RIVER RESEARCH AND APPLICATIONS

River Res. Applic. **33**: 949–958 (2017)

Published online 22 March 2017 in Wiley Online Library (wileyonlinelibrary.com) DOI: 10.1002/rra.3141

RESPONSE OF *MICROCYSTIS* AND *STEPHANODISCUS* TO ALTERNATIVE FLOW REGIMES OF THE REGULATED RIVER NAKDONG (SOUTH KOREA) QUANTIFIED BY MODEL ENSEMBLES BASED ON THE HYBRID EVOLUTIONARY ALGORITHM (HEA)

F. RECKNAGEL[a*], D.-K. KIM[b], G.-J. JOO[c] AND H. CAO[a]

[a] *School of Biological Sciences, University of Adelaide, Adelaide, Australia*

[b] *University of Toronto, Department of Physical and Environmental Sciences, Toronto, ON Canada*

[c] *Pusan National University, Department of Biological Sciences, Busan, South Korea*

ABSTRACT

This study demonstrates the use of inferential models for scenario analyses by simulating direct and indirect effects of predictor variables on state variables through model ensembles. Two model ensembles have been designed to predict the response of the cyanobacterium *Microcystis aeruginosa* and the diatom *Stephanodiscus hantzschii* to modified flow regimes of the River Nakdong (Korea) by a scenario analysis. Whilst flow-independent predictor variables of growth of *Microcystis* and *Stephanodiscus* such as water temperature and pH remain unchanged during the scenario analysis, flow-dependent predictor variables such as turbidity, electrical conductivity, phosphate, nitrate, silica and chlorophyll a are forecasted by inferential models. In the course of scenario analysis, flow-independent and flow-dependent predictor variables feed into the *Microcystis* and *Stephanodiscus* models to make sure that both direct and indirect effects of altered flow regimes are taken into account. The eight inferential models that were incorporated into the model ensembles have been developed by the hybrid evolutionary algorithm based on 19 years of time-series monitored in the River Nakdong between 1993 and 2012. The models achieved good accuracy in terms of timing and magnitudes reflected by coefficients of determination r^2 = 0.94 for *Microcystis* and r^2 = 0.83 for *Stephanodiscus*. The scenario analysis revealed that extreme summer blooms of *Microcystis* as observed between 1994 and 1997, and winter blooms of *Stephanodiscus* as observed between 1994 and 1997 and in 2004 can be prevented in the River Nakdong by adaptive management of seasonal water release from adjacent dams. Copyright © 2017 John Wiley & Sons, Ltd.

KEY WORDS: scenario analysis; model ensemble; hybrid evolutionary algorithm (HEA); river Nakdong; *Microcystis*; *Stephanodiscus*; optimal flow regimes

Received 16 June 2016; Revised 16 January 2017; Accepted 11 February 2017

INTRODUCTION

The ecology of regulated rivers is detrimentally affected by harmonized natural flow patterns, extended water residence times and fragmented river habitats, making rivers more vulnerable to eutrophication and harmful algal blooms (HABs) (e.g. Marker and Collett, 1997; Al-Tebrineh *et al.*, 2012). Recurrent HABs are recently more often observed in regulated rivers in East Asia (e.g. Yoshimura *et al.*, 2005; Harashima *et al.*, 2006; Kim *et al.,* 2007) that are subjected to summer monsoon and sporadic typhoons, and increasingly impacted by fast-growing local economies and global warming.

The Nakdong River stretches 525 km across South Korea with a catchment of 23 380 km^2 and is regulated by dams that supply irrigation and drinking water to adjacent communities. The river has a history of phytoplankton proliferation dominated by cyanobacteria in summer and diatoms in winter (Ha *et al.,* 1999, 2003). Seasonally altered river flow by optimum water release from dams appears as viable option for algal bloom control (e.g. Jeong *et al.,* 2007; Hong *et al.,* 2014), which can be determined by modelling techniques.

Forecasting population dynamics of phytoplankton in rivers requires models with high accuracy and time resolution that reflect both direct effects of flow on algae as well as indirect effects caused by flow-altered physical and chemical water properties. Such models also need to be applicable and valid for long-term time-series data reflecting not only seasonal but also inter-annual dynamics. Even though process-based models are well suited for analysing complex direct and indirect relationships in river ecosystems (e.g. Chapra *et al.,* 2008), the strong influence of hydrodynamic processes in rivers complicates predictive modelling of phytoplankton development and constrains the accuracy required for daily forecasts of species-specific population growth over long-term periods (e.g. Park and Lee, 2002; Kannel *et al.,* 2007). Here, we test ensembles of inferential models as alternative modelling approach in order to overcome these limitations. Scenario analysis is traditionally considered the domain of process-based models by running

*Correspondence to: F. Recknagel, University of Adelaide, School of Biological Sciences, Adelaide, Australia.
E-mail: friedrich.recknagel@adelaide.edu.au

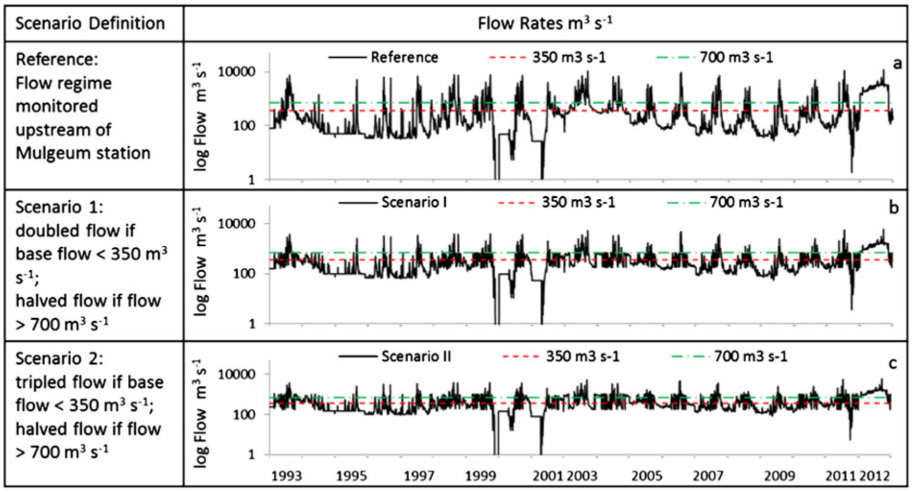

Figure 1. Definition of flow scenarios 1 and 2 in relation to the reference flow regime monitored at Mulgeum Station of the Nakdong River from 1993 to 2012. [Colour figure can be viewed at wileyonlinelibrary.com]

the process equations with scenario specific parameter and input settings, and displaying the likely scenario effect by resulting state trajectories. However, *ad hoc* designed ensembles of inferential models allow to cascade information between key state variables (Recknagel *et al.,* 2014b), thus also enabling scenario analysis.

To control outbreaks of algal blooms in the lower Nakdong River by flow regimes that are managed by optimum water release from dams requires operational models that forecast population dynamics of dominant algal species. This study aims to develop model ensembles by the hybrid evolutionary algorithm (HEA) for forecasting *Microcystis aeruginosa* that is dominant in the Nakdong River in summer and *Stephanodiscus hantzschii* dominant in the river in winter. Hybrid evolutionary algorithm has been developed for inferential modelling of complex ecological data (Cao *et al.,* 2014) and previously successfully applied for assessing

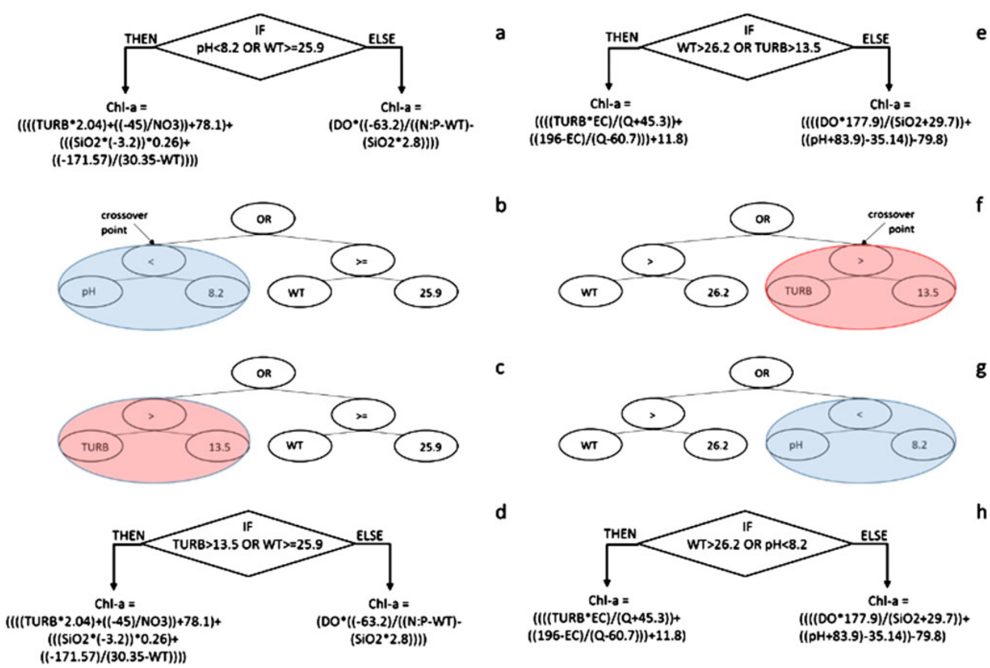

Figure 2. Crossover between the IF-trees of two IF–THEN–ELSE models by GP. (WT = water temperature °C, TURB = turbidity NTU, EC = electrical conductivity μS cm^{-1}, DO = dissolved oxygen mg L^{-1}, NO_3 = nitrate mg L^{-1}, N:P = nitrate to phosphate ratio, SiO_2 = silica mg L^{-1}). [Colour figure can be viewed at wileyonlinelibrary.com]

DOI: 10.1002/rra

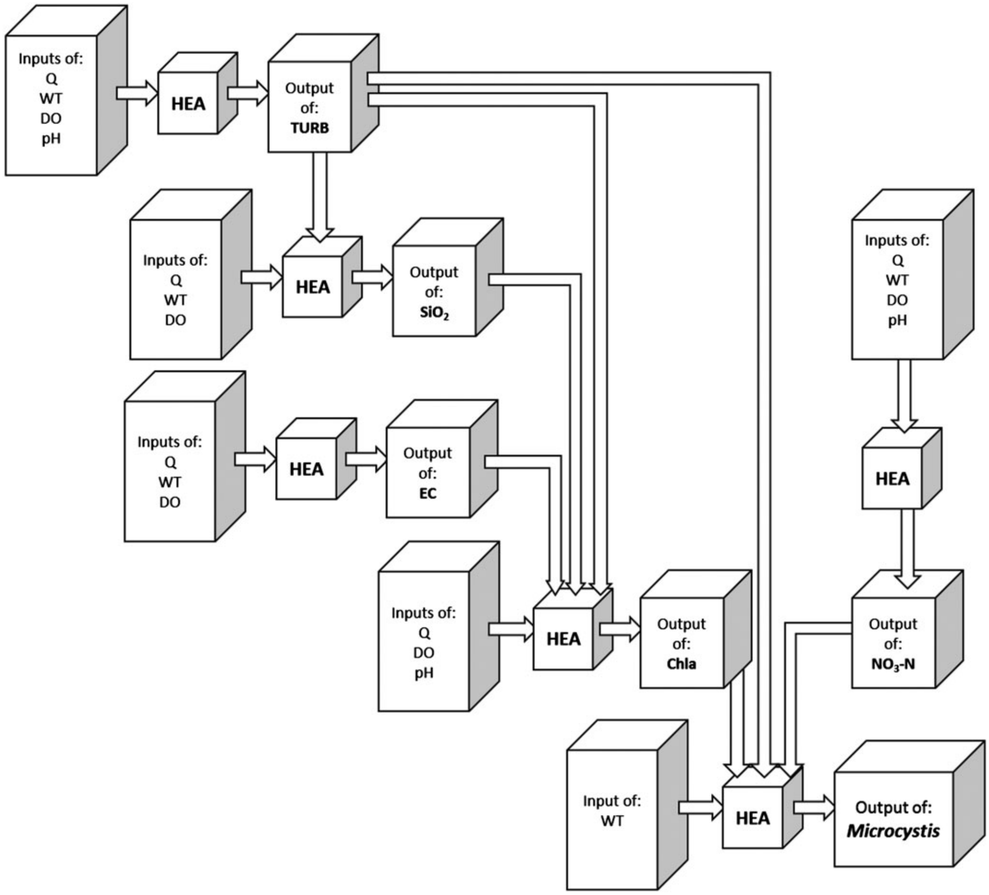

Figure 3. Model ensemble for simulating flow scenarios for *Microcystis*

cyanobacteria blooms in lakes (e.g. Recknagel *et al.,* 2013, Recknagel *et al.,* 2014a, 2014b; Zhang *et al.,* 2015; Recknagel *et al.,* 2016).

In this study, novel model ensembles have been developed by HEA that allow to test the following hypotheses: (i) blooms of *M. aeruginosa* in summer and of *S. hantzschii* in winter are significantly affected by flow regimes of the Nakdong River; (ii) altered flow regimes not only change water residence time that directly affects growth of *M. aeruginosa* and *S. hantzschii*, but also change physical and chemical water quality parameters that indirectly affect growth of *M. aeruginosa* and *S. hantzschii*.

In order to test the hypotheses by scenario analysis, two flow regimes have been created from historical data that maintain the base flow in winter above the threshold of 350 m^3 s^{-1} and limit the peak flow in summer to 700 m^3 s^{-1}. This can be practically managed by maintaining the flow threshold during the dry winter season with

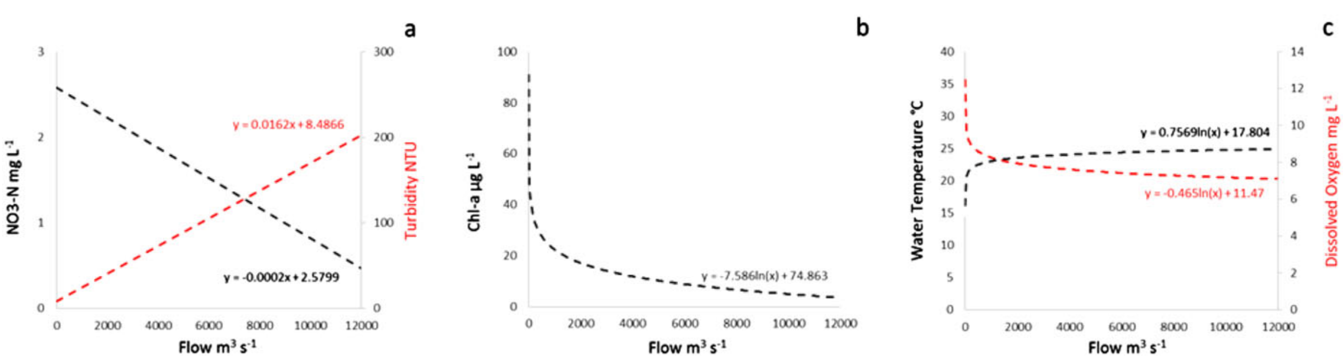

Figure 4. Flow correlations of predictor variables NO_3–N and turbidity (a), Chl-a (b), and water temperature and dissolved oxygen (c). [Colour figure can be viewed at wileyonlinelibrary.com]

DOI: 10.1002/rra

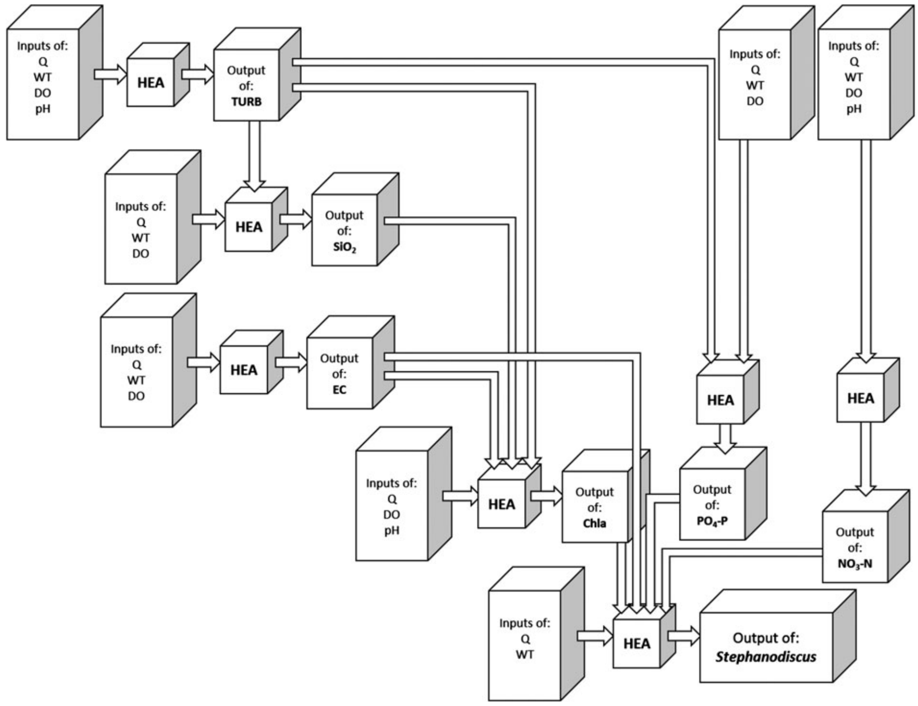

Figure 5. Model ensemble for simulating flow scenarios for *Stephanodicus*

additional water released from adjacent dams and maintaining the peak flow limit by less water released in summer.

MATERIALS AND METHODS

Data of Nakdong River

The study site Mulgeum Station is located 27 km upstream from the estuarine barrage at the river mouth. Water samples were collected from 1993 to 2012 on a weekly/biweekly basis. Water temperature (WT), dissolved oxygen (DO), electrical conductivity (EC), pH and turbidity (TURB) were measured by a YSI multiprobe sonde. Chlorophyll a (Chl-a) was extracted by a 90% acetone method after filtering water samples using 0.45-µm membranes. The filtrates were subsequently analysed for nitrate (NO_3–N), phosphate (PO_4–P) and silica (SiO_2) by a QuikChem Automated Ion Analyser (Model 8000, Lachat Instruments). *M. aeruginosa* and *S. hantzschii* have been counted in sedimentation chambers using an inverted microscope (Utermöhl, 1958). Daily flow rates Q were measured 5 km upstream of the Mulgeum Station by the Korean Meteorological Administration (www.kma.go.kr). Data for the year 2002 were incomplete and have been excluded from this study.

Scenarios have been based on the suggestion, 350 $m^3 s^{-1}$ is the flow threshold above which Chl-a concentrations decline significantly (Hong *et al.,* 2014). Accordingly, the scenario 1 assumes a two-fold increase and scenario 2 a three-fold increase of flow that is below the threshold, whereby flow rates exceeding 700 $m^3 s^{-1}$ (≈83rd percentile of the river flow) have been halved (Figure 1).

Hybrid evolutionary algorithm

Evolutionary computation infers models from data based on principles of natural selection and evolution (Holland *et al.,* 1986). The HEA (Cao *et al.,* 2014, 2016) has been designed to evolve 'fittest' IF–THEN–ELSE rules from ecological data by integrating genetic programming (GP) and differential evolution (DE). It applies GP according to Koza (1992) to evolve the optimum structure of the rule model, and DE according to Storn and Price (1997) to optimize the parameters of the rule model. Because GP typically operates on parse trees rather than on bit strings, it suits well to evolve IF–THEN–ELSE rules for multivariate relationships. Genetic programming uses the logic functions FL = {AND, OR}, comparison functions FC = { $>, <, \geq, \leq$ } and arithmetic functions FA = { +, − , * , /, exp, ln} to represent IF–THEN–ELSE rules as vector of multiple trees. Tree1 denotes the IF condition with the function set $F_{tree1} = FL \cup FC \cup FA$, and tree2 and tree3, respectively, denote the THEN and ELSE branches with the function set $F_{tree2/tree3} = FA$.

Figure 2 illustrates exemplarily one crossover step by GP for the optimization of the IF-trees of two IF–THEN–ELSE models for 5-day-ahead forecasts of the concentration of chlorophyll-a (µg/L) in River Nakdong (see also Figure 6c). Figure 2a and e represents parent models. Figure 2b, c, f and g illustrates the crossover of IF-conditions between the

DOI: 10.1002/rra

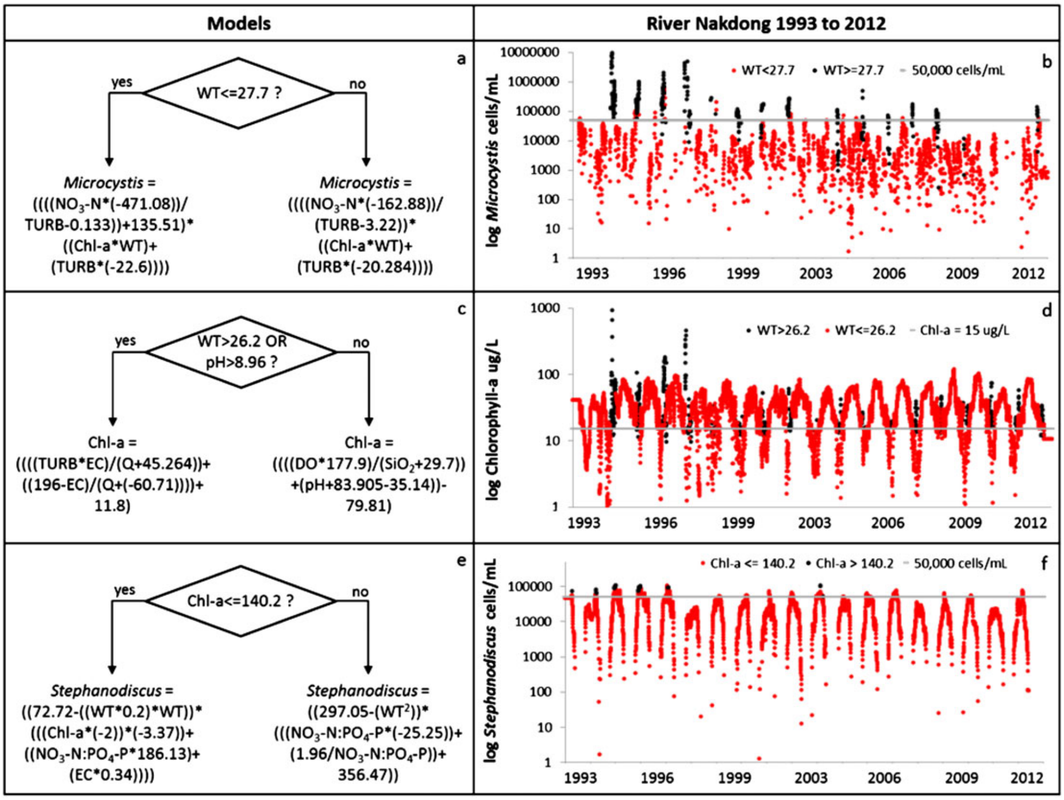

Figure 6. Illustration of IF–THEN–ELSE models and threshold conditions for: *Microcystis* (a, b), chlorophyll-a (c, d) and *Stephanodiscus* (e, f). [Colour figure can be viewed at wileyonlinelibrary.com]

parent models. Figure 2d and h represents two offspring models after the crossover.

Differential evolution extracts information on distance and direction of the current population of solutions towards global optimum to guide the search for optimal parameters in the IF–THEN–ELSE rules. Because DE does not require separate probability distributions, the scheme becomes completely self-organizing. Differential evolution has been implemented in HEA for multi-objective parameter optimization as described by Cao *et al.* (2014).

The daily-interpolated time series data of the River Nakdong from 1993 to 2012 provided a wealth of seasonal and inter-annual patterns of abiotic and biotic limnological properties for modelling by HEA. Daily data interpolation is required in order to match dissimilar monitoring frequencies between physical, chemical and biological data, and to allow short-term forecasting for days ahead. By keeping a time shift of 5 days between predictor and output variables, we aimed to empower resulting models for 5-day-ahead forecasting and avoid possible same-day feedback effects of *Microcystis* and *Stephanodiscus* on physical and chemical parameters.In order to take full advantage of the information content of the data, a cyclic boot-strap scheme was applied that randomly selected different data-subsets for training (75% of all data points) and testing (25% of all data points) for each of 80 generations of models. After 100 boot-strap runs, it determined the overall ‘fittest model’ of all generations by cross-validation for the 19 years of data assuming that there is no bias by the 25% of data points randomly selected for testing during the boot-strap runs. The fitness of each model was evaluated by the root mean squared error between the measured training data $\hat{y}_i$ and the predicted data y_i defined as:

$$\text{Fitness} = \sqrt{\frac{1}{k}\sum_{i=1}^{k}\left(\hat{y}_i - y_i\right)^2}$$

The software HEA automatically carries out sensitivity analyses for the input variables of each discovered model. For this purpose, it calculates output trajectories separately for each input range (mean ± SD) by keeping remaining input variables constant at mean values. Resulting sensitivity curves visualize the output trajectories in percentage terms (0–100%) within their range of each input.

RESULTS

Model ensembles enabling scenario analysis

The model ensemble in Figure 3 has been designed for analysing the impact of alternative flow scenarios of the

DOI: 10.1002/rra

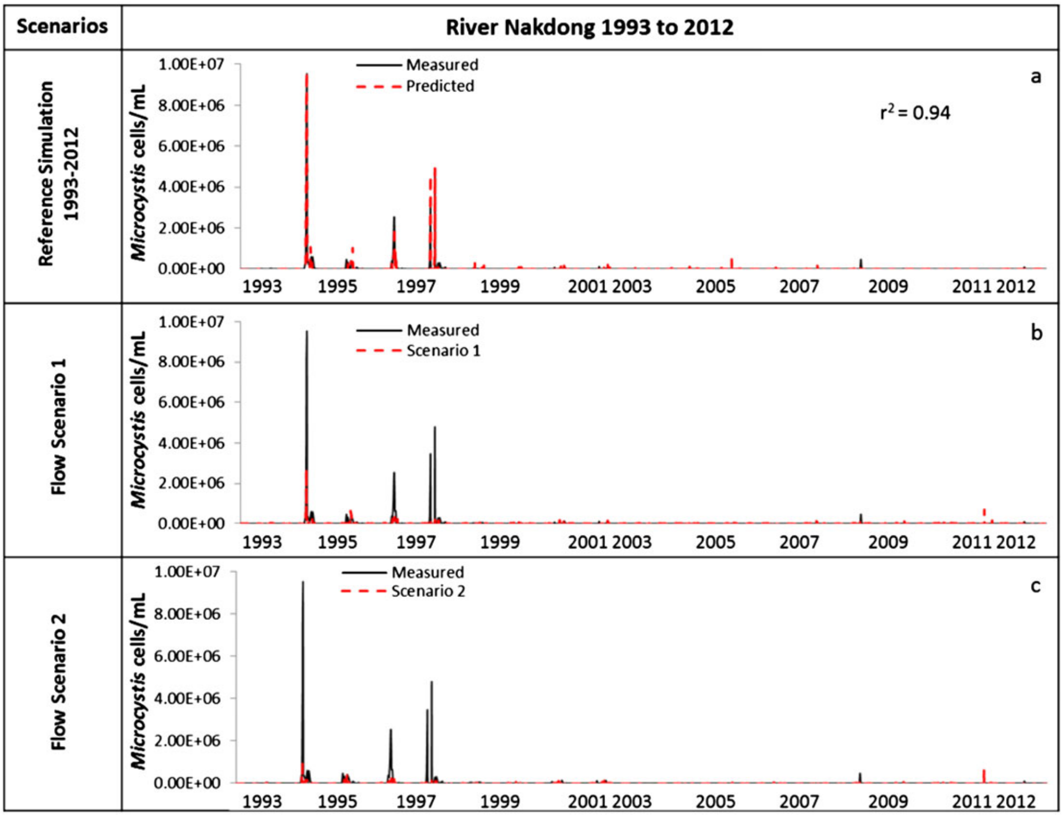

Figure 7. Five-day-ahead forecasting of *Microcystis* in River Nakdong from 1993 to 2012 based on: (a) reference flow, (b) flow scenario 1 (Figure 1b) and (c) flow scenario 2 (Figure 1c). [Colour figure can be viewed at wileyonlinelibrary.com]

River Nakdong on population dynamics of the cyanobacterium *Microcystis*. It was based on the best performing model for 5-day-ahead forecasts of *Microcystis* (Figure 6a) that achieved a coefficient of determination r^2 = 0.94 (see Figure 7a). A WT of 27.7°C has been identified as threshold by HEA above which the model forecasts events of high abundances of *Microcystis* with greater than 50 000 cells mL^{-1} (see Figure 6b). The temperature threshold corresponds well with literature findings suggesting that *Microcystis* tend to have optimum growth rates above 25°C (e.g. Robarts and Zohary, 1987).With regards to the predictor variables of the *Microcystis* model, WT was considered least affected by flow (see Figure 4c) and therefore maintained unchanged for the scenario analysis. However, because TURB as well as NO_3–N and Chl-a was expected to be flow dependent (see Figure 4a, b), following forecasting models have been developed for TURB (r^2 = 0.31) and NO_3–N (r^2 = 0.33):

IF (pH/371.7)*Q<=72 THEN **TURB** =((-25.85/(WT-33.48))+(((Q/15.3)+84.66)/DO))
ELSE **TURB** = (((-489.97/(WT-17.15))/(WT-23.88))-433.49/(WT-31.65))
IF pH>=9.1 OR Q<76.7 THEN **NO_3–N** = (((3.364-(WT/19.24))-0.052)-((31.93/(25.987-Q))/107.28))
ELSE **NO_3–N** = (((3.127-(WT/29.1))-(37.6/(Q+DO)))-((1.84/(7.01-pH))/173.48)),

as well as for Chl-a (Figure 6c), and incorporated into the model ensemble for *Microcystis* (Figure 3). The model for TURB included WT, DO and pH as predictor variables which were considered to be flow independent (see Figure 4c) and therefore maintained unchanged for the scenario analysis. The model for NO_3–N was based on the predictor variables WT, DO and pH which were maintained unchanged for the scenario analysis. The Chl-a model included the flow-dependent predictor variables EC and SiO_2 for which following forecasting models have been developed:

IF (DO>=19.5 AND Q>=46.53) OR (Q>=30.15 AND (pH-Q)>-28.61)
THEN **EC** = (451.96-((-16.32-(WT*(-0.536)))*ln(|(Q-88.43)|)))
ELSE **EC** = (410.95-((18.05-(WT*(-0.536)))*ln(|(Q-44.83)|))), r^2=0.54;

DOI: 10.1002/rra

IF Q>395.35 THEN **SiO_2** = ln(|(((WT*TURB)*(WT*TURB))*((-208.55/DO)/Q))|)
ELSE **SiO_2** = ln(|(((Q*0.03)*(Q*0.102))+(277.9/(WT-0.367)))|), r^2=0.37.

The Chl-a model achieved an r^2 = 0.54 (Figure 8a) assuming WTs greater than 26.2°C and pH values greater than 9.6 as threshold conditions for forecasting of Chl-a concentrations greater than 15 $\mu g\ L^{-1}$ (see Figure 6d). Both thresholds indicate that Chl-a in the River Nakdong is seasonally related to the cyanobacterium *Microcystis* which is dominating in summer at optimum WTs greater than 25°C (see above) and causing pH values to rise above 8.5 (Shapiro, 1984; Reynolds, 1986).The model ensemble in Figure 5 has been designed for analysing the impact of alternative flow scenarios of the River Nakdong on population dynamics of the diatom *Stephanodiscus*. It is based on the 5-day-ahead forecasting model for *Stephanodiscus* (Figure 6e) that achieved a coefficient of determination r^2 = 0.83 (see Figure 9a). Whilst most of its flow-dependent predictor variables were already determined, it required an additional model for PO_4–P in order to provide the NO_3–N/PO_4–P ratio for forecasting *Stephanodiscus*. To suit that purpose, the following PO_4–P model (r^2 = 0.37) has been developed:

IF (TURB<8.2 OR Q<=136.5) OR (WT<28.7 OR (TURB<97.6 AND TURB>=48.5))
THEN **PO_4–P** = ((3.2/(246.9-(WT*27.4)))+54.3-(41.22/(TURB-88.185)))
ELSE **PO_4–P** = (((TURB/0.36)-DO)+62.89).

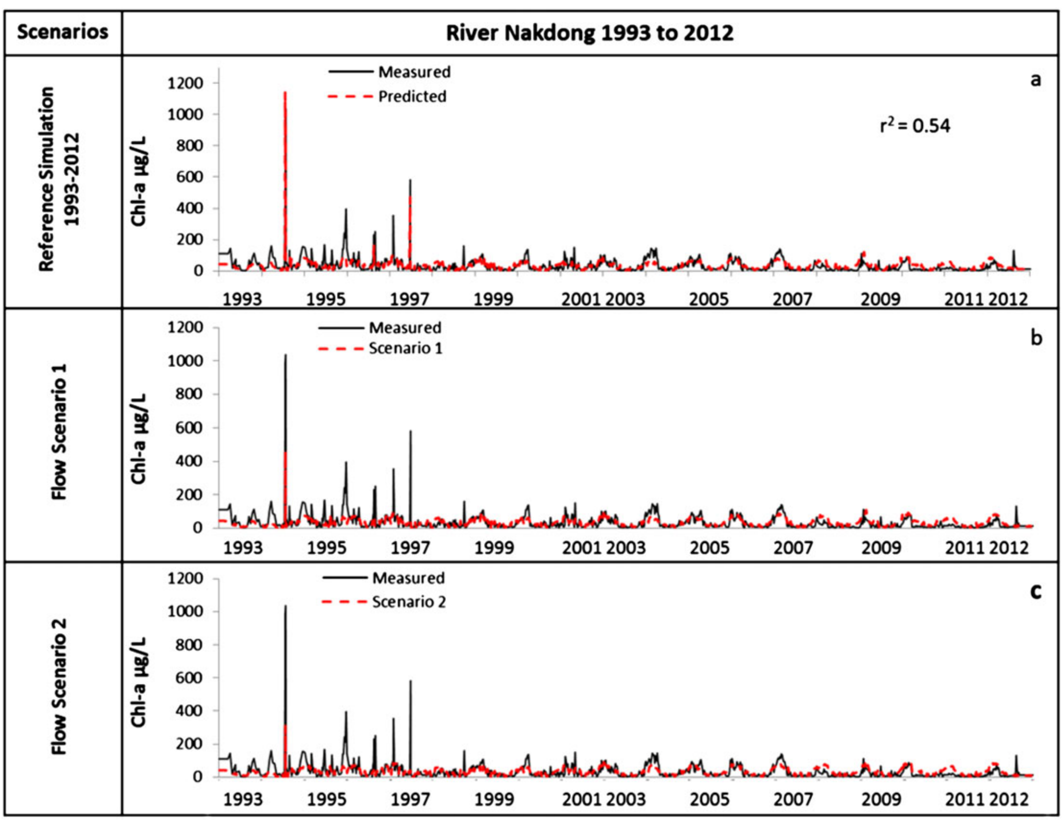

Figure 8. Five-day-ahead forecasting of Chl-a in River Nakdong from 1993 to 2012 based on: (a) reference flow, (b) flow scenario 1 (Figure 1b) and (c) flow scenario 2 (Figure 1c). [Colour figure can be viewed at wileyonlinelibrary.com]

DOI: 10.1002/rra

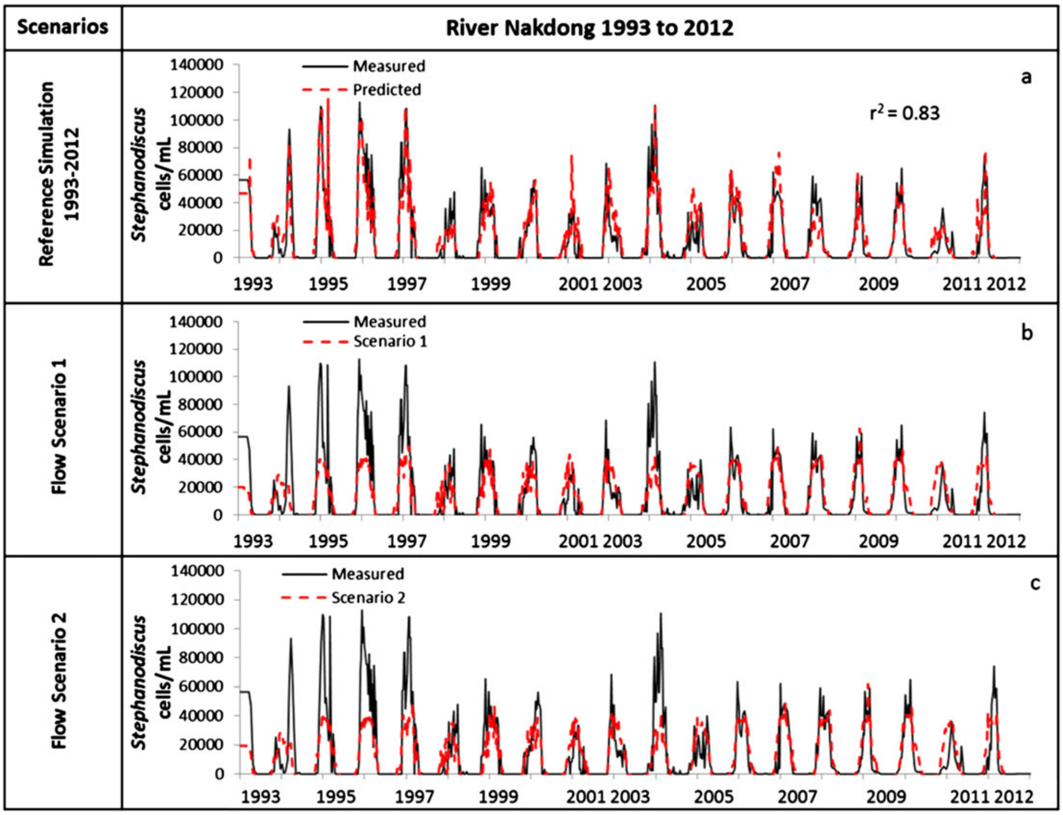

Figure 9. Five-day-ahead forecasting of *Stephanodiscus* in River Nakdong from 1993 to 2012 based on: (a) reference flow, (b) flow scenario 1 (Figure 1b) and (c) flow scenario 2 (Figure 1c). [Colour figure can be viewed at wileyonlinelibrary.com]

The *Stephanodiscus* model assumed a Chl-a concentration of 140.2 μg L^{-1} as threshold for forecasting population densities of greater than 50 000 cells mL^{-1} that would indicate a bloom event (see Figure 6f). As previously discussed, Chl-a is largely reflecting the biomass of the cyanobacterium *Microcystis* that dominates the phytoplankton community of River Nakdong in summer. High Chl-a concentrations in winter, however, seem to be closely associated with *Stephanodiscus* that is dominating in winter.

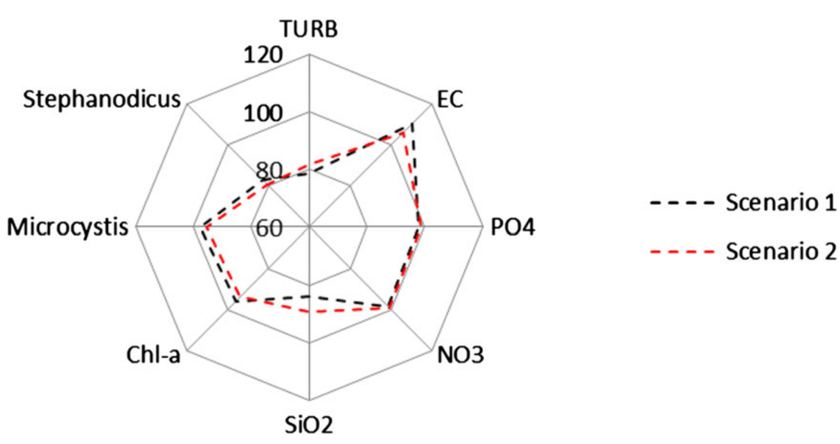

Figure 10. Comparison of percentage changes of water quality parameters and phytoplankton forecasted in response to scenarios 1 and 2. [Colour figure can be viewed at wileyonlinelibrary.com]

DOI: 10.1002/rra

Scenario analysis of alternative flow regimes of the river Nakdong

Whilst bloom events of *Microcystis* with more than 50 000 cells/mL occurred frequently in River Nakdong, major blooms in 1994, 1996 and 1997 exceeding 1 million cells/mL (Figure 7a) were of particular interest and have been forecasted accurately in terms of timing and magnitude by the model documented in Figure 6a. The scenario analysis by means of the model ensemble in Figure 3 predicted a 70% lower magnitude of the *Microcystis* bloom in 1994 and the prevention of major bloom events in 1996 and 1997 (Figure 7b) by the flow regime 1 (see Figure 1b) and the prevention of all three bloom events (Figure 7c) by the flow regime 2 (Figure 1c).

The model for chlorophyll-a predicted the prevention of peak concentrations of Chl-a in 1996 and 1997 by the 2 scenarios, but only a gradual reduction to 50% and 30% of the peak concentration of Chl-a in 1994 (Figure 8b and c).

Results for *Stephanodiscus* in River Nakdong show good accuracy by the model documented in Figure 6e by matching well both timing and magnitudes of population dynamics (Figure 9a). The scenario analysis by means of the model ensemble in Figure 3 has indicated that bloom events of more than 50 000 cells/mL, as observed from 1994 to 1997 and in 2004, can gradually be prevented by adaptive flow management according to scenarios 1 and 2 (Figure 9b and c).

Figure 10 represents results of the scenario analysis in terms of percentage of average change of water quality parameters in response to the two flow scenarios forecasted by the models for TURB, EC, PO_4–P, NO_3–N and SiO_2 as well as the models in Figure 6. It illustrates that EC increased up to 110% under the influence of the scenarios whilst concentrations of PO4, NO_3 and SiO2 decreased. Turbidity decreased most significantly to almost 80%, whilst Chl-a diminished up to 96%. Figure 10 provides further evidence that the altered flow regimes as suggested in Figure 1 can prevent extreme algal blooms in River Nakdong suggesting that average population densities of *Microcystis* decrease to 96% and of *Stephanodiscus* to 81%.

DISCUSSION AND CONCLUSIONS

Results have given evidence that abundances of *M. aeruginosa* in summer and of *S. hantzschii* in winter are significantly affected by flow regimes of the Nakdong River as postulated by hypothesis (i). Whilst increased flow shortens the water residence time at a certain location of the river, it also increases turbulences that prevent *Microcystis* to access optimum nutrient and light conditions by buoyancy. *Stephanodiscus* relies on turbulences to withstand high sedimentation losses and access light, but high flow may also inhibit vital physiological processes (e.g. Reynolds, 1994). It has also been demonstrated that altered flow regimes change physical and chemical water quality parameters that impose indirect effects of flow on abundances of *M. aeruginosa* and *S. hantzschii* as postulated by hypothesis (ii). Whilst the high concentrations of PO_4 and NO_3 in River Nakdong are suggested to decrease only marginally by dilution effects, SiO_2 declined by more than 10% and TURB decreased by 20%. The increase in EC might be attributed by higher loads of ions along with changed flow regimes.

Overall, this research has demonstrated that: (i) inferential models developed by HEA achieved good accuracy in forecasting of population densities of *Microcystis* and *Stephanodiscus* in the regulated River Nakdong and are suitable for scenario analysis provided that both direct and indirect effects of flow are taken into account by *ad hoc* designed model ensembles; and (ii) risks of high population densities of *Microcystis* and *Stephanodiscus* in the Nakdong River can be gradually minimized by adaptive management of seasonal water release from adjacent dams as reflected by scenarios 1 and 2.

REFERENCES

Al-Tebrineh J, Merrick C, Ryan D, Humpage A, Bowling L, Neilan BA. 2012. Community composition, toxigenicity, and environmental conditions during a cyanobacterial bloom occurring along 1,100 kilometers of the Murray River. *Applied and Environmental Microbiology* **78**: 763–272.

Cao H, Recknagel F, Orr PT. 2014. Parameter optimisation algorithms for evolving rule models applied to freshwater ecosystem. *IEEE Transactions on Evolutionary Computation* **18**(6): 793–806.

Cao H, Recknagel F, Bartkow M. 2016. Spatially-explicit forecasting of cyanobacteria assemblages in freshwater lakes by multi-objective hybrid evolutionary algorithms. *Ecological Modelling* 342, 97–112. Queensland (Australia). *Ecological Modelling* **252**: 32–43.

Chapra SC, Pelletier GJ, Tao H. 2008. *QUAL2K: A Modeling Framework for Simulating River and Stream Water Quality, Version 2.11. USA: Documentation and User's Manual. Civil and Environmental Engineering Department*. Tufts University: Medford.

Ha K, Cho E-A, Kim H-W, Joo G-J. 1999. *Microcystis* bloom formation in the lower Nakdong River, South Korea: importance of hydrodynamics and nutrient loading. *Marine and Freshwater Research* **50**: 89–94.

Ha K, Jang M-H, Joo G-J. 2003. Winter *Stephanodiscus* bloom development in the Nakdong River regulated by an estuary dam and tributaries. *Hydrobiologia* **506**(509): 221–227.

Harashima A, Kimoto T, Wakabayashi T, Toshiyasu T. 2006. Verification of the silica deficiency hypothesis based on biogeochemical trends in the aquatic continuum of Lake Biwa- Yodo River-Seto Inland Sea, Japan. *AMBIO: A Journal of the Human Environment* **35**, 36–42.

Holland JH, Holyoak KJ, Nisbett RE, Thagard PR. 1986. Induction. *Process of Inference, Learning, and Discovery*. MIT Press: Cambridge.

Hong D-G, Jeong K-S, Kim D-K, Joo G-J. 2014. Remedial strategy of algal proliferation in a regulated river system by integrated hydrological control: an evolutionary modelling framework. *Marine and Freshwater Research* **65**: 379–395.

DOI: 10.1002/rra

Jeong K-S, Kim D-K, Joo G-J. 2007. Delayed influence of dam storage and discharge on the determination of seasonal proliferations of *Microcystis aeruginosa* and *Stephanodiscus hantzschii* in a regulated river system of the lower Nakdong River (South Korea). *Water Research* **41**: 1269–1279.

Kannel PK, Lee S, Lee YS, Kanel SR, Pelletier GJ. 2007. Application of automated QUAL2Kw for water quality modelling and management in the Bagmati River, Nepal. *Ecological Modelling* **202**: 503–517.

Kim D-K, Jeong K-S, Whigham PA, Joo G-J. 2007. Winter diatom blooms in a regulated river in South Korea: explanations based on evolutionary computation. *Freshwater Biology* **52**: 2021–2041.

Koza JR. 1992. Genetic Programming: On the Programming of Computers by Means of Natural Selection. MIT Press: Cambridge, MA.

Marker AFH, Collett GD. 1997. Spatial and temporal characteristics of algae in the River Great Ouse. I. Phytoplankton. *Regulated Rivers: Research and Management* **13**: 219–233.

Park SS, Lee YS. 2002. A water quality study of the Nakdong River, Korea. *Ecological Modelling* **152**: 65–75.

Recknagel F, Ostrovsky I, Cao H, Zohary T, Zhang X. 2013. Ecological relationships, thresholds and time-lags determining phytoplankton community dynamics of Lake Kinneret, Israel elucidated by evolutionary computation and wavelets. *Ecological Modelling* **255**: 70–86.

Recknagel F, Orr P, Cao H. 2014a. Inductive reasoning and forecasting of population dynamics of *Cylindrospermopsis raciborskii* in three sub-tropical reservoirs by evolutionary computation. *Harmful Algae* **31**: 26–34.

Recknagel F, Ostrovsky I, Cao H. 2014b. Model ensemble for the simulation of plankton community dynamics of Lake Kinneret (Israel) induced from in situ predictor variables by evolutionary computation. *Environmental Modelling and Software* **61**: 380–392.

Recknagel F, Adrian R, Köhler J, Cao H. 2016. Threshold quantification and short-term forecasting of *Anabaena*, *Aphanizomenon* and *Microcystis* in the polymictic eutrophic Lake Müggelsee (Germany) by inferential modelling using the hybrid evolutionary algorithm HEA. *Hydrobiologia* **778**: 61–74.

Reynolds CS. 1994. The long, the short and the stalled: on the attributes of phytoplankton selected by physical mixing in lakes and rivers. *Hydrobiologia* **289**: 9–21.

Reynolds CS. 1986. *The Ecology of Phytoplankton*. Cambridge University Press: Cambridge.

Robarts RD, Zohary T. 1987. Temperature effects on photosynthetic capacity, respiration, and growth rates of bloom-forming cyanobacteria. *NZ J Mar Freshwater Res* **21**: 391–399.

Shapiro J. 1984. Blue–green dominance in lakes: the role and management significance of pH and CO_2. *Limnology and Oceanography* **69**(6): 765–780.

Storn R, Price K. 1997. Differential evolution–A simple and efficient heuristic for global optimization over continuous spaces. *Journal of Global Optimization* **11**, 341-359.

Utermöhl H. 1958. Zur vervollkommnung der quantitativen phytoplankton-methodik. *Verhandlung Internationale Vereinigung Limnologie* **9**: 1–38.

Yoshimura C, Omura T, Furumai H, Tockner K. 2005. Present state of rivers and streams in Japan. *River Research and Applications* **21**: 93–112.

Zhang X, Recknagel F, Chen Q, Cao H, Li R. 2015. Spatially-explicit modelling and forecasting of cyanobacteria growth in Lake Taihu by evolutionary computation. *Ecological Modelling* **306**: 216–225.

DOI: 10.1002/rra