



Predicting food web responses to biomanipulation using Bayesian Belief Network: Assessment of accuracy and applicability using *in-situ* enclosure experiments

R.B.H. Lim, J.H. Liew, J.T.B. Kwik, D.C.J. Yeo*

Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore 117543, Republic of Singapore



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ABSTRACT

Ecological networks are useful for describing the complex trophic interactions within an ecosystem and hold great potential for ecosystem-based management. However, owing to the complexity and limited knowledge on the trophic interactions of natural food webs, it is challenging to make quantitative predictions about ecological community response to management interventions. Here, we use stable isotope mixing models in conjunction with Bayesian Belief Networks (BBN) to develop and examine the trophic interactions for six empirically determined aquatic food webs in tropical reservoirs. Using BBN, we predicted potential trophic cascade outcomes to predator removals, validated the predictions against data observed from *in-situ* biomanipulation experiments, and identified influential species using sensitivity analyses. Comparisons among various food web modelling frameworks demonstrated the importance of weighted connectance and network-centric approach for quantitative predictions, suggesting that the Bayesian Belief Network framework can play an important role in ecosystem-based management.

1. Introduction

Food webs describe the realized network of trophic interactions among species within a given community where each node represents a species or functional trophic group, while links between nodes represent biotic interactions (e.g., feeding relationships) (May, 1973; Pimm et al., 1991). The patterns and strength of trophic interactions within the food web are crucial in maintaining the stability and function of ecosystems (de Ruiter et al., 1995; McCann, 2000). However, the lack of congruence between theoretical and experimental definitions of interaction strength hampers efforts to quantify such complex interactions in real food web systems (McDonald-Madden et al., 2016). This is partly the reason why food web studies are conventionally based on a static “topological” approach determined solely by food web structure or simplified food chains (Dunne et al., 2002; Solé and Montoya, 2001) instead of a “dynamic” approach that quantifies species interaction strength and simulates species biomass over time using the bioenergetics consumer-resource model (Stouffer and Bascompte, 2011). Further, effective management of food webs requires a clear understanding of the complex relationships among a multitude of biotic interactions (e.g., competition, predation, mutualism) and broader ecological processes (e.g., nutrient and chemical cycling). Overlooking such

interactions (species–ecosystem–services) in management decisions may lead to unintended consequences or failed objectives (Dee et al., 2017).

The Green World Hypothesis (HSS), which was originally proposed by Hairston et al. (1960) suggests that predators (i.e., top-down regulation) are the predominant force regulating herbivore abundance and keeping them in check to maintain vegetation cover. Subsequently, this concept led to the emergence of the Trophic Cascade Hypothesis (TCH) by Paine (1980), which proposed that the removal of top predators (or organisms in higher trophic position) in aquatic system will cascade across the food web in a downward direction to influence primary productivity at the base of the food web (i.e., top-down effect) (Carpenter et al., 2001; Pace et al., 1999). While it is clear that top-down and bottom-up forces act complementarily in freshwater systems, their relative importance in regulating food web structure is debatable (Brett and Goldman, 1996; McQueen et al., 1986; Ripple et al., 2016; Taylor et al., 2015). Notably, a meta-analysis of 102 experimental studies suggests that the trophic cascade (i.e., top-down regulation) effect is stronger in aquatic (especially lentic ecosystems) than in terrestrial food webs (Casini et al., 2008; Halpern et al., 2005; Shurin et al., 2002). Recognizing the significance of trophic cascades, especially in freshwater lentic systems, has given new impetus to the

* Corresponding author.

E-mail addresses: dbslblr@nus.edu.sg (R.B.H. Lim), jh.liew@nus.edu.sg (J.H. Liew), jkwik@nus.edu.sg (J.T.B. Kwik), dbsyeod@nus.edu.sg (D.C.J. Yeo).

‘classical’ biomanipulation approaches (i.e., altering top-down food web interactions) (Lazzaro, 1997). However, difficulties in empirically measuring species interactions strengths, often requiring substantial computational resources, had impeded the development of a more mechanistic understanding of trophic cascades through food webs (Hodgson, 2005; Ripple et al., 2016).

Bayesian Belief Networks (BBN) and other ecological network approaches (e.g., Ecopath) offer an integrative management framework to overcome the computational and graphical limitations associated with complexity and uncertainty in food webs by combining biodiversity—ecosystem functioning (BEF) and food web theory (FWT) into a “two-mode network” (species—ecosystem and ecosystem—services), thus integrating ecological dynamism with socio-economics (Bohan, 2016; Dee et al., 2017; Hines et al., 2015; Pauly et al., 2000). Bayesian Belief Networks, introduced by Judea Pearl in 1985, are multivariate probabilistic models comprising two components: (1) directed acyclic graph (DAG) made up of directed linkages among variables describes the causal relationship among them; and (2) conditional probability tables (CPTs) that measure the strength of dependencies among these variables (Aguilera et al., 2011; Landuyt et al., 2013; Pearl, 1985). The network structure is capable of incorporating expert opinion and empirical data-based learning forms the basis of an operational BBN. Potential applications include informing decision-making via the assessment of potential management actions and identification of important drivers of network outcomes (e.g., in species conservation management or in biomanipulation of food webs) (McDonald-Madden et al., 2016).

In this study, we attempted to predict the effect of species removal on aquatic food webs using BBN by focusing on the response of a ubiquitous and abundant group of invertebrates, the Chironomidae (Diptera: Chironomidae). The chironomids play an important ecological role in the aquatic and terrestrial communities (Ali, 1980; Oliver, 1971) owing to their role as a major link between producers and consumers, making chironomids excellent model organisms for aquatic food web biomanipulation studies (Barnard, 1993; Butakka et al., 2016; Lilley et al., 2012). Here, we first developed a BBN framework to characterize six aquatic food webs, incorporating inter-species interaction strengths based on empirical data. We quantified the degree of predation pressure among consumers and their resources using dietary information derived from stable isotope signatures (^{13}C and ^{15}N) for all components in our food web models. Second, we constructed six empirically-derived food webs using BBN to investigate and predict chironomid abundance trends in response to species removal. Finally, we assessed the predictive performance of the BBN food web models using *in-situ* enclosure experiments to simulate predator removal. Data collected from these experiments were used to validate our food web model predictions. We also applied sensitivity analysis to identify influential species on specific target variables from the BBN models to inform prioritization of management actions.

2. Materials and methods

2.1. Study sites and sample collection

Comprehensive surveys of the aquatic communities were carried out in six reservoirs in Singapore (Res1–6) from January 2014 to June 2016 (Fig. 1). These man-made reservoirs vary in terms of their species assemblage, land-use history, anthropogenic disturbances and riparian forest cover (Yeo and Lim, 2011). Survey methods used included electrofishing, fish traps, cast-nets, artificial substrate colonizers, plankton trawls and hand nets to capture samples of populations of representative taxa in the aquatic community in each reservoir (see Liew et al., 2018 for details). Isotopic profiles ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of all fish species, representative benthic invertebrate taxa, zooplankton, phytoplankton, and riparian plants were investigated with Bayesian mixing models using the SIAR package (Parnell and Jackson, 2013). This allowed us to determine the mean dietary contribution of each resource

to its respective consumers and construct a network matrix summarizing predator-prey associations.

2.2. BBN food web construction

The Bayesian Belief Network (BBN) is a probabilistic model that examines the causal interactions among a set of variables. Generally, such causal networks comprise three features: nodes, links, and probabilities. In this case, the nodes represent living components in the aquatic food web; links depict the consumer-resource interactions; and conditional probabilities describe the dependencies of the presence or absence of a prey or given the state of its predators. In contrast to McDonald-Madden et al. (2016) who examined species persistence (bottom-up measure of resource availability), we focused on the “classical” top-down biomanipulation approach and constructed a predation-based BBN food web (e.g., incorporates measure of consumption intensity) for each reservoir using the GeNIe Modeler software (BayesFusion).

First, the probabilistic dependencies among species in the food web (prey-preference) were determined by taking the inverse of the normalized dietary proportion resource i contributes to its consumer ($diet_{ik}$) as follows:

$$pred_{ki} = \frac{diet_{ik}}{\sum_{w=1}^{W_i} diet_{ik}}$$

where $pred_{ki}$ is a relative measure of predation pressure of consumer k on resource i , $diet_{ik}$ is the dietary contribution of resource i for consumer k , and W_i is the full suite of consumers on resource i .

Two states (increase and decrease) were assigned to each node, representing predicted changes to the species’ population based on the conditional probability tables (CPTs). The conditional probability for resource abundance to increase, $p_i(\text{Increase} | \bar{f}_k)$ was defined as a function of predation pressure ($pred_{ki}$) and consumer availability (f_k) where the probability for resource abundance to increase diminishes to zero (that is, $p_i(\text{Increase} | \bar{f}_k) = 0$) when the full suite of consumers (F_k) are present ($f_k = F_k$). Conversely, the conditional probability, $p_i(\text{Increase} | \bar{f}_k) = 1$, when all the consumers are absent ($f_k = 0$). The initial conditional probability of all species to persist was defined as $p_i(\text{Increase}) = 0.5$. This implies that at equilibrium (i.e., without any management actions), a species has an equal chance to increase or decrease in their relative abundance. Similarly, for apex predators, which are independent of any predatory influence, their conditional probability of persistence was also assumed to be 0.5. However, as sets of predators (f_k) are introduced or removed from the full suite of predators (F_k), the conditional probability of prey abundance will scale proportionally to an increase or decrease in predation pressure (Eklöf et al., 2013). If $f_k \neq 0$ and if $f_k \neq F_k$, then:

$$p_i(\text{Increase} | f_k) = 1 - \frac{\sum_{k \in f_k} pred_{ki}}{\sum_{k \in f_k} pred_{ki} + \sum_{k \notin f_k} pred_{ki}}$$

and,

$$p_i(\text{persist} | \bar{0}) = 0.5$$

Therefore, this network provides a probabilistic investigation of the changes to relative abundance in the ecological communities in relation to the top-down trophic interactions given the static condition of the stable isotope profiles for each species or functional group during the survey period. The predictive ability of the BBN was then evaluated and validated against independent data collected from a biomanipulation experiment of these food webs (Fig. 2).

2.3. Assessment of prediction accuracy using food web biomanipulation experiment

The food web biomanipulation experiment simulated predator

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