5 mg/L
Water movement		
Sediment resuspension	80 mg/L	5 mg/L

Notes: The percentage difference in the child node represents how much the child node changes when toggling between the high and low state of the parent node. For example, with the highest state of the parent node “Fishing effort,” the “biomass of large predatory fish” is 80% lower than if fishing effort were low. Relevance categories for inclusion, in order of preference, are studies that focused on (1) *Zostera muelleri*; (2) other *Zostera* species; and (3) other subtropical species. When these were not available, we accepted studies from (4) non-subtropical seagrass species. Abbreviations are WM, wet mass; DM, dry mass; ind, number of individuals; Chl *a*, chlorophyll *a*; AFDM, ash-free dry mass.

† Algal grazing pressure is the ratio of algal epiphyte dry mass to leaf dry mass.

#### Step 5: determining the effect of starting seagrass biomass on the likelihood of increased seagrass biomass

To determine the effect that starting seagrass biomass has on the likelihood of increased seagrass biomass, we used the 45 input combinations described in Appendix A: Table A1. For each input combination, we recorded the percentage likelihood of the high state of the increased seagrass biomass node for each state of the starting seagrass biomass node (high, low, and absent).

#### Case study: location description

Moreton Bay in southeast Queensland, Australia (Fig. 2), contains a mosaic of coastal habitats that have been affected by multiple impacts operating along multiple gradients (Maxwell et al. 2014). The Bay is bordered on its eastern side by three sand islands that allow exchange with oceanic water through three passages, and in the west by the mainland, from which four large and several small river estuaries drain a highly developed catchment. This has resulted in a

TABLE 1. Extended.

Child node difference, high vs. low parent state	Relevance	Reference(s)
80% lower	2	Baden et al. (2012)
72% lower	3	Alcoverro and Mariani (2004)
90% lower	2	Baden et al. (2012)
76% lower	3	Heck et al. (2000)
40% higher	3	Heck et al. (2000)
40% higher	2, 3	Neckles et al. (1993), Heck et al. (2000)
50% lower	2, 3	Neckles et al. (1993), Hays (2005)
70% lower	2	Hootsmans and Vermaat (1985)
80% lower	1, 1	Gray et al. (1996), Burfeind et al. (2009)
50% lower	3, 1	Arrivillaga and Baltz (1999), Fonseca et al. (2011)
90% higher	1, 3	Boon et al. (1986), Thomas et al. (2000)
85% higher	1, 1	Gray et al. (1996), Burfeind et al. (2009)
74% lower	1	Longstaff et al. (1999)
30% higher	3, 3	Tomasko and Lapointe (1991), Lewis et al. (2002)
50% higher	1	Abal et al. (1994)
41% higher	4, 1	Thursby and Harlin (1984), Udy and Dennison (1997)
46% higher	3	Gil et al. (2006)
25% higher	3, 3	Stapel et al. (1996), Apostolaki et al. (2011)
30% higher	2	Hauxwell et al. (2001)
30% higher	3, 3	Tomasko and Lapointe (1991), Heck et al. (2000)
99% lower	1	O'Brien et al. (2012)
72% higher	4, 1, 2	Ward et al. (1984), Pattiaratchi and Harris (2002), Hansen and Reidenbach (2012)

strong water quality gradient across the Bay, with elevated nutrients and poor light availability in the western and southern zones adjacent to riverine discharge (e.g., EHMP 2010). In contrast, the eastern zones of the Bay, proximal to oceanic passages, are typically nutrient limited, with saturating light levels and low water residence times (e.g., Dennison and Abal 1999). The Brisbane River is the largest river discharging into Moreton Bay (Fig. 2a) and typically contains nutrient and sediment levels well above local and national water quality guidelines (EHMP 2010). The majority of flow from the Brisbane River runs north from the mouth into the western embayments, impacting the seagrass meadows of Deception Bay to the north and Waterloo Bay to the south via a small channel (Fig. 2a). Seagrass in Moreton Bay has been

steadily declining, particularly in Bramble Bay since the 1940s (Dennison and Abal 1999), and in Deception Bay following floods in 1974 (Kirkman 1978) and 1996 (Moss 1998). The distribution and abundance of meadows in the Bay are also predicted to change significantly with the effects of sea level rise (Saunders et al. 2013). Currently, there are ~190 km<sup>2</sup> of seagrass meadows in Moreton Bay, composed of seven species, with *Zostera muelleri* predominant and present in 70–80% of the meadows (Roelfsema et al. 2009, 2013). Consequently, we focused on *Z. muelleri*, modeling the relationships between environmental impacts and subsequent seagrass responses. This allowed us to assess the strength of feedback processes that enable seagrasses to mitigate impact and maximize growth

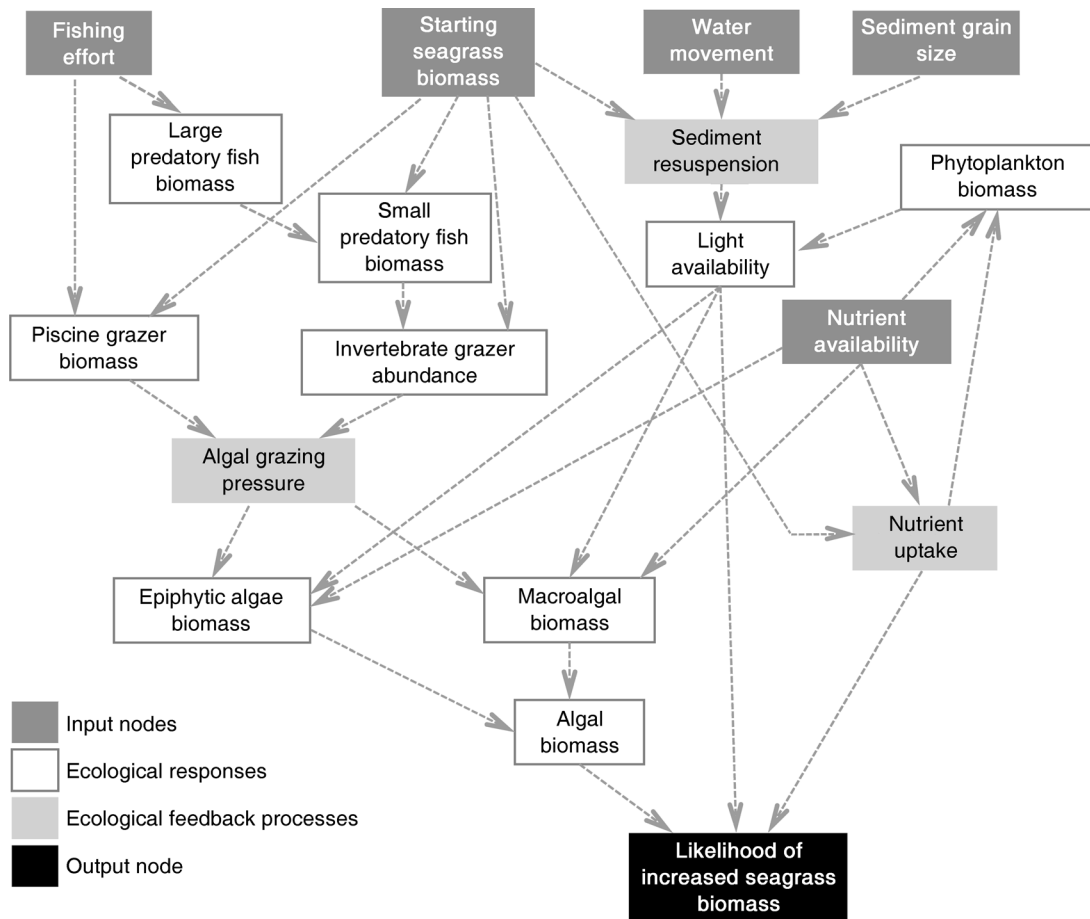


FIG. 1. Conceptual diagram based on the relationships in Table 1. Each box represents a node in the Bayesian network; each node represents a key environmental impact or an expected ecological response with directional links between nodes. The network contains five input nodes; two nodes based on anthropogenic impacts (i.e., fishing effort and nutrient availability) and three based on the physical characteristics of the seagrass meadow (i.e., starting seagrass biomass, water movement, and sediment grain size). Light gray nodes represent key processes that comprise essential feedback loops in seagrass meadows. The feedback processes are enhanced by a higher starting biomass, which in turn leads to a greater likelihood of increased seagrass biomass. Hence, these feedback processes act to stabilize shallow coastal areas that contain seagrass in the seagrass-dominant state.

potential. Hereafter, the term seagrass in the context of the model refers to *Z. muelleri*.

*Predicting regions of bistability in Moreton Bay*

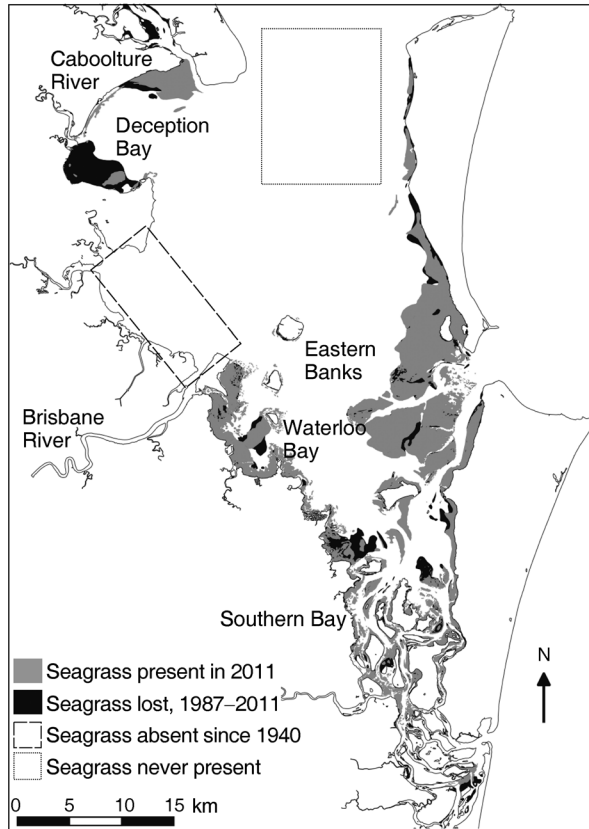
We first used the model to determine the likelihood of seagrass presence at 23 locations in Moreton Bay (Fig. 2b; Appendix B: Table B1). These locations were chosen because they either have seagrass present, previously had seagrass present (locations 4–6), or were of a depth and substrate type that supports seagrass elsewhere in the Bay (e.g., location 22). Data were drawn from a range of sources to populate each of the input nodes for each location. For each input node, we calculated the percentage likelihood of the high state. Nutrient availability data were taken from a local monitoring program, the Ecosystem Health Monitoring Program (EHMP). The program collects nutrient data at 72 sites monthly in the Bay. We calculated the median monthly total nitrogen concentration from the monitoring sites closest (<100 m)

to each location using data from 2009–2010 (EHMP 2010). Nodes were populated by the total nitrogen (TN) in each region as the proportion of the highest monthly median value recorded in the Bay that year (e.g., percentage likelihood of high nutrient availability =

TABLE 2. Conditional probability table for invertebrate grazer abundance with respect to starting seagrass biomass and small predatory fish biomass.

Starting seagrass biomass	Small predatory fish biomass	Likelihood (%)	
		High invertebrate grazer abundance	Low invertebrate grazer abundance
High	high	24	76
High	low	100	0
Low	high	16	84
Low	low	70	30
Absent	high	12	88
Absent	low	50	50

a) Moreton Bay seagrass distribution



b) Case study results

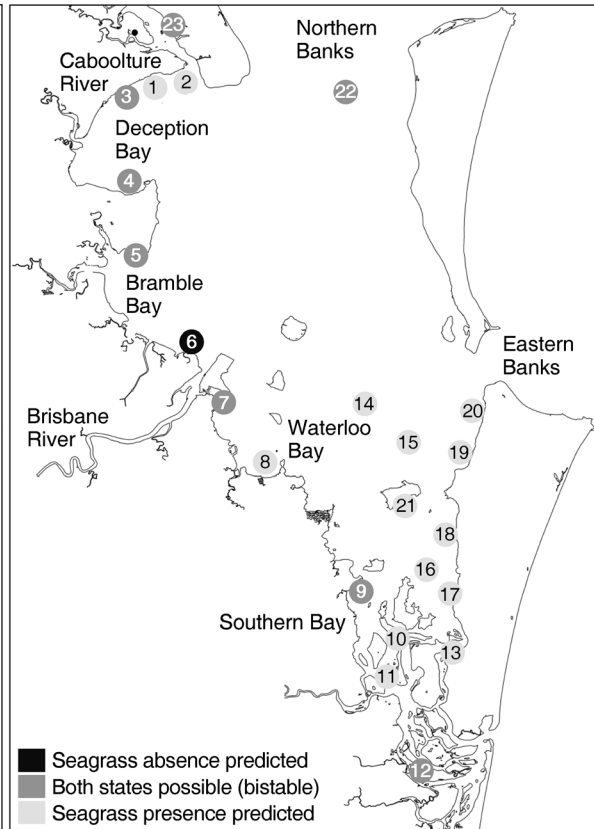


FIG. 2. (a) Distribution of seagrass in Moreton Bay as measured in 2011 (dark gray fill), as well as areas of seagrass lost since 1987 (black fill), areas that have never supported seagrass since 1940 (Bramble Bay, thick dashed outline) and areas that were predicted to be bistable but have never supported seagrass (Northern Banks, thin dotted outline). (b) Regions of Moreton Bay, with the 23 numbered locations in the case study, that are predicted for seagrass presence, bistability, and seagrass absence based on the impact levels at each. The regions are based on data from a single location within each region, and are extrapolated only to illustrate how the approach can be used to prioritize larger regions of seagrass meadows for conservation or protection. Properties of regions (by numbered case study locations) are given in Appendix B: Table B1.

median monthly TN value for the region/highest monthly median value recorded in Moreton Bay).

Official records of fishing effort cannot be resolved spatially for different locations of Moreton Bay, so the fishing effort node was defined using marine park zones (DERM 2008). In regions with no fishing restrictions (General Use Zones), fishing effort was defined as 100% likelihood of high fishing effort. For regions where restrictions on trawling and net fishing apply (Conservation Park), fishing effort was defined as 50%. For regions where all fishing is prohibited (Marine National Park Zones), fishing effort was defined as 0%.

The sediment grain size node was populated using sediment grain size data collected from 56 sites across Moreton Bay (A. Grinham, unpublished data; but see Grinham et al. (2011) for data from a selection of sites). Data from the closest sites to the model locations (<200 m) were used. The percentage of sand fraction (i.e., >0.063–2 mm) from each site was used to calculate the

percentage likelihood of the high state, so that muddier sites have lower percentage likelihoods than sandier sites.

Data for the water movement node were calculated from wind-wave height and tidal-flow modeling. Wind-waves (as distinct from ocean swells, which do not occur in Moreton Bay due to the protection provided by the sand islands to the east) are generated by the local wind patterns. These waves cease once local wind patterns change. Wind-wave height was calculated for each region using average wind speed, wind fetch length, and water depth data for each region for the year 2009–2010 (BOM 2012) using fetch and depth-limited wave calculations (CERC 1984). Average tidal flow data were calculated from hydrodynamic modeling results (CSIRO 2012). To get a percentage value to enter into the water movement node, we calculated the wind-wave height in each region as the proportion of the highest wind-wave height recorded for all regions in Moreton Bay (e.g., percentage likelihood of high water movement = wind-wave height/highest wind-wave height recorded in Moreton Bay).

TABLE 3. Sensitivity of the output node (increased seagrass biomass) to values of the remaining nodes.

Node affecting sensitivity of output node (more seagrass biomass)	Entropy reduction value
Algal biomass	0.04509
Light availability	0.04323
Algal grazing pressure	0.03671
Nutrient uptake	0.03522
Starting seagrass biomass	0.03357
Sediment resuspension	0.02991
Piscine grazer biomass	0.02381
Macroalgal biomass	0.02226
Epiphytic algal biomass	0.01107
Phytoplankton biomass	0.01056
Invertebrate grazer abundance	0.00367
Large predatory fish biomass	0.00367
Fishing effort	0.00367
Nutrient availability	0.0021
Sediment grain size	0.00203
Water movement	0.00036
Small predatory fish biomass	0.00001

Notes: Outcomes of the Bayesian network are assessed by ranking the effect that each node has on the output node. Nodes with greater entropy reduction values have a greater influence on the output node.

## RESULTS

### Model sensitivity

The nodes that link directly to the output node (i.e., algal biomass, light availability, and nutrient uptake) and algal grazing pressure had the greatest effect on the output node (Table 3). Each of these nodes had similar entropy reduction values, suggesting that they had similar effect on the outcomes of the output node. Of the five input nodes, seagrass starting biomass had the greatest effect on the output node (Table 3). The remaining four input nodes (fishing effort, nutrient availability, sediment

grain size, and water movement) had low entropy reduction values, suggesting that they had less effect on the BN outcome than starting seagrass biomass. Water movement and sediment grain size, however, still have a significant effect on the output node through their influence on sediment resuspension, which has a relatively high entropy reduction value considering the high number of links between it and the output node.

Starting seagrass biomass is linked to five child nodes, thereby affecting all of the pathways that lead to the output node. In contrast, the four remaining input nodes are only linked to one or two child nodes and therefore affect only one or two of the BN pathways. Following starting seagrass biomass, fishing effort had the most effect on the output node, followed by nutrient availability and sediment grain size. The influence of the input nodes on the output node changed with differing levels of starting seagrass biomass. For example, changing the fishing effort node from 100% to 0% High state only had a 4% influence on the output node when starting seagrass biomass was absent. When starting seagrass biomass was set to “high,” however, changing the fishing effort node from 100% to 0% High state had a 20% influence on the output node.

### Effect of changing impact on the likelihood of seagrass biomass

The predicted likelihood of seagrass biomass for each input combination ranged from 100% to 30% (likelihood of seagrass biomass = percentage likelihood of high biomass state + low biomass state). The effect of increasing impact levels on the presence of seagrass biomass was not simply linear ( $R^2 = 0.64$ ,  $P = 0.001$ ) (Fig. 3a), with the relationship being equally well

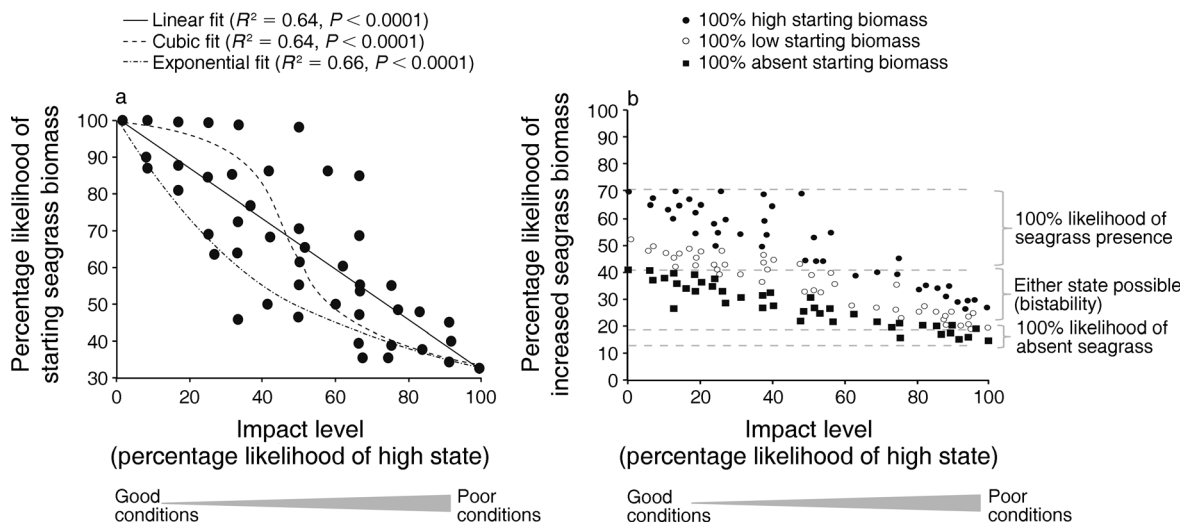


FIG. 3. Output of the Bayesian network. (a) The likelihood of starting seagrass biomass at different impact levels (see Step 4) and (b) the effect of starting seagrass biomass on the likelihood of increased seagrass biomass (percentage of the high state of the node) at different impact levels (see Step 5). The amount of initial seagrass biomass has a mitigating effect on the level of impact a meadow can withstand without loss. This mitigating effect resulted in the middle ranges of impact levels having a wide likelihood of seagrass presence, a situation known as bistability.



explained by cubic polynomial ( $R^2 = 0.64$ ,  $P = 0.001$ ) and exponential ( $R^2 = 0.66$ ,  $P = 0.001$ ) functions. Three of the possible functions that significantly described variation in the relationship between impact and seagrass biomass have been included in Fig. 3a. This results from the large variability in predictions for seagrass biomass in the middle range of impact levels (e.g., 25–70%), but narrowing at both high and low impact averages. The variability in the likelihood of starting seagrass biomass being present or absent at the same impact levels in this range is an indication of bistability.

*Effect of starting seagrass biomass on likelihood of increased seagrass biomass and calculation of bistability*

Seagrass presence has a strong positive effect on the likelihood of increased seagrass biomass at all impact levels. For each combination of input values (Appendix A: Table A1), the predicted likelihood of increased seagrass biomass when high starting seagrass biomass was present was greater than that for both low starting seagrass biomass and absent starting seagrass biomass (Fig. 3b). The predicted likelihood of increased seagrass biomass for each of the starting biomass categories (high, low, and absent) decreased with increasing impact. The likelihood of high starting seagrass biomass was more variable at lower impact levels, suggesting that high starting biomass results in a better chance of increased biomass at a larger range of impact levels than low starting biomass.

In order to determine the likelihood of bistability at each location in the case study, we had to define bistability in terms of the BN's output node, likelihood of increased seagrass biomass. Bistability was therefore defined as the range where the likelihood of increased biomass when starting biomass was present (e.g., high starting biomass + low starting biomass) overlapped with the likelihood when starting biomass was absent. Based on the model, when the likelihood of increased biomass is between 19% and 40% (Fig. 3b) it is possible that starting biomass could be present or absent. This range was used to determine the likelihood of bistability in the case study.

*Case study: model validation and the predicted locations of bistability in Moreton Bay*

The model output was validated by comparing the prediction for each of the case study locations (Fig. 2b) with the 2011 seagrass map for Moreton Bay (Roelfsema et al. 2013) (Appendix C: Table C1). Model validation was only possible for the locations that were predicted as having seagrass present or absent, because the locations that were predicted as bistable could either be present or absent in the 2011 map. For the locations that were predicted by the BN as only seagrass presence possible (14 of 23 locations), seagrass was present in 2011 and in all four of the previous distribution maps. For locations predicted as having seagrass absent (one

of 23), seagrass was absent in 2011, in each of the four previous maps, and anecdotally since 1940. Therefore the model accurately predicted seagrass presence or absence in 100% of the relevant locations.

Bistability was assigned to the locations in Moreton Bay based on two criteria. First, the impact levels for bistable regions had to fall between 25% and 70% (based on the criteria outlined in *Methods* and Fig. 3a), and second, the likelihood of increased seagrass biomass had to fall between 20% and 40% (based on Fig. 3b). Only southern Bramble Bay (location 6 in Fig. 1b) experienced impact levels resulting in the likelihood of increased biomass below 20%, leading to the predicted absence of seagrass in that location (Fig. 1b). The model did not predict seagrass absence in any locations where seagrass has been recorded previously. Eight locations experienced combined impact levels and likelihood of increased biomass that resulted in model predictions of bistability (locations 3, 4, 5, 7, 9, 12, 22, and 23). All of those locations, with the exception of the Northern Banks, were adjacent to the mainland. The model predicted bistability in many of the areas that have experienced seagrass loss since 1987 (based on Hyland et al. 1989), most notably southern Deception Bay (location 4) and parts of the Southern Bay channels (locations 9 and 12); see Fig. 2b.

## DISCUSSION

Effective conservation and management of ecosystems requires an understanding of complex nonlinear relationships that may exist between impact gradients, ecosystem structure, and the processes that mediate the two (e.g., Suding and Hobbs 2009). Timely collation of such information can be difficult, given the urgency with which conservation and restoration goals need to be met (e.g., Holzkämper et al. 2012), and practitioners are often unable to wait for rigorous testing of nonlinear ecosystem dynamics. Our results demonstrate the capacity for simple modeling tools to facilitate collation and synthesis of disparate information, and provide for preliminary assessments of nonlinear dynamics in ecosystems such as seagrasses. This approach can be adopted to support the development of programs for ecosystem conservation, restoration, and management (e.g., Renken and Mumby 2009) and to direct any data collection activities needed to underpin management decisions.

Nonlinear ecosystem dynamics, such as the bistability we describe here, are notoriously difficult to predict and identify (deYoung et al. 2008). The apparent irreversibility of shifts in ecosystem structure and function is of increasing concern as intensifying human impacts shift the dynamics of ecosystems from being regulated by local- to global-scale stressors (e.g., Brown et al. 2013). Bistable ecosystems exhibit high variability in response to impact and, therefore, may fluctuate abruptly between regimes (Gunderson 2000). This means that relatively small increases in impact levels may result in

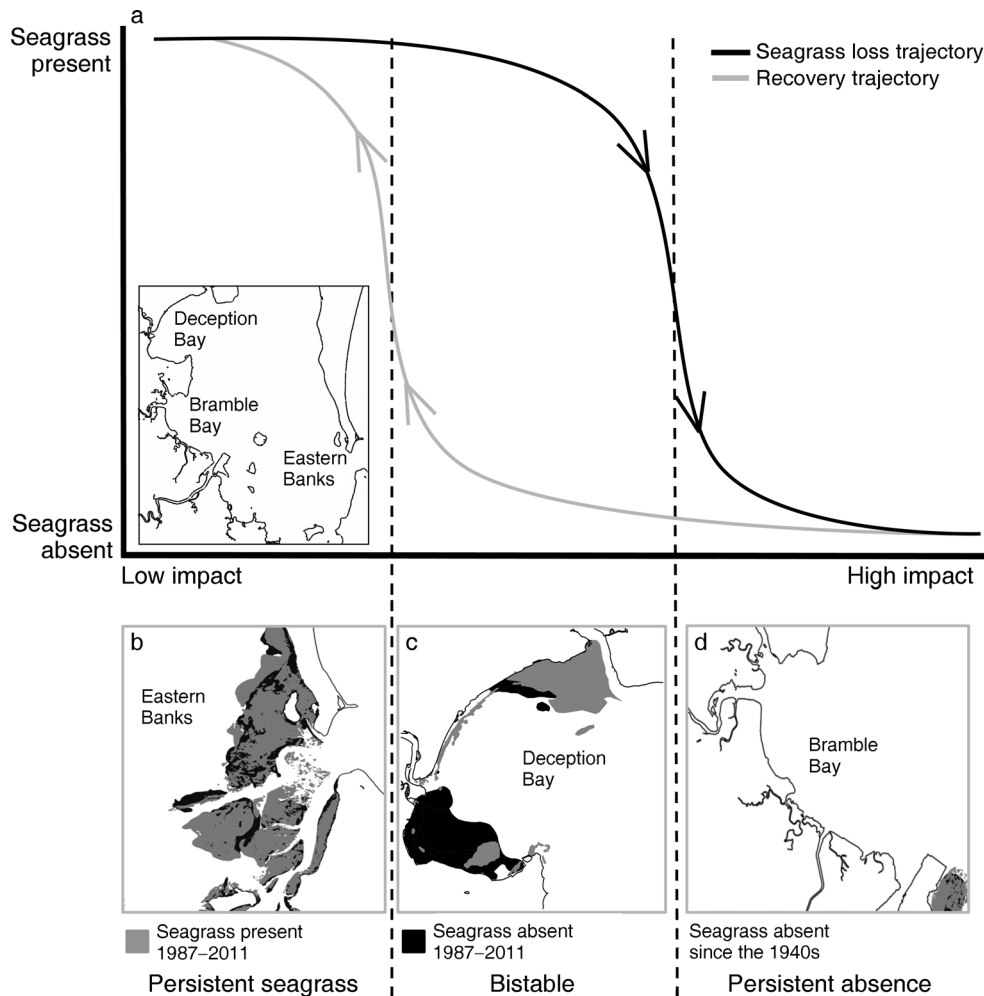


FIG. 4. (a) Idealized trajectories of seagrass meadows with changes in impacts based on the Bayesian network output. Both the loss and recovery trajectory exhibit considerable lag in their response to changes in conditions. (b) When impact levels are low and the likelihood of increased seagrass biomass is high, there is a high likelihood of seagrass presence (e.g., Eastern Banks). (c) When impact levels are in the middle range, the likelihood of seagrass biomass is variable, which in turn can lead to temporal fluctuations in seagrass biomass (e.g., Deception Bay). (d) At high levels of impact, the likelihood of seagrass biomass is low (e.g., Bramble Bay). The gray and black keys for seagrass presence and absence apply to all three lower panels (b–d).

disproportionately large changes to the structure and functioning of bistable ecosystems. Once these ecosystems shift regimes, disproportionately large decreases in impact levels may be required to reverse such changes (e.g., Fig. 4) (e.g., Beisner et al. 2003). These nonlinear ecosystem dynamics can dramatically reduce the likelihood of success with succession-based approaches to management and conservation.

In soft-sediment coastal habitats, shifts in ecosystems are often associated with changes in the cover of habitat-forming species, which influence sediment stability and positively affect water quality (Lohrer et al. 2004, van Nes et al. 2007). The results of our study demonstrate that seagrasses have a significant positive effect on their growing conditions, which leads to bistability across a range of impact levels. As in other recent studies (Carr et al. 2010, 2012, van der Heide et al. 2011), bistability in

our model results from the coupling of feedback loops between starting seagrass biomass and the enhancement of conditions required for the addition of seagrass biomass.

Through the process of developing the conceptual diagram, we identified three feedback loops that occur in seagrass ecosystems. First, seagrass meadows, and the bacterial and microbial communities associated with them, sequester nutrients from the water column. This limits the nutrients available for micro- and macroalgal growth and prevents them from reducing light penetration through the water column. The sequestration of nutrients from the water column maintains the dominance of seagrasses and other macrophytes under low to medium levels of nutrients; however, it can lead to phytoplankton dominance once the key biogeochemical processes break down with high levels of nutrients (e.g.,

Webster and Harris 2004, Anton et al. 2011). Second, seagrasses trap and bind sediment, limiting resuspension and increasing light availability. Sediment resuspension has been the focus of various studies of bistability in seagrass ecosystems (e.g., van der Heide et al. 2007, Carr et al. 2010) and a review (de Boer 2007), and has been suggested as the factor primarily limiting seagrass occurrence and recovery. Third, denser seagrass canopies provide habitat for algal grazers, which reduce the negative effects of algal overgrowth and improve light availability. Seagrass–herbivore interactions exert considerable influence on a meadow’s morphology and algal control, triggering the recruitment of new shoots and an increased number of leaves (e.g., Heck and Valentine 2006), thus affecting the photosynthetic capacity and subsequent growth rates of plants.

The bistability that appears to exist in some Moreton Bay seagrass meadows is likely to result from the mitigating effects of the three feedback processes at medium and lower levels of impact. As a result, it is possible that the trajectory for seagrass loss may exhibit a substantial delayed response to increases in impact levels (Fig. 4a). When impacts breach some threshold level, the feedback processes break down, leading to a potentially rapid loss of seagrass biomass, as suggested by previous studies (e.g., Viaroli et al. 2008). Once unvegetated, sediments are more easily resuspended, light availability is reduced (e.g., Carr et al. 2010), nutrient loads increase in the water column (e.g., Boon 1986), and grazing rates decrease (e.g., Gray et al. 1996). These processes facilitate perpetuation of the unvegetated state even after substantial reductions in impact levels. Although each of the three feedback processes has been previously modeled or studied in isolation, this is the first attempt at modeling their combined effects on seagrass ecosystem dynamics.

The results from our case study show that the model was able to predict how different impact levels affected the likelihood of seagrass presence at different locations in Moreton Bay. In areas where impact levels are low, we found a high likelihood of seagrass presence only (e.g., Eastern Banks; Figs. 2b and 4b). In these regions, the loss of seagrass is unlikely to reduce growth conditions to levels that would result in long-term seagrass absence. In areas of the Bay where impact levels are in the middle ranges, seagrass loss would significantly reduce growth conditions and thereby lower the likelihood of seagrass recovery. This has already occurred in some of the predicted bistable locations; for example, seagrasses were lost from southern Deception Bay in 1996 following flooding of the Caboolture River (Moss 1998). Recovery in the region has been limited, with a smaller meadow recorded in the 2011 survey than was present in 1987 (Figs. 2a and 4c), despite improvements in water quality since 1996 (P. Maxwell, *unpublished data*). We suspect that this was due to the resuspension of the fine sediments in the region that prevents seagrass recolonization. In regions

of the Bay with high impact levels, conditions are not conducive to seagrass growth, so seagrass has been lost and not recovered (e.g., Bramble Bay; Figs. 2b and 4d). Once seagrass is lost from bistable regions of Moreton Bay, recovery would require significant improvements to impact levels to ultimately improve conditions for seagrass recolonization. Seagrass recovery in bistable regions, therefore, requires the suppression of the feedbacks responsible for the stability of unvegetated regimes (e.g., the stabilization of sediments to prevent resuspension). Sediment stabilization using shell armoring (van Katwijk and Hermus 2000, Suykerbuyk et al. 2012) and mussel beds (Bos and van Katwijk 2007) has been shown to favor seagrass transplant survival. This approach has also been widely discussed as the key to restoring degraded ecosystems generally (see examples in Suding et al. 2004).

Our results suggest that the current catchment management efforts underway in southeast Queensland are unlikely to have a short-term positive effect on seagrass recovery in bistable regions of Moreton Bay, even though these actions are, in part, aimed at aiding the recovery of significant marine habitats (e.g., Abal et al. 2006). Reducing sediment and nutrient loads from diffuse and point sources in the catchment, particularly in the western and southern regions, will have little immediate effect on the level of sediment resuspension, nutrient uptake, and algal grazing rates, and, as a result, seagrass recovery. The restoration of coastal habitats generally has traditionally focused on reversing the impacts that lead to the initial degradation (e.g., Young 2000). Although we strongly support catchment management and restoration efforts to reduce sediment and nutrients and limit further seagrass loss, we recommended that additional measures be included to enhance the likelihood of seagrass recovery. These are based on our results, guidelines for seagrass restoration (e.g., van Katwijk et al. 2009), and the suggestion of restoration ecologists generally (e.g., Suding et al. 2004, Suykerbuyk et al. 2012).

We recommend that the additional actions focus on enhancing the biomass of existing seagrass meadows, particularly in bistable areas, and reducing the direct negative effects of sediments and nutrients. Seagrass transplantation is one possibility, but this can be costly, with limited and variable success (e.g., van Katwijk et al. 2009). We recommend that seagrass restoration and management plans include management actions that enhance feedback processes that promote resistance to impact, and actions that break down the feedback processes that prevent recovery. For example, managing to enhance grazing rates, through the protection of herbivores or designation of no-take areas that prohibit fishing for herbivores, is likely to limit algal loads and improve seagrass growth and abundance (Valentine and Heck 1999, Hays 2005). Actions could include sediment stabilization strategies in unvegetated areas to improve the success of restoration efforts (e.g., van Katwijk et al.

2009). Seagrass monitoring programs should include measures of feedback processes to better understand the relationship between changing impact and seagrass response. For example, measuring algal grazing rates can help to better understand how the temporal and spatial variation in grazing rates affects algal production and, ultimately, seagrass resilience. Monitoring should include measures of sediment resuspension and nutrient uptake rates, to improve understanding of how these processes might mitigate changing levels of impact.

Our study has shown that Bayesian networks are a useful tool for combining disparate data sets to measure ecological responses to changing impact gradients (Pollino et al. 2007). The utility of the BN enabled us to conceptualize an ecosystem within a quantitative and probabilistic framework and define the relationship between changing impacts and ecological function. We combined information from multiple sources, integrating locally relevant studies with those from farther afield, to fully populate the network. The utility of the BN means that as the network becomes more developed, the relationships between nodes can be used to develop dynamic models capable of more complex spatial predictions of seagrass distribution. For example, the model could be linked with spatially explicit input data (e.g., wind, water current, sediment grain size mapping, seagrass biomass mapping) through GIS platforms in order to provide high-spatial-resolution risk maps for bistable seagrass meadows that could be used in environmental risk assessments. The BN that we present here has been compiled using relationships most relevant to the case study location, Moreton Bay. For example, although water temperature is a significant stressor in many regions, particularly in *Zostera marina* meadows in the northern hemisphere, it is not significant in Moreton Bay, where water temperature in subtidal areas rarely exceeds the tolerance limits of *Z. muelleri*. Water temperature, therefore, was not included in the network. The flexibility of BNs, however, makes it relatively simple to add or remove nodes depending on their local relevance. Therefore, the extent to which our BN is relevant for other seagrass systems is only limited by the relevance of the nodes included in the network.

Although BNs provide managers with the flexibility to incorporate a range of data types, including quantified data sets and expert opinion (e.g., Stewart-Koster et al. 2010), the ecosystem knowledge gained through their development is also invaluable for enhancing management outcomes. For example, the approach used to develop the BN is similar to that used for environmental risk assessments and could therefore be used to provide an early step for managers to use in that process. The initial step of developing a conceptual diagram of the ecosystem, and seeking relevant local information to populate it, helps to highlight the deficiencies in local knowledge and can be used to better focus further research. For example, although the sensitivity analysis (Table 3) showed the algal grazing to be important, the

uncertainties outlined in Table 1 highlighted the lack of local knowledge about the role that it plays in enhancing seagrass resilience. Accordingly, the need to better quantify this relationship should provide a focus for future research. This step is vitally important to the relevance of such models to local ecosystem management. Locally relevant information is often unavailable in the initial planning stages of conservation or restoration projects, which can detract from the forecasting capacity of reliant models (e.g., Syphard et al. 2011). Local relevance and additional precision can be incorporated in models such as ours as further information comes to hand.

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## SUPPLEMENTAL MATERIAL

## Ecological Archives

Appendices A–C are available online: <http://dx.doi.org/10.1890/14-0395.1.sm>