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ECOSYSTEMS

Artificial intelligence to explain the variables that favor the cyanobacteria steady-state in tropical ecosystems: A Bayeasian network approach

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Abstract: The steady-state is a situation of little variability of species dominance and total biomass over time. Maintenance of cyanobacteria are often observed in tropical and eutrophic ecosystems and can cause imbalances in aquatic ecosystem. Bayeasian networks allow the construction of simpls models that summarizes a large amount of variables and can predict the probability of occurrence of a given event. Studies considering Bayeasian networks built from environmental data to predict the occurrence of steady-state in aquatic ecosystems are scarce. This study aims to propose a Bayeasian network model to assess the occurrence, composition and duration of cyanobacteria steady-state in a tropical and eutrophic ecosystem. It was hypothesized long lasting steady-state events, composed by filamentous cyanobacteria species and directly influenced by eutrophication and drought. Our model showed steady-state lasting between 3 and 17 weeks with the monodominance or co-dominance of filamentous species, mainly *Raphidiopsis raciborskii* and *Planktothrix agardhii*. These evens occurred frequently under drought and high turbidity, however higher nutrients concentrations did not increase the probability steady-state occurrence or longer duration. The proposed model appears as a tool to assess the effects of future warming on steady-state occurrence and it can be a useful to more traditional process-based models for reservoirs.

Key words: abiotic variables, phytoplankton, predictive models, eutrophication, climate.

INTRODUCTION

The growth and dominance of phytoplankton species in reservoirs is regulated by a complex combination of physical, chemical and hydrological factors (Huszar et al. 2003, Çelik & Ongun 2008). These variables are nested and interact each other, creating a spacial and temporal heterogeneity that influence systems on different scales (Naselli-Flores & Barone 2003).

Depending on environmental conditions, some dominant species in the environment may not show significant variation in their biomass over a period of time, constituting an event called steady-state, regulated by the production and loss of biomass in a balanced way (Rojo & Álvarez-Cobelas 2003, Teubner et al. 2003, Hui et al. 2014).

The term steady-state originates in culturing experiments with microrganisms, including algae (Naselli-Flores & Barone 2003). In phytoplankton ecology, the steady-state concept emerged to describe a situation of little variability of species dominance and total biomass over time (Hui et al. 2014). According to Sommer et al. (1993), the criteria for identifying the steady-state phases in natural systems are: maximum of three species contributing at least 80% of the total biomass for more than 2 weeks without considerable variation in the total biomass.

The mechanisms or factors controlling the steady-state phytoplankton assemblage would be trophic relationships, biogeochemistry processes, climate variables, diffusion mechanisms, etc, under certain conditions (Rojo & Álvarez-Cobelas 2003, Mei & Zhang 2012). Since the steady-state is the result of a dynamic process (Sommer et al. 1993) and the time generation of microalgae is from 0.3 to 3 days, sampling for assessment this status must be weekly. Thus, it is requisite to find a similar assemblage over a period of at least three successive weeks in order to suggest that it is stable (Rojo & Álvarez-Cobelas 2003).

In natural freshwaters, historical observations showed cyanobacterial blooms were a successive process, lasting for several months in a year. Cyanobacteria steady-has often been seen in hypertrophic conditions, in stressed shallow water bodies and usually occur in summer (Hui et al. 2014). Studies suggest the characteristics of cyanobacteria, including cell-density, toxin fate etc. favour the maintenance of cyanobacteria on the ecosystem (Li et al. 2020). Due to their relative stability and higher temperatures, steady-state cyanobacteria are supposed to be more likely to occur in tropical environments and are characterized by their lasting duration and seasonality dependence, in addition to being predominantly monospecific of *Microcystis aeruginosa* (Kützing) Kützing and *Raphidiopsis raciborskii* (Woloszynska) Aguilera, Berrendero Gómez, Kastovsky, Echenique & Salerno (previously classified as *Cylindrospermopsis raciborskii* (Woloszynska) Seenaya and Suba Raju) (Komárková & Tavera 2003, Rojo & Álvarez-Cobela 2003, Stoyneva 2003, Becker et al. 2008, Baptista & Nixdorf 2014).

Studies show that increased environmental heterogeneity leads that species occupies a different niche, reduces direct competition and thus species composition is more or less stable according to environmental predictability. Hence, both temporal and spatial niche segregation is essential to maintain communities in equilibrium. In tropical aquatic environments, this segregation could be reached in the absence of disturbance and would result in an eternal steady-state where diversity is reduced to minimal levels by competitive exclusion (Naselli-Flores & Barone 2003, Çelik & Ongun 2008).

The steady state is influenced, among other variables, by nutrients both present in the water column and present in the sediment and which are resuspended in periods of flooding or drought. Due to low water levels in reservoirs during drought periods, mixing proceses, with resuspension of nutrients and other sediments are posible, in addition to facilitating the light penetration. These conditions create a scenario that favors cyanobacteria steady-sate (Peeters et al. 2013, Oliveira & Dantas 2019).

High densities of cyanobacteria are often observed in tropical and eutrophic ecosystems and can cause imbalances in aquatic ecosystem biodiversity. Additionally, some species can compromise the water quality of a certain ecosystem, as they are potentially producers of cyanotoxins and other secondary metabolites, which impart taste and odor to water, such as 2-methylisoborneol (MIB) and geosmin. This scenario requires the investment of large amounts for operational adjustments in order to guarantee the quality of the water to be distributed by the supply companies. Therefore, predicting the occurrence and duration of steady-state is essential, as it allows immediate adjustments to be made in the water supply, avoiding excessive expenditure on chemicals and other operational maneuvers.

Studies have been conducted mainly in laboratories and propose mathematical models and algorithms for direct or indirect estimation of the concentration of phytoplankton organisms in a water body, considering a constant stoichiometric relationship between a limited set of abiotic variables and monospecific phytoplankton cultures (Persaud et al. 2015, Abakumov et al. 2019).

Bayeasian networks (BN) are a simplified data entry model, which allow the construction of a structure that summarizes a large amount of information (independent variables) and can predict the probability of occurrence of a given event. They are a low-cost and operationally easy tool, which allows assessing the relation between variables, where changes in each of the components can be visualized, supporting in decision-making (Moe et al. 2016).

Studies considering BN built from environmental data to predict the occurrence of steady-state in aquatic ecosystems are scarce. This approach allows considering the oscillations of biotic and abiotic variables over time, relating them to the steady-state occurrence of one or more phytoplankton species. Therefore, BN allow the generation of a model closer to reality in the ecosystem, contributing to fill this scientific gap in the study of the ecology of phytoplankton communities.

Thus, this work aims to propose predictive models, through BN, to assess the occurrence, composition and duration of cyanobacteria steady-state in a tropical and eutrophic ecosystem, considering rainfall and physicochemical variables of water. We hypothesized that the steady-state events observed in this work will be long lasting and will be composed by filamentous cyanobacteria species. We also believe that the increase of the level of eutrophication, evaluated by the concentrations of nitrogen and phosphorus in the ecosystem, as well as the drought, will have a direct impact on the occurrence and duration of the steady-state.

MATERIALS AND METHODS

Study area

Pedro Moura Júnior (8°20’9’’S, 36°25’28’’W) is a eutrophic reservoir located in the municipality of Belo Jardim (Northeast of Brazil) and is part of the Ipojuca River basin, one of the largest in the region. It is responsible for the supply of approximately 80,000 inhabitants, and has a maximum accumulation volume of 30,740,000 m^3 and an average depth of 14 m. The climate of the region is semiarid (Alvares et al. 2013) with rainfall concentrated between March and August. During the study, the rainfall ranged from 0.00m to 116.4mm and the average monthly air temperature ranged from 23.0ºC to 24.2ºC.

Sampling procedures and laboratory analysis

Water samples were taken weekly between July 2016 and December 2019 in the limnetic region of the reservoir for 130 monitoring weeks. Phytoplankton samples were collected in duplicate for qualitative and quantitative analysis under the water surface of the reservoir (approximately 30 cm depth), around 11 a.m., due to the higher intensity of sunlight, and then preserved and stored according to American Public Health Association (APHA 2017). We carried out our investigation in surface water, considering: (I) the absence of thermal stratification in the reservoir throughout the study period; (II) the deep-water nutrient concentration is insufficient to sustain the stability of any biomass in the mixed layer through vertical transport of nutrients into the mixed layer, as pointed out by Kovac et al. (2020).

Cyanobacteria were identified to the lowest possible taxa, according to the literature (Komárek & Anagnostidis 1989, 1999, 2005, Komárek & Cronberg 2001). Other phytoplankton groups did not show significant biomass in this ecosystem, compared to cyanobacteria, and were identified to the genus level, according to Bicudo & Menezes (2006).

Phytoplankton density (cells.mL^{-1}) was determined following the methodology described in APHA (2017), using Sedgewick-Rafter counting chambers and optical microscope (Leica, Germany). Species biomass ($mm^3.L^{-1}$) was calculated from the cell biovolume values (n = 30), based on Hillebrand et al. (1999).

All parameters were analyzed in the laboratory. Values of turbidity (NTU), color (UC) and pH were obtained from measurements with turbidimeter (Hach, USA), colorimeter (Hach, USA) and potentiometer (Digimed, Brazil), respectively. Measurements of total inorganic nitrogen (TIN, mmol.L^{-1}) and phosphate (PO4, mmol.L^{-1}) were made according to APHA (2017). Data of rainfall (mm) were provided by Pernambuco Water and Climate Agency (APAC), and were obtained from a research station located about 2 km from the sampling sites.

Previous studies carried out by Oliveira & Dantas (2019) in a tropical ecosystem also located in the Northeast region of Brazil, showed that high concentrations of nitrogen together with higher values of turbidity and color favored the development of steady state of cyanobacteria in these ecosystems. For this reason, these variables were selected to compose the model proposed in this manuscript.

Bayeasian network modelling

Three BN models were performed: I. Steady-state; II. Cyanobacteria species in steady-state; III. Duration of cyanobacteria steady-state. For constructing the BN models, we followed the guidelines for use of BN in ecological modelling (Marcot et al. 2006): (1) Defining the objective of the model and its final node; (2) generating a model (nodes and arrows) based on monitoring data; (3) establishing the model states and quantifying the relationships. The BN model was developed and run in the software Netica version (https://www.norsys.com).

Model structure

In a BN model, each node (variable) is typically defined by a discrete probability distribution across a number of alternative states (i.e., intervals or categories). This structure enables different types of information to be linked by conditional probability tables (CPT). All nodes with outgoing arrows are termed “parent nodes”, while all nodes with incoming arrows are termed “child nodes”. In a CPT, the probabilistic dependencies between a child node and its parents are defined. When the model is run, probability distribution of the child node is updated accordingly, given the states of the parent nodes, following the Bayes’ theorem for conditional probability calculation (Koski & Noble 2009). The probability distributions in the CPTs can represent the natural variability in the system as well as any other type of uncertainty concerning the relationship between the variables. The complexity of a BN grows exponentially with the number of nodes and arrows; therefore it is often desirable to limit the number of nodes (Varis & Kuikka 1999). In this study, we aimed at including only the nodes that were necessary to assess the effect of rainfall and water physicochemical variables for the cyanobacteria steady-state status.

Tredictions of a BN can represent the probability of realising different outcomes during a specified period. The BN in our study represents the samples collected between 2016 and 2019.

The BN model developed in this study comprises three modules, corresponding to the sources of information described above.

Module 1 constains the observed data for rainfall.

Module 2 contains the observed series for a set of water physicochemical variables.

Module 3 contains the observed steady-state status.

This enables prediction of the probability of cyanobacteria steady-state status for each indicator. For the causal links between the nodes (i.e., the arrows and their directions), we let the software estimate suggest a set of arrows and their directions given specific criteria.

Node states and prior probability distributions

Continuous variables must be discretised into intervals (states) for use in discrete nodes in a BN. The number of states for each node is typically kept low, because the model complexity also grows quickly with the number of states. In this study, therefore, we tried to minimise the number of states, while still obtaining a model with sufficient sensitivity to respond to the cyanobateria steady-state. In the child module, we discretised the states into:

I. Model 1 (steady-state occurrence): nSS (non steady-state occurrence) and SS (steady-state occurrence).

II. Model 2 (cyanobacteria species in steady-state): PA; PA+RR and PA+RR+MA, where PA = *Planktotrhrix agardhii,* RR = *Raphidiopsis raciborskii* and MA = *Microcystis aeruginosa.*

III. Model 3 (duration of cyanobacteria steady-state): 3-6 weeks; 7-12 weeks and 13-17 weeks.

An overview of the states of all nodes is given in Table I.

The prior probability distributions were defined as follows. For parent nodes representing rainfall and water physicochemical variables (Modules 1 and 2), the prior probability distribution was determined by their CPT

Table I. Overview of nodes in the Bayeasian network model. Module 1: rainfall; Module 2: physicochemical variables; Module 3: steady-state status. Model 1: steady-state occurrence; Model 2: cyanobacteria species in steady-state; Model 3: duration of cyanobacteria steady-state; PO_4: phosphate; TIN: total inorganic nitrogen; nSS: non steady-state; SS: steady-state; PA: *Planktothrix agardhii*; RR: *Raphidiopsis raciborskii*; MA: *Microcystis aeruginosa*.

Module	Model	Node name	Unit	Node states		
				1	2	3
1	1	Rainfall	mm	0.0-38.8	38.9-77.6	77.7-116.4
1	2; 3			0.0-29.0	30.0-59.0	60.0-89
2	1; 2; 3	PO_4	$mg.L^{-1}$	0.005-0.127	0.128-0.249	0.250-0.371
2	1; 2; 3	TIN	$mg.L^{-1}$	0.33-1.17	1.18-2.01	2.02-2.85
2	1	pH	-	7.0-7.4	7.5-7.8	7.9-8.2
	2; 3			7.0-7.5	7.6-8.0	-
2	1; 2; 3	Turbidity	uT	0.84-3.59	3.60-6.34	6.35-9.10
2	1	Color	uC	31-61	62-91	92-121
	2; 3			36-71	72-96	97-111
3	1	Steady-state occurrence	-	nSS	SS	
3	2	Cyanobacteria species in steady-state	-	PA	PA+RR	PA+RR+MA
3	3	Duration of cyanobacteria steady-state	weeks	3-6	7-12	13-17

in combination with the prior probability distributions of their parente nodes. For child nodes (Module 3), representing the cyanobacteria steady-state status, that is, frequency of occurrence of states in each of the three models.

Construction of conditional probability tables (CPT)

Table II contains examples of CPTs for each module. The CPT of each child node was calculated as the frequency distribution of this variable across each of its parent nodes. For example, the probability of the steady-state, under a given combination of states of the parent nodes (rainfall, PO_4, TIN, pH, turbidity and color), was determined by the count of variable obtained for each particular combination of states of the parents nodes divided by the total number of observations for this combination.

Running the BN model

A BN model can be run by altering the probability distribution of one or more nodes and thereby updating the probability distribution in all the nodes that are linked by CPTs throughout the network. A common way to run the model is to "set evidence" for one or more of the parent nodes, i.e. to select one of the states (assign 100% probability for this state). In this study, three models were performed by setting evidence for each combination of abiotic variables (water physicochemical and rainfall) and: I. steady-state occurrence; II. Cyanobacteria species in steady-stateSS; III. Duration of cyanobacteria steady-state. Then, the probabilities were recorded.

Model evaluation

Model evaluation is an important step in good modelling practice, but evaluation of BN models is often neglected (Moe et al. 2016). We used one part of a dataset for "training" (model calibration) while another part was reserved for evaluation by comparison with model predictions and we could test the behaviour of the model (Chen & Pollino 2012).

Besides, the sensitivity analysis was perfomed to evaluate the intensity of interaction (sensitivity) of each input variable to the output variable, indicating, in decreasing order, the variables with the greatest impact.

RESULTS AND DISCUSSION

We would like to begin this section keeping in mind that our results allow us to establish a pattern, but not to make definite conclusions about the underlying mechanisms.

Table II. Examples of conditional probability tables (CPT) for each module of the Bayeasian network model. Each column contains the probability distribution of a child node for a given combination of states of the parent nodes. The bottom row ("Experience") contains the total count of observations for each combination of parent nodes. The table shows the first 9 columns for rainfall, PO_4 and turbidity. The full table contains 3 (rainfall intervals) x 3 (PO_4 intervals) x 3 (TIN intervals) x 3 (pH intervals) x 3 (turbidity intervals) x 3 (color intervals) = 729 columns.

Rainfall (mm)	0.0-38.8			38.9-77.6			77.7-116.4		
pH	**7.0-7.4**	**7.5-7.8**	**7.9-8.2**	**7.0-7.4**	**7.5-7.8**	**7.9-8.2**	**7.0-7.4**	**7.5-7.8**	**7.9-8.2**
Turbidity (uT)									
0.84-3.59	0.25	0.00	0.00	0.50	0.83	0.00	0.00	0.91	0.00
3.60-6.34	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.04	0.00
6.35-9.10	0.75	100.00	0.00	0.48	0.17	0.00	0.00	0.05	0.00
Experience	4	92	22	2	7	0	0	3	0

Effects of rainfall and pH on water physicochemical variables

Turbidity, PO_4 and TIN were affected by the rainfall as well as by the pH. The rainfall had a effect on the PO_4, TIN, pH and color nodes: the probabilities of intermediate values of PO_4, TIN and pH (0.128-0.249mg.L^{-1}; 1.18-2.01mg.L^{-1} and 7.5-7.8, respectively) and higher values for color (92-121uC) and turbidity (6.35-9.10uT) were higher in the drier periods (Figure 1a).

Studies carried out by Komárková & Tavera (2003) point out higher nutrients concentrations during rainy months. According the authors, the rains can help in mixing the whole water column and probably lifted up a lot of sedimented nutrients. Runoff from the surrounding agricultural lands can also introduce nutrients into the lake.

Concerning the pH, the results show a limited effect on the turbidity and color nodes: the probabilities of higher values (6.35-9.10uT and 92-121 uC, respectively) were higher in the period of lower pH values. Nevertheless, pH had a pronounced effect on nutrients nodes: the 100% probability of higher TIN concentrations (2.02-2.85mg.L^{-1}) and lower PO_4

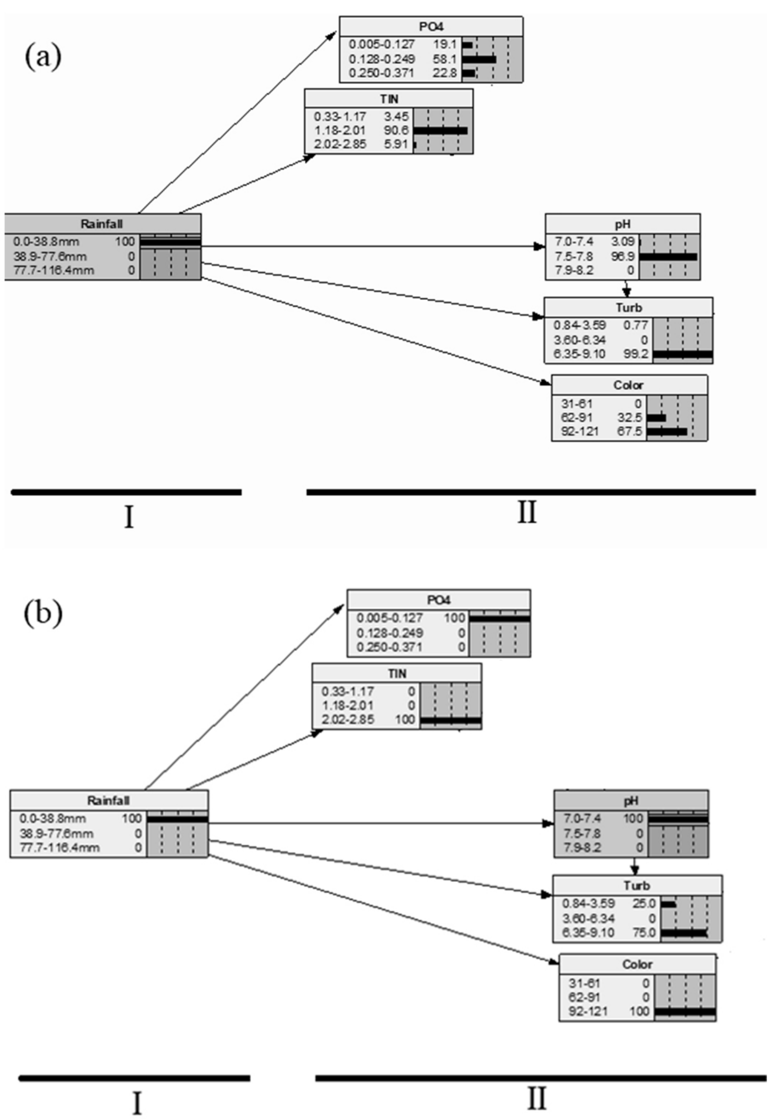

Figure 1. **Structure of the Bayesian network model showing the effects of rainfall and pH on water physicochemical variables in the Pedro Moura Jr reservoir, Northeast of Brasil. (a) Effect of rainfall (drough scenario); (b) Effect of pH. The model consists of two modules: (I) Rainfall; (II) Physicochemical variables of water. The prior probability distribution for each node is displayed both as horizontal bars and by percentages (the second column in each node), across the states (the first column). The set of arrows pointing to one node represents the conditional probability table for this node. PO_4 = phosphate; TIN = total inorganic nitrogen; Turb = turbidity.**

concentrations (0.005-0.127mg.L^{-1}) was reached on lower pH values (Figure 1b), while in samples with intermediate pH values, the probabilities decreased to 2.98% and 16.3%, respectively.

Effects of rainfall and water physicochemical variables on cyanobacteria steady-state occurence

The steady-state occurrence was more influenced by turbidity, TIN and rainfall. In the proposed model, the probability of 100% of steady-state status occurred in 69.8% of the waters with greater color values (92-122uC), 95.4% of the most turbid waters (6.35-9.10uT), in the intermediate ranges of pH (7.5-7.8, 96.5%), TIN (1.18-2.01mg.L^{-1}, 93.0%) and PO_4 (0.128-0.249mg.L^{-1}, 59.6%) and during drier periods (below 38.8mm, 95.0%) (Figure 2a).

Considering a scenario with elevation only in PO_4 concentrations, thus decreasing the N/P ratio, the probability of steady-state occurrence decreases to 86.8% (Figure 2b). On the other hand, considering a hypothetical situation in which the volume of rainfall increases and dilutes the PO_4 in the reservoir, remaining the intermediate concentrations of TIN, the probability of steady-state occurrence decreases to 12.1% (Figure 2c). However, if the TIN concentration reaches higher concentrations, increasing the N/P ratio, the steady-state probability increases to 78.2% (Figure 2d). Taking into account the proposed model, the probability of steady-state occurrence under more diluted values of TIN as well as under with higher concentrations of both nutrients, concomitantly is null. In other words, enhancing both nutrient concentrations, concomitantly, counteracted the increased steady-state status risk associated with lower rainfall.

We consider that the volume of rainfall has an indirect effect on the steady-state occurrence, due to changes in the physicochemical variables of the water. The model allowed us to observe that in the drier months, the optimal conditions for steady-state occurrence were reached. As the volume of rain increases, the probability of occurrence of the event decreases to 52.5% (Figure 2e) and 0.0% in the ranges of 38.9-77.6mm and 77.77-116.4, respectively. This reduction was mainly accompanied by a reduction in turbidity values. We also understand that pH can exert an indirect effect on the steady-state occurrence, due to the influence on nutrient concentrations and turbidity. The model showed that rainfall, turbidity and TIN were the variables that presented, separately, the greatest contribution in relation to the occurrence of steady-state, with sensitivity percentages of 3.88%, 3.82% and 3.25%, respectively.

The steady-state occurrence reflects available resources, quality of light and the possibility of organism distribution in the water column. The assemblage is formed by species with different rates of resources, uptake, mobility and light necessity usages. The different species are together because they do not compete, and have different niches (Rojo & Álvarez-Cobelas 2003).

The effects of rainfall considered in this study affected physicochemical variables and, consequently, the steady-state status in the ecosystem. Precipitation has the potential to influence physicochemical variables of water. For example, periods of drought decrease the run-off of nutrients from agriculture and likely to give lower PO_4 concentrations (Oliveira et al. 2018). Besides, the lowering of the level of aquatic ecosystems may increase the concentration of cyanobacteria, which tend to have faster growth rate and permanence in the ecosystem (Carvalho et al. 2011, Elliott 2012). Consequently, their populations would disappear during the flooding periods (Mihaljevic et al. 2011).

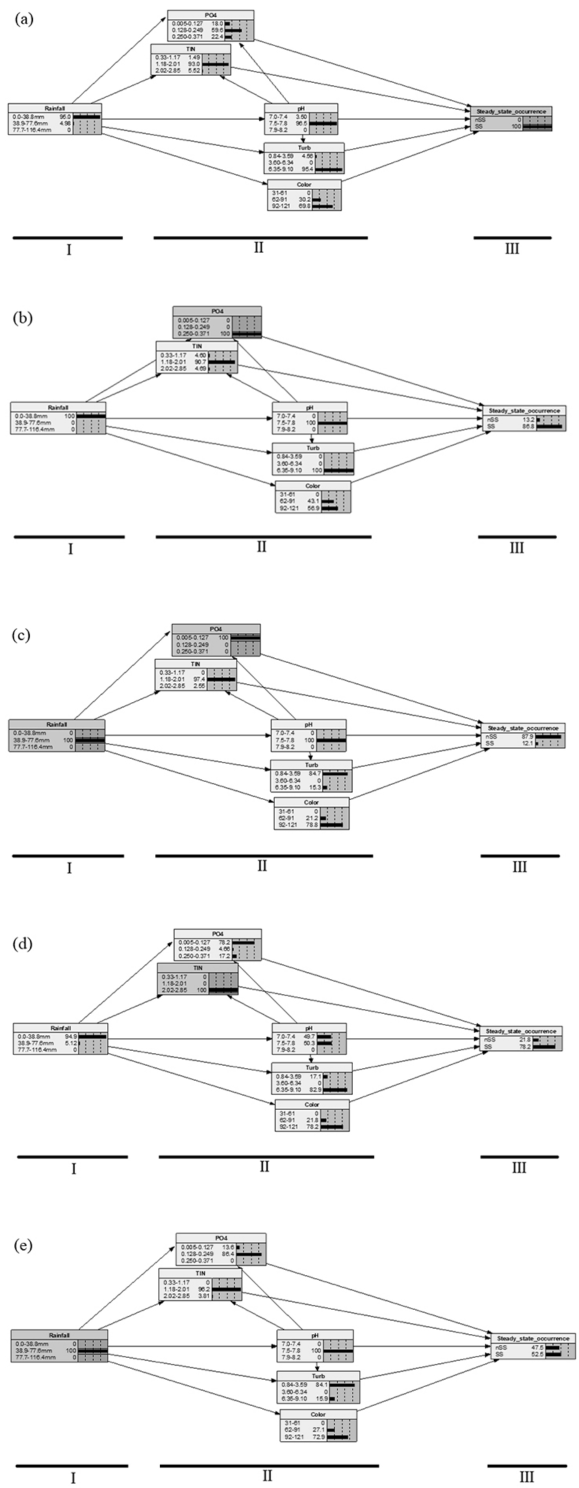

Figure 2. Structure of the Bayesian network model showing the effects of rainfall and water physicochemical variables on cyanobacteria steady-state occurrence in the Pedro Moura Jr reservoir, Northeast of Brasil. (a) scenario for 100% probability of steady-state; (b) scenario with elevation only in PO_4 concentrations; (c) scenario with increased rainfall and diluted PO_4 concentrations; (d) scenario with elevation only in TIN concentrations; (e) scenario with increased rainfall. The model consists of three modules: (I) Rainfall; (II) Physicochemical variables of water; (III) Steady-state occurrence. The prior probability distribution for each node is displayed both as horizontal bars and by percentages (the second column in each node), across the states (the first column). The set of arrows pointing to one node represents the conditional probability table for this node. PO_4 = phosphate; TIN = total inorganic nitrogen; Turb = turbidity; SS = steady-state; nSS = non steady-state.

It is noteworth that although high concentrations of nutrients favor the bloom of cyanobacteria, it does not necessarily increase the probability of steady-state occurrence (Moe et al. 2016). At steady-state, the downward flux of particulate material has to be balanced by an upward flux of the dissolved nutrient. The assumption of steady-state will not be fullfilled during episodic events of nutrient injection (Stoyneva 2003). These observations corroborate our results, since we the occurrence of steady-state was not favored at higher concentrations of nutrients.

Chakraborty et al. (2008) observed that, in an ideal laboratory condition, theoretical analysis model demonstrates that in nutrient-limited condition influences the competitive interaction of two species. Therefore, an ideal concentration of nutrients is necessary to create niches in the ecosystem and avoid competition between species, leading the steady-state of the species. In this study, we believe this scenario was achieved at intermediate nutrient concentrations.

Shallow ecosystems may be more disturbed and Valenti et al. (2016) observed that the high intensity of environmental perturbation influences on steady-state of some phytoplankton groups, leading permanent algal blooms in surface water. Kovac et al. (2020) mention that the steady-state sets a limit on the maximum attainable biomass in case all nutrients to be utilized and, without additional perturbations, the system very rapidly mantain the occurrence.

According to Naselli-Flores & Barone (2003), within a specific climate, disturbance can alter the phytoplankton on at a much smaller temporal scale. While the community reacts to the disturbance, it is still constrained by the current climate in how it can react. Thus, disturbance is nested within the climatic regime. Theses observations may explain why steady-state occurred mainly in dry periods. Thus, we suggest further studies in tropical and stratified ecosystems, considering a vertical distribution of the phytoplankton community, in order to assess whether disturbances disfavor the steady-state in some layers, but favor it in others.

As seen above, steady-state was more frequent in periods of greater turbidity. Higher amount of suspended particles can limit the penetration of light into the water and it seems to have selected for continued dominance of some species. As reviewed in the work published by O'Farrel et al. (2003), photosynthesis in cyanobacteria is allowed even under unfavourable light conditions. Moreover, in addition to normal aerobic photosynthesis, several species are capable of anoxygenic photosynthesis or the microbial mats are capable of fermentation. Thus, low light availability affects algal competition and phytoplankton diversity and can favour steady-state occurrence (Iachetti & Llames 2014, Izaguirre et al. 2012).

Effects of rainfall and water physicochemical variables on cyanobacteria species in steady-state

Throughout the study, steady-state events were observed in all color and turbidity ranges and frequently during drought periods. The species *Planktothrix agardhii* was observed in all steady-state periods, either alone or in co-dominance with *M. aeruginosa* and/or *R. raciborskii*. *P. agardhii* monospecific steady-state events occurred in 90.4% and 98.7% of samples with intermediate concentrations of PO_4 and TIN, respectively (Figure 3a), while shared steady-state with co-dominance of the three species was seen in 100% of samples with intermediate concentrations of these nutrients (Figure 3b).

The co-existence of *R. raciborskii* and Oscillatoriales species, both considered R-strategists well adapted to low light conditions, has been often reported in tropical ecosystems (Dokulil & Teubner 2000). Scenarios with lower concentrations of PO_4 were characterized by steady-state with co-dominance of *R. raciborskii* and *P. agardhii* (Figure 3c). Mischke & Nixdorf (2003) point out that different members of cyanobacteria show a differential tolerance for nutrient conditions, therefore the ecological niches of the two habitats can be were occupied either by *P. agardhii* or *R. raciborskii*. This condition, unfavorable for the steady-state of *M. aeruginosa*, leads to the conclusion that the increase in the N/P ratio seems to contribute to the steady-state with co-dominance of filamentous species, although Dokulil & Teubner (2000) have shown steady-state of *Planktothrix* under highest phosphorous concentrations, highlighting that the strongly multimodal distribution of *P. agardhii* reflects the tendency of this species to occur in different scenarios due its ability to adapt to the most different environmental conditions and to co-dominate with other species.

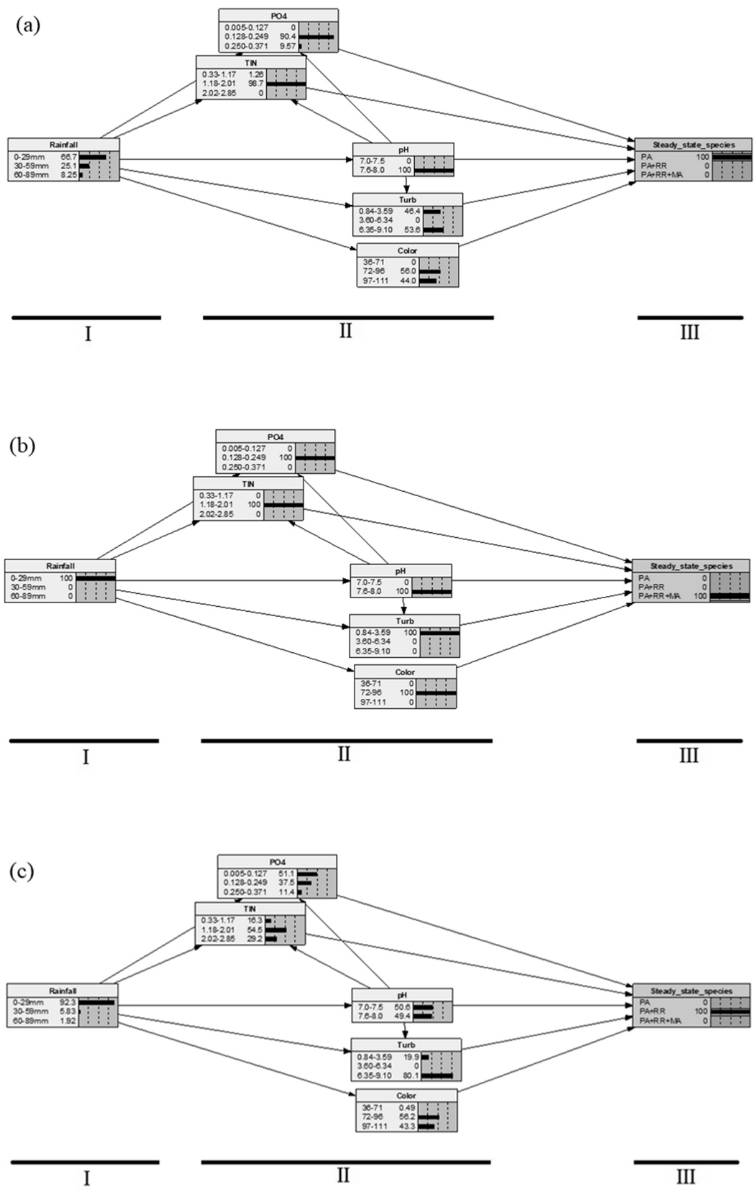

Figure 3. **Structure of the Bayesian network model showing the effects of rainfall and water physicochemical variables on cyanobacteria species in steady-state in the Pedro Moura Jr reservoir, Northeast of Brasil. (a) scenario for steady-state with monodominance of *Planktothrix agardhii*; (b) scenario for steady-state with co-dominance of *P. agardhii, Raphidiopsis raciborskii* and *Microcystis aeruginosa*; (c) scenario for steady-state with co-dominance of *P. agardhii* and *R. raciborskii*. The model consists of three modules: (I) Rainfall; (II) Physicochemical variables of water; (III) Cyanobacteria species in steady-state. The prior probability distribution for each node is displayed both as horizontal bars and by percentages (the second column in each node), across the states (the first column). The set of arrows pointing to one node represents the conditional probability table for this node. PO_4 = phosphate; TIN = total inorganic nitrogen; Turb = turbidity; PA = *Planktothrix agardhii;* RR = *Raphidiopsis raciborskii*; MA = *Microcystis aeruginosa*.**

According to Moustaka-Gouni et al. (2007) and Moe et al. (2016), the total nitrogen concentration seems to play a role in favouring certain N-fixating cyanobacteria taxa (order Nostocales), especially in drought months, when nitrogen use to be depleted. Growth (Becker et al. 2008) and steady-state (Komárková & Tavera 2003) of *Cylindrospermopsis* (*Raphidiopsis*) spp. are observed under low nitrogen concentration, which decreased greatly due to low precipitation levels in the drier years.

The ecological success of *R. raciborskii* is attributable to many factors, including buoyancy regulation, tolerance of low light, high affinity for phosphorus and ammonia, high phosphorous storage capacity, resistance to grazing by zooplankton and presence of heterocysts (nitrogen fixing ability), aerotopes (buoyancy control) and akinetes (dispersal and environmental resistance), allowing easy dispersal and environmental resistance; wide thermal tolerance and allelopathic interference.

Its presence may modify the general structure of other species or cause a substantial decrease in plankton diversity (Mihaljevic et al. 2011, Izaguirre et al. 2012).

Mischke & Nixdorf (2003) and Figueredo & Giani (2009) point out that the Oscillatoriales and Nostocales growth during drier months induces light deficient conditions by high shading effects, that other phytoplankton association are suppressed. Steady-state with co-dominance of *R. raciborskii* and *P. agardhii* ocurred mainly under higher turbidity values (Figure 3c), while steady-state with *M. aeruginosa* occurred more frequently in samples with lower values of color and turbidity (Figure 3b). This result corroborates with the study carried out by Naselli-Flores & Barone (2003) and Moustaka-Gouni et al. (2007), who pointed out steady-state of *M. aeruginosa* under lower turbidity values. According to these authors, when the colonies lying on the bottom receive sufficient light, it activates anoxygenic photosynthesis and the cells start producing gas-vesicles that allow them to become buoyant.

Under high underware light, the dominance and maintenance of *M. aeruginosa* can be explained by its photoadaptation and buoyancy regulation, to effectively exploit resources. In this way, *M. aeruginosa* avoids direct competitition with the other species and thus increases its number (Çelik & Ongun 2008). Thus, *M. aeruginosa* and *R.* raciborskii and *P. agardhii* partially did not compete, but may have different niches separated vertically in the water column (Moustaka-Gouni et al. 2007). On the other hand, *P. agardhii* and *R. raciborskii* are frequently favoured in turbid and light deficient layers. The relative darkness combined with low phosphorous concentration supported the development of the filamentous Nostocales and Oscillatoriales (Nixdorf et al. 2003).

M. aeruginosa are classified as S-species. The táxons belonging this group are defined by Reynolds et al. (2002) as acquisitive strategists; they are generally large unicells or large colonies which, through compounding motility or the ability to control buoyancy, may self-regulate their position in the water column. These organisms are typically K-selected strategists, that is, they are individuals who use all their energy in order to grow and survive for a long period of time.

Studies show that *Microcystis* reaches rather high biomass values under a condition of stable stratification and when epilimnetic nutrient values tended to be exhausted (Naselli-Flores & Barone 2003). Once the temperature is high, the nitrogen in the sediments is released to the overlying water, leading to a high concentration of nitrogen. However, depending on the stratification of the reservoir this may not cause disturbance in the surface waters, resulting in a lower nitrogen concentration in surface waters in the southern location. The sudden rise in phosphorous concentration could be the factor that inhibited the formation of a steady-state phase (Hui et al. 2014). Conversely, Mischke & Nixdorf (2003) and Çelik & Ongun (2008) observed that blooms of *Microcystis* may be suppressed by the relatively low phosphorous concentrations.

Effects of rainfall and water physicochemical variables on duration of cyanobacteria steady--state

The steady-state events observed in this work lasted from 3 to 17 weeks and all of them were more frequent in dier periods, on waters with intermediate concentrations of PO_4 and TIN, pH between 7.6 and 8.0 and higher color values. Longer steady-state periods (13-17 weeks) were more frequent in samples with lower turbidity values (Figure 4), in which a greater predominance of *M. aeruginosa* was observed.

It is observed that there is a threshold maturation value so that the population is destined to extinction and that this steady-state depends on the maturation time. As the maturation time increases, the density of the phytoplankton species will decrease, and finally the species could die out (Chen & Shi 2019).

Studies have shown that at higher trophic levels, equilibrium is easily reached and sometimes maintained for considerable periods of time, mainly because environmental conditions constrain species diversity to one or two dominating species, unless when rapidly flushed or in the metalimnetic niche. The main factor of persistence that causes and maintained the steady-state seems to be the lowering nutrient concentrations. Constancy of hidrological conditions, during 3 or 4 weeks, leads to dominance and maintenance of particular species. What matters to promote and maintain persistent species is the environmental constancy, independently of its relation with a particular physical condition (Dokulil & Teubner 2000).

As observed by Moe et al. (2016), possibly in waters with higher turbidity values, the photosynthetic rate decreases and nitrogen-fixing cyanobacteria have an advantage, increasing their concentrations, corroborating the observation of this work that points some steady-state periods with dominance of *R. raciborskii* when the turbidity values are higher. However, nitrogen fixation involves energetically costly reactions, therefore, maintaining these blooms for long periods is not possible. With the reduction of turbidity, photosynthesis should increase and the oxidized forms of nitrogen are more used to maintain cyanobacterial concentrations for long periods.

Studies have pointed out that steady-state stages are not frequently attained in phytoplankton successions and, once reached,

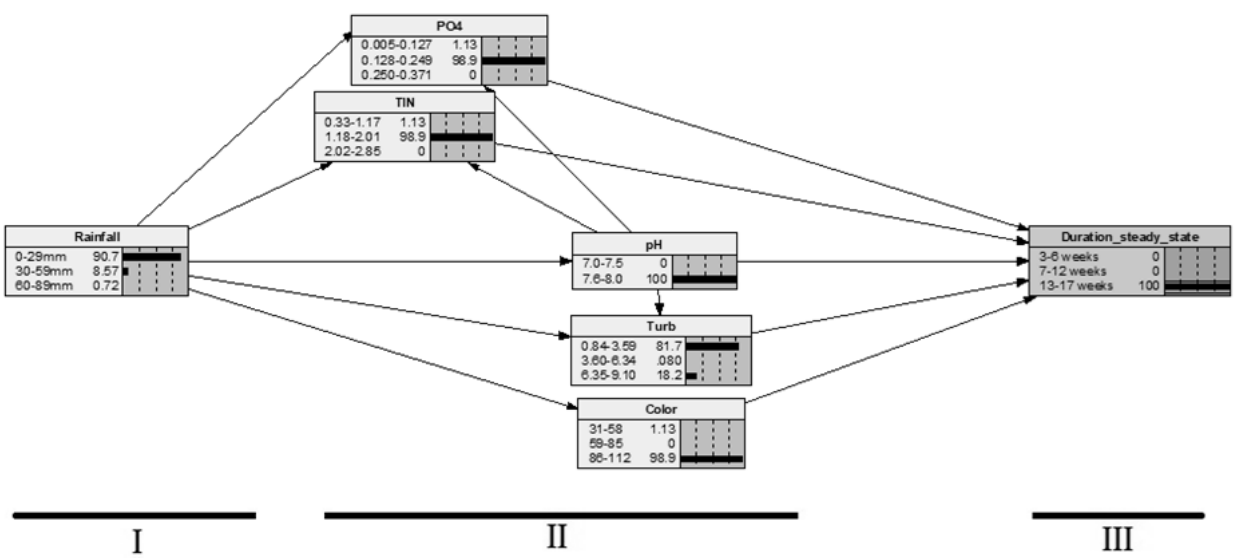

Figure 4. Structure of the Bayesian network model showing the effects of rainfall and water physicochemical variables on duration of cyanobacteria steady-state in the Pedro Moura Jr reservoir, Northeast of Brasil (scenario for steady-state lasting 13-17 weeks). The model consists of three modules: (I) Rainfall; (II) Physicochemical variables of water; (III) Cyanobacteria species in steady-state. The prior probability distribution for each node is displayed both as horizontal bars and by percentages (the second column in each node), across the states (the first column). The set of arrows pointing to one node represents the conditional probability table for this node. PO_4 = phosphate; TIN = total inorganic nitrogen; Turb = turbidity.

the equilibrium phase generally covers a short periods. The rarity and the ephemeral nature of these events might be attributed to the frequently changing aquatic environment, to the fast response time of phytoplankton, and to the diferente scenarios upon which phytoplankton play (Naselli-Flores & Barone 2003). It is remarkable to underline that the majority of available studies still comes from temperate climates, where seasonal changes of physical conditions terminate the equilibrium phase. Probably, in tropical systems these changes are smoother or quite absent allowing long-lasting equilibrium phases, as reported by Komárková & Tavera (2003) and Baptista & Nixdorf (2014).

Evalution of model: a hypothetical situation

The inclusion of rainfall, pH, turbidity, color and nutrients nodes was important for obtaining a more correct overall steady-state status assessment. Turbidity, TIN and PO_4 nodes, alone, showed better interaction with steady-state status in the designed models, corroborated by the sensitivity analysis showed in Table III.

We can assume that TIN is one of the three nodes that most influenced all designed models. Rainfall and turbidity were the nodes that had the greatest influence on steady-state occurrence, while its duration model had more influence of PO_4 and turbidity. Conversely, color was the node that showed the lowest sensitivity in the designed models. Turbidity, nutrients and color were, sinergistically, influenced by rainfall and pH. However, only the color showed the lowest sensitivity percentuals or steady-state status. A common problem for BN models that incorporate several sources of uncertainty is that nodes further down the causal chain have greater predictive uncertainty (Marcot et al. 2006, Borsuk et al. 2012). This may explain the low sensitivity of the steady-state status in the three designed models to a color node.

Hence, all of the five indicator nodes (rainfall, PO_4, TIN, pH, turibidity and color) played important roles in the overall assessment of steady-state status.

Effects of rainfall

One way to inspect the rainfall effects in the BN was to select the samples that showed drought. The full model is based on all data that showed drier and rainier months. However, since there is large seasonal variation in many of the variables, selecting only drier months would reduce the temporal variation, and might therefore improve the precision of the model (i.e., result in narrower probability distributions of the indicators).

Turbid water and higher probability of steady-state occurrence can be seen in the samples from drier months. This result shows that the model behaves as expected regarding

Table III. Sensitivity of steady-state occurrence, cyanobacteria species in steady-state and duration of steady-state to a finding at another nodes. PO_4: phosphate; TIN: total inorganic nitrogen. Underlined values indicate higher percentages; SS = steady-state.

Nodes	% (SS occurrence)	% (cyanobacteria species in SS)	% (duration of SS)
Rainfall	<u>3.88</u>	7.16	1.40
PO_4	0.61	<u>27.20</u>	<u>13.90</u>
TIN	<u>3.25</u>	<u>19.50</u>	<u>6.27</u>
pH	1.24	<u>24.50</u>	5.47
Turbidity	<u>3.82</u>	11.50	<u>11.60</u>
Color	0.71	3.71	0.05

rainfall on turbidity values and steady-state status.

Assessment of the BN approach for modelling of ecological status

In this study we used an external, larger dataset for evaluation by constructing an alternative CPT for steady-state occurrence and comparing the results with the default model version.

Overall, the BN model satisfied our objective: to integrate information from climate, water physicochemical scenarios, and steady-state status. The BN approach gives a possibility to account for mismatch between predictions and observations for steady-state occurence, by incorporating this uncertainty in their CPTs and evaluating its consequences. Since the selected model does not account for the mismatch between prediction and observations of steady-state occurence, the results predicted by the BN should not be interpreted in terms of absolute probability values. Nevertheless, the qualitative effects of the scenarios on the different indicators predicted by the BN should be valid.

The components included in the BN model had importance to the overall assessment of steady-state occurence, implying that our approach can be used for other ecosystems where steady-state occurence is likely. For ecosystems with more limited data, we suggest that filling the data gaps using observations from other ecosystems in combination with expert knowledge on ecosystem type, local conditions etc. is a viable option, as demonstrated by Rigosi et al. (2015), in which a BN was constructed to analyse the sensitivity of cyanobacterial bloom development to different environmental factors and to determine the probability that cyanobacterial blooms would occur.

A more complete representation of climate change in the BN would include effects of changed precipitation patterns (Lehikoinen et al. 2014), and potentially other meteorological or hydrological variables. Inclusion of micronutrientes and other water physicochemical in the BN would make the assessment of physicochemical status more complete. According to Carvalho et al. (2011), alkalinity may be even more importante to cyanobacteria development than the phosphorous concentration. Oliveira & Dantas (2019) pointed out that higher concentrations of nitrate together with higher values of color favored the development of steady-state.

A complete steady-state status assessment should also include other variables, such as macrophytes, benthic invertebrates and fish communities in order to reduce the uncertainty of the model. When there is high uncertainty associated with the data, assessments based on this combination rule tend to underestimate the prediction status (Moe et al. 2016). A probabilistic result such as the outcome of a BN can be helpful, giving a more nuanced and more informative result than only a single status class (Gottardo et al. 2011).

We limit our considerations without considering explicit details of zooplankton dynamics at this stage. According to Kovac et al. (2020), inclusion of zooplankton changes the dynamical picture by lifting the model from two to three dimensions where more complex trajectories can emerge. Thus, although zooplankton grazing and natural mortality may also play a stabilizing role in phytoplankton fluctuations, we do not consider these processes explicitly.

Although much knowledge is available on effects on climate change on ecosystems, including specific effects on biological quality elements in aquatic ecosystems (Moe et al. 2016), incorporating such information in predictive models is a challenge. The BN methodology can facilitate the use of such knowledge, manifested as expert judgement of probabilities under given climatic scenarios. Furthermore, a BN model may be relatively easy to understand for end users who do not have any modelling background (Borsuk et al. 2012). Therefore, BNs are promising tools for supporting informed decision making and thus the work of water managers. There are of course also several limitations associated with the BN methodology in the context of environmental management. The fact that the dynamic network can contain loops puts constraints on the ecological processes that can be modelled (Saloranta & Andersen 2007). For example, high cyanobacteria biomass can reduce the turbidity; on the other hand, higher turbidity can limit further cyanobacteria growth due to light limitation.

The accumulation of uncertainty with the length of the network implies that it can be difficult to draw conclusions from the final output nodes (Borsuk et al. 2012). The current BN model can be further developed in several ways by reducing the predictive uncertainty though a more quantitative sensitivity analysis of the model, such as calculation of entropy reduction that can help identify nodes to which the final output is particularly sensitive (Chen & Pollino 2012).

We can state that the hypothesis presented in this work was partially confirmed. Long lasting steady-state periods (until 17 weeks) occurred in Pedro Moura Jr reservoir along with the monodominance or co-dominance of filamentous species, mainly under drought, high turbidity and colors values, however higher nutrients concentrations did not increase the probability steady-state occurrence or longer duration.

The steady-state staus must be viewed considering a complex interactions between biotic and abiotic variables. In summary, the BN approach was able to model effects of combined scenarios of rainfall and water physicochemical on steady-state status of a tropical and eutrophic aquatic ecosystem. The BN model showed higher probability of steady-state in drought periods and it appears as a tool to assess the effects of future warming on steady-state occurence. Thus, the BN modelling approach can be a useful supplement to more traditional process-based models for reservoirs.

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