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PRIMARY RESEARCH PAPER

Modelling and forecasting the heterogeneous distribution of picocyanobacteria in the tropical Lajes Reservoir (Brazil) by evolutionary computation

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Abstract Five years of water quality data from six stations across the mesotrophic and oligomictic Lajes Reservoir (Brazil) were utilized to develop 7-day ahead forecasting models for the picocyanobacteria *Cyanodictyon imperfectum, Cyanogranis ferruginea* and *Synechococcus* sp. by means of the hybrid evolutionary algorithm HEA. The data included physical and chemical water quality parameters as well as abundance data of the three picocyanobacteria. Models based on site-specific data of six monitoring stations forecasted population dynamics of *Synechococcus* with coefficients of determination (r^2) between 0.58 for and 0.88, of *Cyanodictyon* with r^2 between 0.5 and 0.89 and of *Cyanogranis* with r^2 between 0.53 and 0.77. Despite phosphorus limiting conditions the sensitivity analysis revealed that the three picocyanobacteria responded much stronger to nitrate rather than to phosphate concentrations throughout the Lajes Reservoir suggesting that cyanobacteria may have adopted the sulphur-for-phosphorus strategy by utilizing sulfolipids instead. *Cyanogranis* displayed a negative relationship with increasing water temperature indicating its higher competitiveness at internal nutrient supply and low light levels during winter turnover. The resulting models will inform operational intervention and prevention of fast growth and dispersal of picocyanobacteria in Lajes Reservoir, and reveal environmental thresholds for outbreaks of such events.

Keywords Spatial heterogeneity · Picocyanobacteria · Evolutionary computation

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Introduction

The Lajes Reservoir is situated in the Rio de Janeiro State of Brazil and fed by the Piraí and Ribeirão das Lajes rivers. Hydroelectric power generation of up to 612 MW per year is the main purpose of Lajes Reservoir, but it is also used for water supply, irrigation, aquaculture and recreation. The occurrence of cyanobacteria in the reservoir is of major concern since it supplies just chlorinated domestic water to one million people, and feeds water into the Guandu River which is the main source of water for around nine million people in the Rio de Janeiro Municipality.

Picocyanobacteria have been intensively studied in deep oligotrophic and mesotrophic temperate lakes where they comprise the majority of picophytoplankton (Callieri, 2007), but little is known about picocyanobacteria in tropical lakes. Peculiar features of picocyanobacteria that were found in the tropics are high abundances throughout the year (Sarmento et al., 2008) and seasonal variations in biomass according to dry or wet season (Macek et al., 2009; Stenuite et al., 2009), and may not be fully explained by benefits from small cell size for nutrient uptake, lower cost metabolism, negligible sedimentation as well as acclimation to varying light and temperature (Callieri et al., 2012).

Picocyanobacteria tend to be abundant in the metalimnion and upper hypolimnion of stratified lakes exhibiting low nutrient availability in the epilimnion, and are favoured by stable thermal stratification and long water retention time (Camacho et al., 2003). The oligomictic mesotrophic Lajes Reservoir with an average water retention time of 297 days provides favouring growth conditions for picocyanobacteria.

The picocyanobacteria species *Cyanodictyon imperfectum, Cyanogranis ferruginea* and *Synechococcus* sp. accounted for 46% of the abundance of the phytoplankton community in Lajes Reservoir between 2007 and 2009. The colonial *C. imperfectum* has reportedly caused cyanobacteria blooms in Lake Trummen (Sweden) (Callieri et al., 2012) and Lake Kinneret (Israel) (Hickel & Pollinger, 1988). The colonial *C. ferruginea* has been observed both in temperate lakes and lentic oxbows (Híndak, 1982; Borics et al., 2011) as well as in rivers in the southeast part of Brazil (Soares et al., 2007). The single-celled *Synechococcus* sp. appears to be common in oligotrophic to eutrophic tropical reservoirs (Honda & Azevedo, 2004; Callieri, 2007; Gentil et al., 2008; Delazari-Barroso et al., 2009) and can produce hepatotoxic microcystins (Furtado et al., 2009).

The present study uses long-term limnological data of Lajes Reservoir to better understand bottom-up mechanisms that control population dynamics of picocyanobacteria in a tropical environment. Following hypotheses are tested: (1) the hybrid evolutionary algorithms HEA allows to build spatially explicit short-term forecasting models for the three picocyanobacteria based on 5 years of limnological time series across six monitoring stations of the Lajes Reservoir and (2) resulting models reveal ecological thresholds and relationships that determine fast population growth of the three picocyanobacteria within the Lajes Reservoir. The hybrid evolutionary algorithm HEA (Cao et al., 2013) has been designed to perform inductive reasoning and forecasting from complex ecological data (Recknagel et al., 2014a) and quantify environmental thresholds for recurrent outbreaks of population densities (Recknagel et al., 2014b, c).

Materials and methods

Lajes Reservoir

Lajes Reservoir was constructed in 1902 and is located in a preserved watershed area of 305 km^2, that is covered by up to 50% by tropical rain forests. The main tributary is the Piraí River that carries water from the Piraí Creek watershed situated in a farming region receiving waste water from adjacent villages (Guarino et al., 2005; Soares et al., 2008). The Lajes Reservoir is characterized by a surface area of 30–47.8 km^2, an average depth of 15 m and a maximum depth of 40 m, a volume of 450,106 m^3 and a retention time of 297 days. The reservoir is stratified for most time of the year with occasional mixing in winter (Branco et al., 2009) and is considered to be mesotrophic (Guarino et al., 2005; Soares et al., 2008).

Physical and chemical water quality parameters as well as cell concentrations of the three cyanobacteria species have been monitored monthly at six sampling sites of Lajes Reservoir (see Fig. 1) from 2005 to 2009. Table 1 displays the annual means of the physical–chemical parameters and Table 2 the annual mean and maximum densities of the picocyanobacteria observed at the six sampling stations of Lajes Reservoir. The sampling sites reflect conditions of the riverine zone where the Piraí River enters the reservoir (site 1), the transitional zone (site 2), the lacustrine zone (site 3 and 4) and areas of fish farming by net-cages (site 5). The site 6 is located near the dam wall where water is supplied for power generation and domestic uses. Surface samples (0.3 m) for phytoplankton and chemical analysis were monthly taken from each site from January 2005 to December 2009. Water temperature (WT), electrical conductivity (EC), dissolved oxygen (DO) and pH were measured in situ

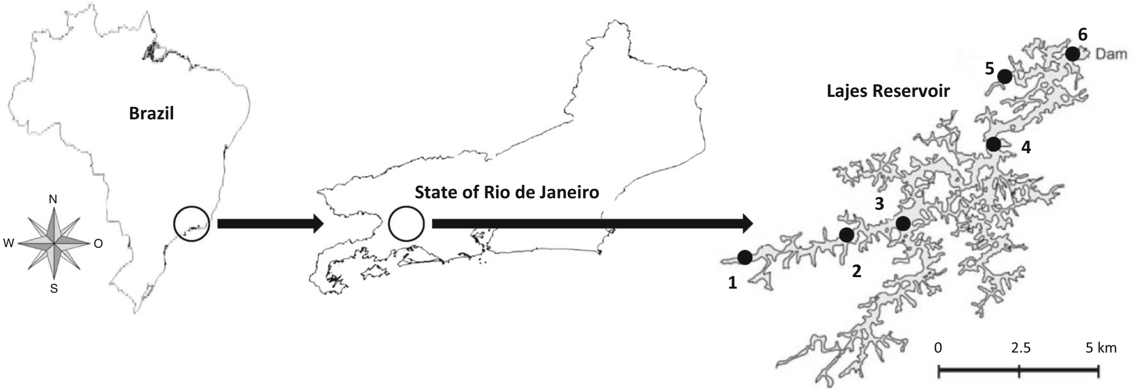


Fig. 1 Location and sampling sites of Lajes Reservoir

by an YSI multi-sensor probe. Water transparency was estimated by Secchi depth (SD).

Samples for dissolved nutrients (P-PO_4^{3-}, N-NH_4^+, N-NO_3^- and N-NO_2^-) were filtered using GF/C filters (Whatman); total phosphorus (TP) and nitrogen (TN) were determined in unfiltered samples which were kept frozen before the analysis. Laboratory analyses for nutrients were performed according to standard spectrophotometric techniques (APHA, 2005). Samples for phytoplankton analysis were placed in dark bottles and fixed with Lugol-acetic solution. Picoplankton population densities (ind. ml^{-1}) were estimated as cells per litre using the sedimentation technique (Utermöhl, 1958) under an inverted microscope (400× magnification). Organisms were identified by main morphological and morphometric characteristics under microscopes with 1,000× magnification. At least 100 individuals of the dominant species were counted in each sample (error <20%, $P < 0.05$, Lund et al., 1958). This number increased during periods of higher cell numbers, when at least 400 individuals of the dominant species were counted in each sample (error <10%, $P < 0.05$, Lund et al., 1958). An underestimation of the counts of single-celled *Synechococcus* by this method cannot be ruled out.

Hybrid evolutionary algorithm HEA

The research was conducted by means of the hybrid evolutionary algorithm HEA (Cao et al., 2013) that previously has been successfully applied for predictive modelling of cyanobacteria growth in a variety of lake and rivers worldwide (e.g., Chan et al., 2007; Kim et al., 2007; Recknagel et al., 2008, 2013, 2014a, b). It has been designed to evolve "fittest models" spiral-like over time from ecological data by combining genetic programming (GP) for optimizing the model structure and differential evolution (DE) for optimizing model parameters (see Fig. 2). GP is applied to search for the optimum model structure by continually recombining arithmetic and logic operators based on principles of crossover, mutation and reproduction as explained in great detail in Recknagel et al. (2014c). The DE is an evolutionary algorithm designed for parameter optimization (Storn and Price, 1997) that extracts the differential information (i.e., distance and direction to global optimum) from the current population of solutions as guide to search for the global optimum.

The monthly time series from 2005 to 2009 provided a wealth of seasonal and inter-annual patterns of abiotic and biotic limnological properties. In order to take full advantage of the information content of available data, the boot-strap scheme has been implemented for the training of HEA that randomly selects different data-subsets for training and testing for each of which 80 generations of models are evolved (see Recknagel et al., 2013). After 100 boot-strap runs, it determines the overall "fittest model" of all generations. The fitness of each model is evaluated by the root mean squared error (RMSE) between the measured training data and the predicted data defined as

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

Table 1 Annual averaged data of physical and chemical variables measured at six sites of Lajes Reservoir from 2005 to 2009

Variable	St.	2005	2006	2007	2008	2009	Variable	St.	2005	2006	2007	2008	2009
Surface water temperature (°C)	P1	22.7	21.8	23.1	21.6	21.5	Dissolved oxygen (mg l^{-1})	P1	8.2	9.5	7.9	7.4	7.8
	P2	26.3	25.9	26.1	25.1	25.8		P2	8.1	9.0	7.6	7.3	7.4
	P3	26.3	25.8	26.1	25.0	25.8		P3	8.1	8.6	7.6	7.1	7.4
	P4	26.7	26.1	26.2	25.3	25.9		P4	7.9	8.3	7.2	7.0	7.3
	P5	26.6	26.4	26.4	25.3	26.1		P5	7.7	8.0	7.0	6.7	6.5
	P6	26.2	25.6	25.6	24.8	25.4		P6	7.9	8.4	7.2	6.5	7.0
Electrical conductivity (µS cm^{-1})	P1	22.5	22.0	27.3	23.7	25.0	pH	P1	6.5	6.3	6.5	6.3	5.9
	P2	28.2	28.0	29.8	28.0	27.8		P2	7.4	6.9	7.3	6.6	6.2
	P3	28.2	27.5	29.5	28.0	27.7		P3	7.4	7.0	7.3	6.7	6.5
	P4	28.0	27.0	29.0	27.6	27.7		P4	7.3	6.8	7.1	6.6	6.4
	P5	29.4	28.4	30.3	29.0	29.3		P5	7.2	6.7	7.0	6.5	6.1
	P6	27.5	26.5	28.5	27.3	27.7		P6	7.1	6.5	6.9	6.3	5.9
Secchi depth (m)	P1	1.3	1.5	2.1	1.2	1.4	Chlorophyll *a* (µg l^{-1})	P1	2.2	1.6	1.6	3.0	3.2
	P2	3.2	3.1	2.9	3.1	2.5		P2	1.7	2.7	1.8	3.2	3.0
	P3	3.7	3.9	3.8	3.5	2.8		P3	1.7	2.2	1.7	2.4	2.6
	P4	4.0	4.3	3.8	3.8	3.2		P4	1.4	1.8	1.1	1.6	1.5
	P5	2.8	2.6	3.4	2.8	2.6		P5	3.5	6.1	3.6	2.8	4.7
	P6	4.0	4.1	4.1	4.0	3.3		P6	1.3	1.8	1.1	1.2	1.5
Ammonium (µg l^{-1})	P1	42.3	471.3	347.3	273.7	411.5	Nitrite (µg l^{-1})	P1	2.0	1.3	18.7	28.2	26.9
	P2	37.3	252.0	203.4	180.8	291.3		P2	1.8	1.0	11.2	13.2	16.5
	P3	38.1	213.9	152.8	152.4	177.6		P3	1.5	1.0	9.9	11.7	14.9
	P4	29.3	206.8	173.7	140.8	165.1		P4	1.5	0.9	8.6	10.2	12.7
	P5	58.5	523.5	235.8	164.1	223.1		P5	2.2	1.0	13.9	11.4	21.1
	P6	63.0	327.2	248.2	220.4	376.6		P6	1.5	1.1	10.4	10.5	12.6
Nitrate (µg l^{-1})	P1	77.7	103.2	264.5	312.7	358.7	Phosphate (µg l^{-1})	P1	8.0	12.0	10.5	11.7	12.0
	P2	26.1	45.5	88.1	181.8	265.2		P2	7.1	9.7	10.0	15.9	11.7
	P3	24.1	46.2	67.7	177.4	212.0		P3	5.4	8.0	7.7	8.9	10.7
	P4	31.2	36.3	77.1	189.2	225.7		P4	5.2	7.5	8.6	9.4	8.0
	P5	38.4	36.4	90.4	187.2	258.4		P5	7.1	8.1	9.7	13.2	13.8
	P6	24.0	39.0	80.2	230.9	179.4		P6	8.9	7.4	8.2	9.5	9.0
Total phosphorus (µg l^{-1})	P1	27.9	43.7	43.7	54.6	49.2	N/P (DIN/PO_4 ratio)	P1	15.3	48	60	52.5	66.4
	P2	15.8	19.3	18.7	42.9	34.7		P2	9.2	30.8	30.3	23.6	49
	P3	12.8	14.8	14.3	19.8	21.0		P3	11.8	32.6	29.9	38.4	37.8
	P4	12.1	12.1	13.7	19.2	16.7		P4	11.9	32.5	30.2	36.2	50.4
	P5	26.3	24.2	16.3	15.4	15.8		P5	14	69.2	35.1	27.5	36.4
	P6	17.6	21.8	25.6	26.3	35.8		P6	9.9	49.6	41.3	48.6	63.2

The software HEA automatically carries out sensitivity analyses for the input variables of each discovered model. 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

Site-specific models

Figures 3, 4, 5, 6, 7, 8 document the best-performing models for the three picocyanobacteria developed specifically for each of the 6 monitoring stations of

Table 2 Annual average and maximum densities of picocyanobacteria (cells ml^{-1}) measured at six sites of Lajes Reservoir from 2005 to 2009

Picocyanobacteria cells (ml)	2005	2006	2007	2008	2009
P1					
Cyanodictyon imperfectum	0	26 (149)	10 (113)	31 (262)	71 (452)
Cyanogranis ferruginea	54 (447)	80 (1,760)	334 (2,336)	1,473 (7,432)	1,072 (2,939)
Synechococcus sp.	0	5 (128)	64 (226)	858 (5,214)	2,143 (14,496)
P2					
Cyanodictyon imperfectum	0	50 (590)	568 (1,243)	328 (1,130)	319 (1,724)
Cyanogranis ferruginea	9	18 (182)	992 (4,719)	1,041 (2,561)	2,465 (4,776)
Synechococcus sp.	0	271 (6,493)	856 (8,657)	726 (2,435)	7,084 (64,426)
P3					
Cyanodictyon imperfectum	0	43 (359)	520 (1,281)	639 (8,991)	975 (11,869)
Cyanogranis ferruginea	30 (251)	5 (46)	1,018 (4,185)	1,055 (10,238)	3,569 (13,650)
Synechococcus sp.	0	9 (212)	426 (2,043)	1,246 (8,355)	2,468 (13,960)
P4					
Cyanodictyon imperfectum	0	37 (424)	464 (1,047)	154 (565)	262 (1,507)
Cyanogranis ferruginea	72 (787)	6 (46)	839 (3,297)	658 (2,155)	2,480 (6,181)
Synechococcus sp.	0	13 (318)	278 (1,281)	15,125 (160,944)	2,155 (8,167)
P5					
Cyanodictyon imperfectum	0	17 (368)	571 (1,170)	213 (767)	529 (4,352)
Cyanogranis ferruginea	20 (179)	45 (446)	1,535 (5,181)	772 (1,798)	4,239 (13,947)
Synechococcus sp.	0	2 (56)	176 (746)	1,004 (5,445)	2,146 (17,352)
P6					
Cyanodictyon imperfectum	0	44 (1,026)	765 (2,520)	173 (584)	340 (2,261)
Cyanogranis ferruginea	9 (57)	18 (92)	742 (2,741)	584 (2,091)	2,311 (6,217)
Synechococcus sp.	0	0	767 (3,985)	700 (5,878)	3,600 (34,816)

Lajes Reservoir using site-specific water quality data as inputs. The r^2 values of models for *Cyanodictyon* (Figs. 3, 4) ranged between 0.5 for station 1 (Fig. 3d) and 0.89 for station 3 (Fig. 3f). However, all six models forecasted well timing and cell concentrations of peak events in the population dynamics of *Cyanodictyon* observed over the 5 years. It is apparent that nitrate concentrations triggered at all six sites fast growth events of *Cyanodictyon* whereby measurements indicated a distinct gradient from high nitrate concentrations at inlet site 1 towards low nitrate concentrations at outlet site 6. This is reflected in the site-specific modelling results suggesting that the peak cell concentration of *Cyanodictyon* at station 1 in 2009 coincided with the nitrate concentrations greater than 360.6 N-NO$_3$ µg/l (Fig. 3g) and peak cell concentrations of *Cyanodictyon* at station 6 in 2007 and 2009 corresponded with the nitrate concentrations greater than 64.6 N-NO$_3$ µg/l (Fig. 4i).

The r^2 values of models for *Cyanogranis* (Figs. 5, 6) ranged between 0.53 for station 3 (Fig. 5f) and 0.77 for station 5 (Fig. 6e). The six site-specific models performed well by forecasting timing and magnitudes of most of the events with high cell concentration. Exceptions are two medium high events at station 2 in 2007 and at station 3 in 2007/2008. The thresholds discovered by the *Cyanogranis* models for stations 1–5 also indicated high sensitivity of population growth to changing nitrate concentrations. The highest cell concentrations of *Cyanogranis* have been observed and forecasted for station 3 in 2008/2009 coinciding with the nitrate concentrations greater than 165 N-NO$_3$ µg/l (Fig. 5i) and for station 5 in 2009 coinciding with the nitrate concentrations greater than 183.7 N-NO$_3$ µg/l (Fig. 6h). The model for station 6 suggests that pH values greater than 5.7 trigger high cell concentrations of *Cyanogranis* from 2007 to 2009 (Fig. 6i).

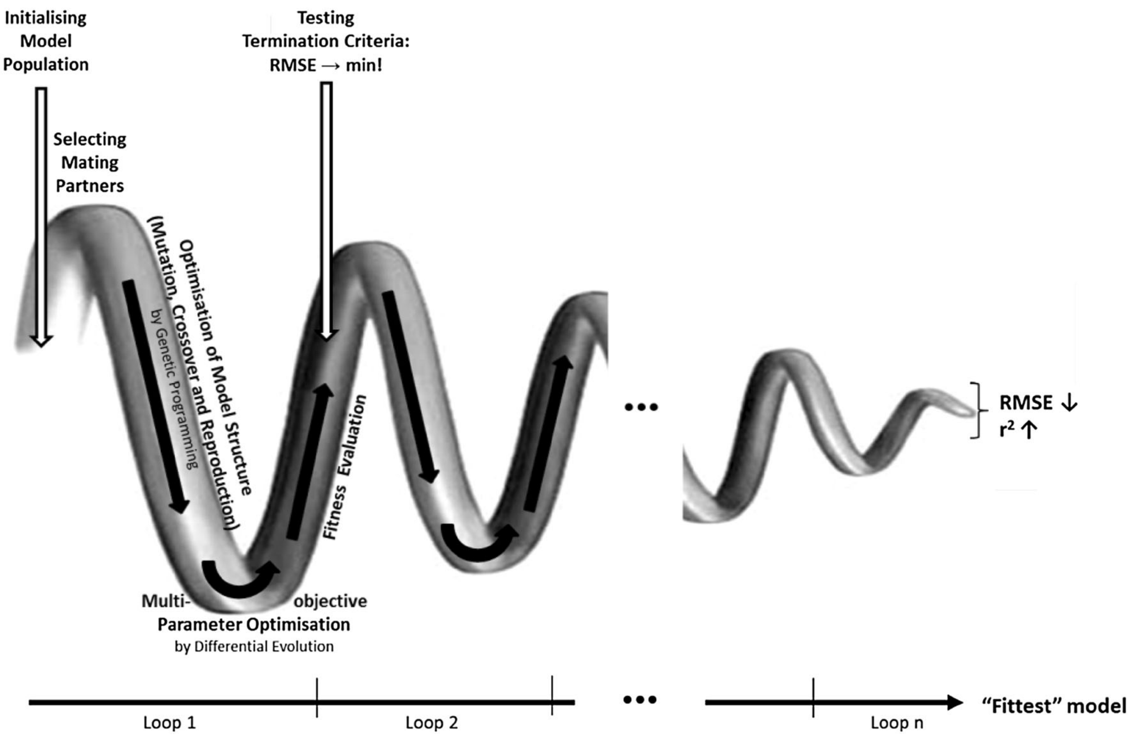


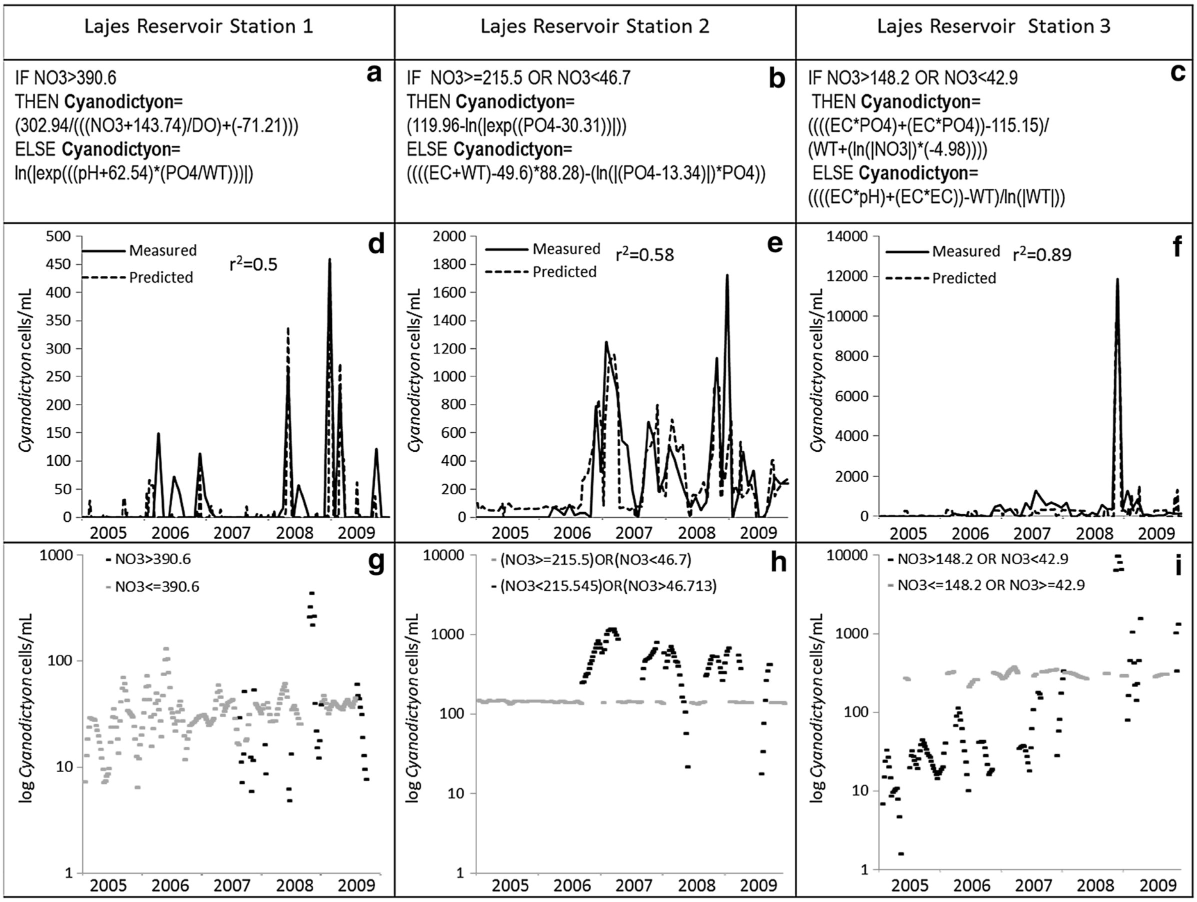
Fig. 2 Conceptual diagram of the functioning of the hybrid evolutionary algorithm HEA

The r^2 values of models for *Synechococcus* (Figs. 7, 8) ranged between 0.58 for station 6 (Fig. 8f) and 0.88 for station 2 (Fig. 7e). High cell concentrations of *Synechococcus* have been observed at stations 1–3, 5, and 6 in 2008/2009 and at station 4 in 2008 with 1.6×10^5 cells per ml, with virtually no major growth events before 2007 at all stations. The six site-specific models performed well by forecasting timing and magnitudes of the few events with high cell concentrations. Thresholds indicating fast growth of *Synechococcus* as discovered by models for the stations 1–4 and 6 included nitrate concentrations. In contrast, the fast growth event at station 5 in 2008 appeared to be triggered by phosphate concentrations smaller than 21.05 P-PO_4 µg/l (Fig. 8h). Another interesting finding is the inclusion of water temperature greater than 28.2°C in the threshold conditions for the high cell concentrations at station 2 in 2009 (Fig. 7h).

Ecological relationships

Figure 9 summarizes the results of sensitivity analyses conducted for the ten best-performing picocyanobacteria models by focusing on water temperature, nitrate and phosphate that were selected as input variables by all models discussed in the section above. Even though ammonium showed similar annual trends as nitrate, it had not been selected as key driving variable in any of the models documented in Figs. 3, 4, 5, 6, 7, 8 and therefore was not subject to sensitivity analysis.

Within the temperature range of 20.5–31.5°C, *Cyanodictyon* responded on average almost linearly to temperature increases, reaching highest cell concentrations at temperatures at near 30°C (Fig. 9a). This result appeared in strong contrast to cell concentrations of *Cyanogranis* that were highest at temperatures in the low 20s but exponentially declined towards and remained very low beyond 26°C (Fig. 9b). *Synechococcus* sp. seems to be tolerant to the temperature range observed in Lajes Reservoir by not showing any distinct trend in response to temperature changes (Fig. 9c). All three picocyanobacteria responded linearly to increasing nitrate concentrations within the range from 5.5 to 350 µg N-NO_3/l (Fig. 9d–f), corresponding with findings in the section above where N-NO_3 concentrations were identified as thresholds for fast growth events. *Cyanogranis* was



IF NO3>390.6
THEN **Cyanodictyon**=
(302.94/(((NO3+143.74)/DO)+(-71.21)))
ELSE **Cyanodictyon**=
ln(|exp(((pH+62.54)*(PO4/WT)))|)

IF NO3>=215.5 OR NO3<46.7
THEN **Cyanodictyon**=
(119.96-ln(|exp((PO4-30.31))|))
ELSE **Cyanodictyon**=
((((EC+WT)-49.6)*88.28)-(ln(|(PO4-13.34)|)*PO4))

IF NO3>148.2 OR NO3<42.9
THEN **Cyanodictyon**=
((((EC*PO4)+(EC*PO4))-115.15)/
(WT+(ln(|NO3|)*(-4.98))))
ELSE **Cyanodictyon**=
((((EC*pH)+(EC*EC))-WT)/ln(|WT|))

Fig. 3 Seven-Day ahead forecasting models and ecological thresholds for *Cyanodictyon* at station 1 (**a**, **d**, **g**), station 2 (**b**, **e**, **h**) and station 3 (**c**, **f**, **i**)

responding strongest to increasing N-NO_3 concentrations indicated by a slope of 19.4 (Fig. 9b), whilst *Cyanodictyon* was responding slowest reflected by a slope of 1.6 (Fig. 9a). Similar positive trends were discovered for relationships between the three picocyanobacteria and changing P-PO_4 concentrations within the range of 1.5–20 µg P-PO_4/l where *Cyanogranis* was responding strongest with a slope of 37 (Fig. 9h) and *Cyanodictyon* weakest with a slope of 1.6 (Fig. 9g).

Discussion

The present study aimed at forecasting population dynamics of picocyanobacteria across the horizontal sampling sites of the Lajes Reservoir and to determine environmental thresholds that cause fast growth events of picocyanobacteria. Models based on site-specific data of the six monitoring stations forecasted population dynamics of *Cyanogranis* with coefficients of determination (r^2) ranging between 0.53 for station 3 and 0.77 for station 5, and achieved an average r^2 for all stations of 0.67. Similar results were achieved by models for *Cyanodictyon* where r^2 ranged between 0.5 for station 1 and 0.89 for station 3, and averaged with 0.66, as well as for models for *Synechococcus* with r^2 ranging between 0.58 for station 6 and 0.88 for station 2, and averaged with 0.73 for all stations. These results are consistent with findings by Van de Bogert et al. (2012) that only spatially-explicit models meet requirements for forecasting heterogeneously distributed

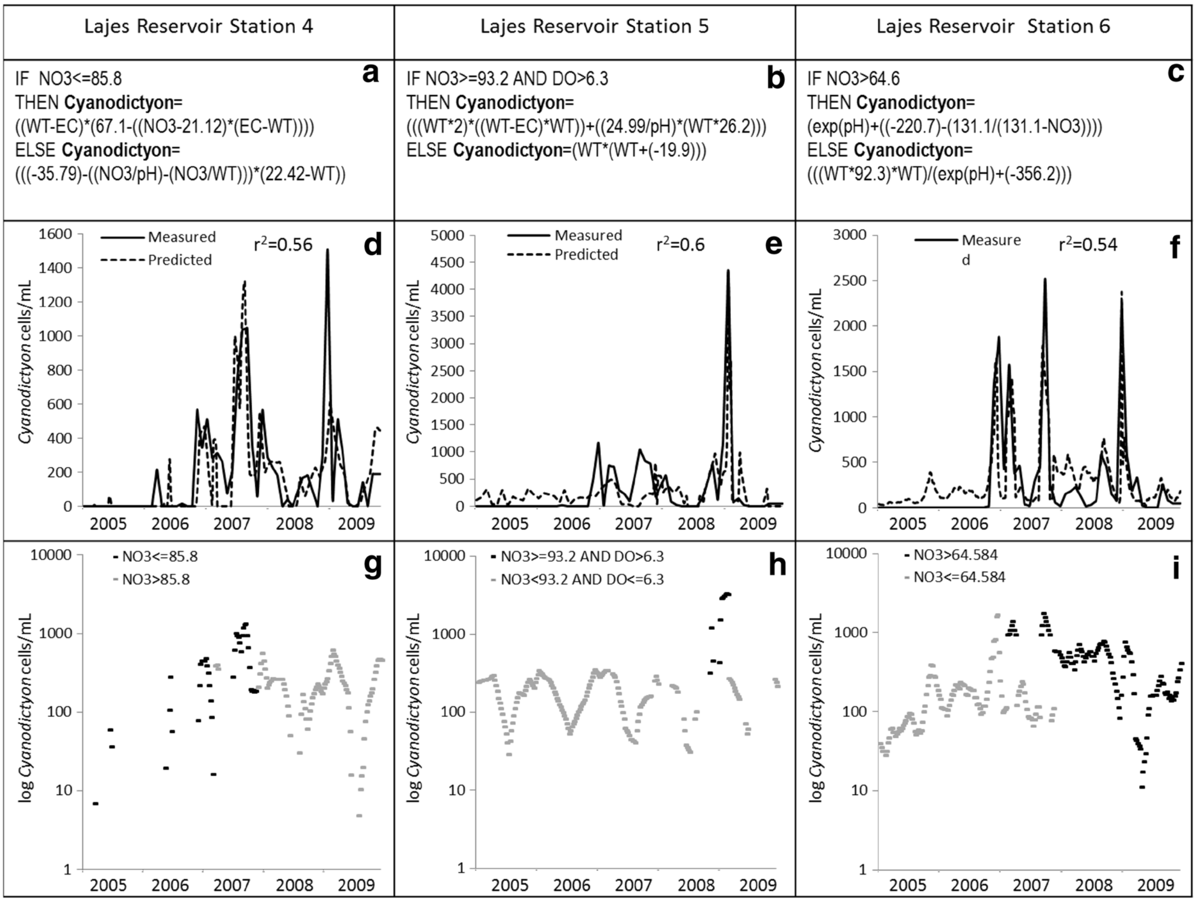


Fig. 4 Seven-Day ahead forecasting models and ecological thresholds for *Cyanodictyon* at station 4 (**a**, **d**, **g**), station 5 (**b**, **e**, **h**) and station 6 (**c**, **f**, **i**)

aquatic communities in lakes, and that in the case of picocyanobacteria in Lajes Reservoir most likely are caused by long water residence times (Soares et al., 2012) and aquaculture at site 5. Moreover, picoplankton communities may adapt to local conditions, making their behaviour less predictable on a long-term basis without local predictor variables (Callieri, 2007).

Sensitivity analysis revealed nitrate as the main factor for population growth of *C. imperfectum, C. ferruginea* and *Synechococcus* sp. throughout Lajes Reservoir. Phosphate concentrations of 5–10 µg/l frequently observed in Lajes Reservoir matched half-saturation concentrations for most algal species as suggested by Reynolds (2006), and were also identified as growth factor for the picocyanobacteria species in this mesotrophic tropical lake. The lesser importance of phosphate may be related to alternative phosphate acquisition strategies adopted by picocyanobacteria. The sulphur-for-phosphorus biochemical strategy allows cyanobacteria at low phosphorus concentrations to substitute sulphate phosphate in lipids (Van Mooy et al., 2006), and may explain the success of picocyanobacteria despite oligotrophic to mesotrophic conditions of Lajes Reservoir. It can be concluded from these results that nitrate concentrations predominately stimulate growing cell concentrations of each species in combination with other environmental factors. Nitrate and water temperature were important driving variables for *Cyanodictyon* at all sampling stations according to site-specific modelling results, whilst phosphate appeared as important driving variable only at sampling sites 1, 2 and 3. Despite the small range of water temperature as observed for Lajes Reservoir, slight

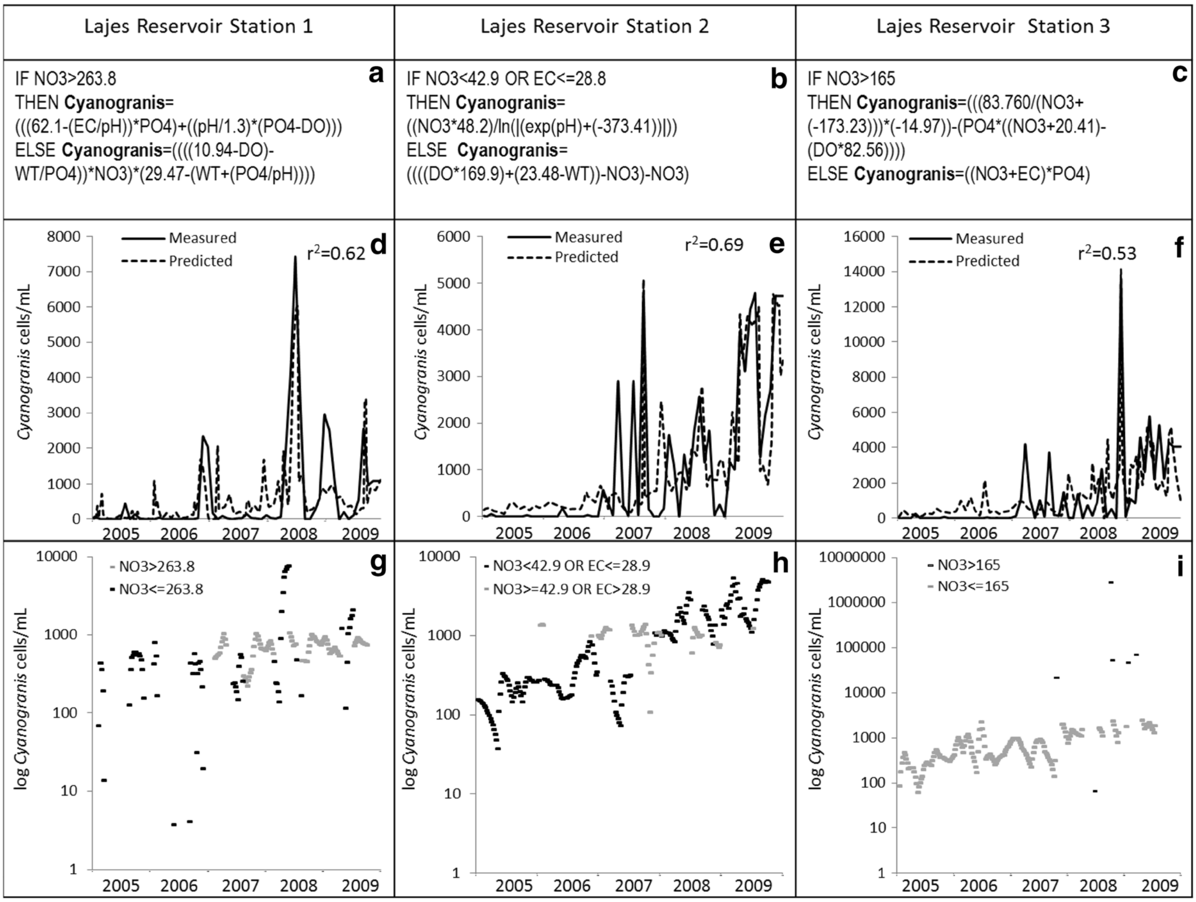


Fig. 5 Seven-Day ahead forecasting models and ecological thresholds for *Cyanogranis* at station 1 (**a**, **d**, **g**), station 2 (**b**, **e**, **h**) and station 3 (**c**, **f**, **i**)

seasonal increases in temperature may stimulate the growth of cyanobacteria in tropics (Soares et al., 2009), as discovered for *Cyanodictyon*. Improved understanding of environmental conditions that stimulate the growth of *C. imperfectum* is of fundamental importance since colonial picocyanobacteria can be disrupted during the treatment process for drinking water and release cyanotoxins, posing a risk for human health (Callieri et al., 2012).

Nitrate concentrations and electrical conductivity (EC) appeared to be important predictor variables for *Cyanogranis* at all sampling stations, whilst PO_4 was important at sampling stations 1, 3, 5 and 6. Water temperature (WT) and EC displayed low variation in Lajes Reservoir, and changes are typically associated with heavy rains and water column mixing in winter (Branco et al., 2009). Since *C. ferruginea* was negatively correlated with increasing WT, it may indicate its reliance on surface nutrient supply from lake turnovers since mixing of a long-term stratified reservoir stimulates growth of phytoplankton species requiring high surface concentration of nutrients (Delazari-Barroso et al., 2009). Moreover, picocyanobacteria may be more competitive during mixing at low light levels (Callieri & Stocker, 2002; Camacho et al., 2003). *C. ferruginea* can also form clusters of cells incorporating grains of precipitating iron-oxides, indicating their capability to mobilize phosphate from these deposits (Hindák, 1982; Whitton, 1992).

The present research has also revealed that nitrate-to-phosphate ratios and epilimnion depth are indicative properties for high cell concentrations of *Synechococcus* sp. in Lajes Reservoir. By looking at site-

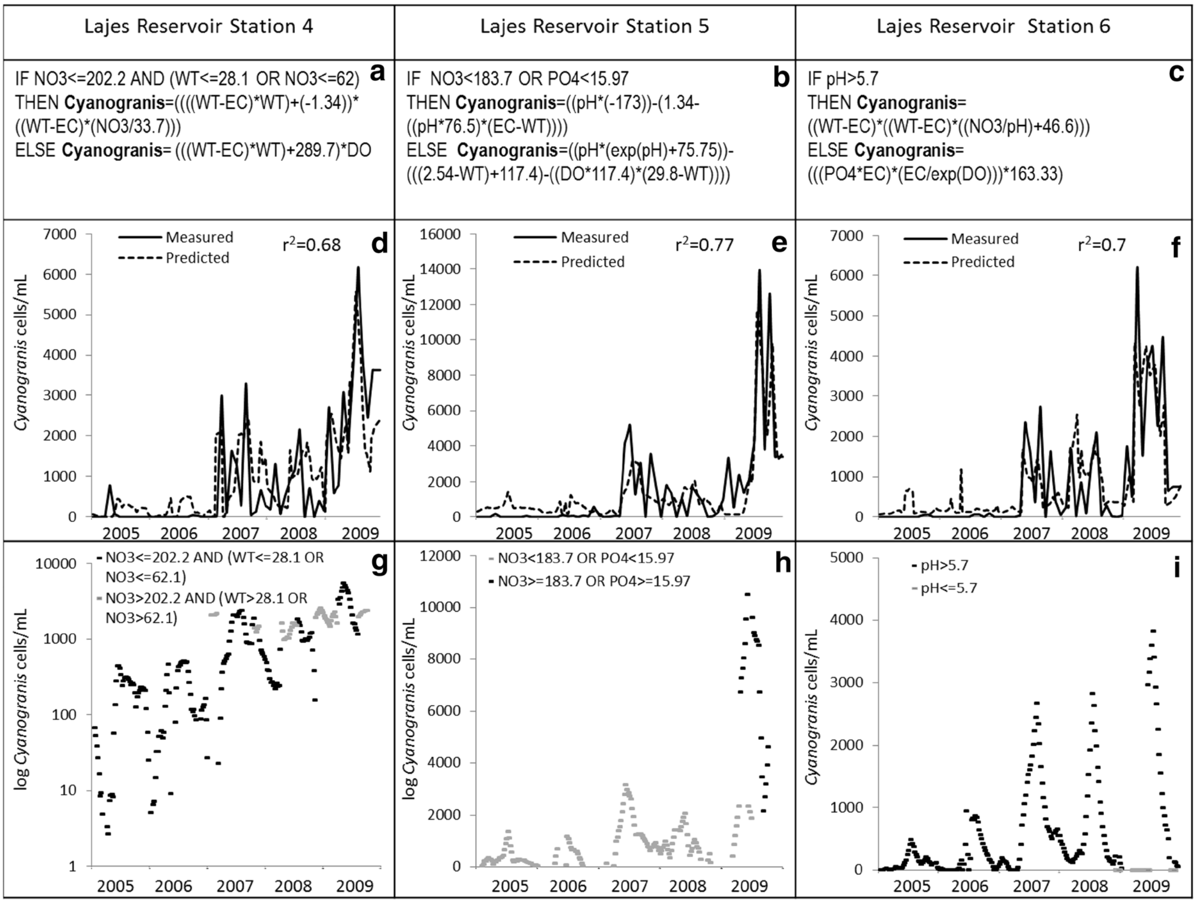


Fig. 6 Seven-Day ahead forecasting models and ecological thresholds for *Cyanogranis* at station 4 (**a**, **d**, **g**), station 5 (**b**, **e**, **h**) and station 6 (**c**, **f**, **i**)

specific conditions, modelling results suggested that nitrate was less important at sampling site 5, where fish-cage farming activities release nitrogen compounds to the water and cause phosphorus limitation. Accordingly, modelling results revealed phosphate concentrations of $PO_4 < 21.05$ µg/l as threshold for the growth of *Synechococcus* at this site. Since *Synechococcus* spp. have a high affinity for orthophosphate, they are favoured in situations of low PO_4 concentration and competitively superior to other algae and bacteria under pulsing supply (Vadstein, 2000; Moutin et al., 2002). This also corresponds with findings of Schallenberg and Burns (2001) that picocyanobacteria can respond negatively to experimental additions of nutrients, particularly of phosphorus.

The prediction of fast growth of *Synechococcus* sp. in Lajes Reservoir is of high importance to inform management for domestic water supply, since only chlorination is applied prior to human consumption. The recommended limit of 20,000 cells ml^{-1} according to Brasil (2011) was exceeded two times at sampling stations 2 and 6 in 2009. Since strains of picocyanobacteria can produce cyanotoxins (Bláha and Marsálek, 1999; Furtado et al., 2009) and may pass through filters of water treatment plants (Callieri et al., 2012), monitoring and early warning of high cell concentrations are crucial for sustainable management of Lajes Reservoir.

This study has confirmed that nutrient concentrations determine fast growth of picocyanobacteria in a mesotrophic tropical lake. Experimental studies of Schallenberg and Burns (2001) have shown that picocyanobacteria respond sensitive to extremely small changes of nutrient concentrations in

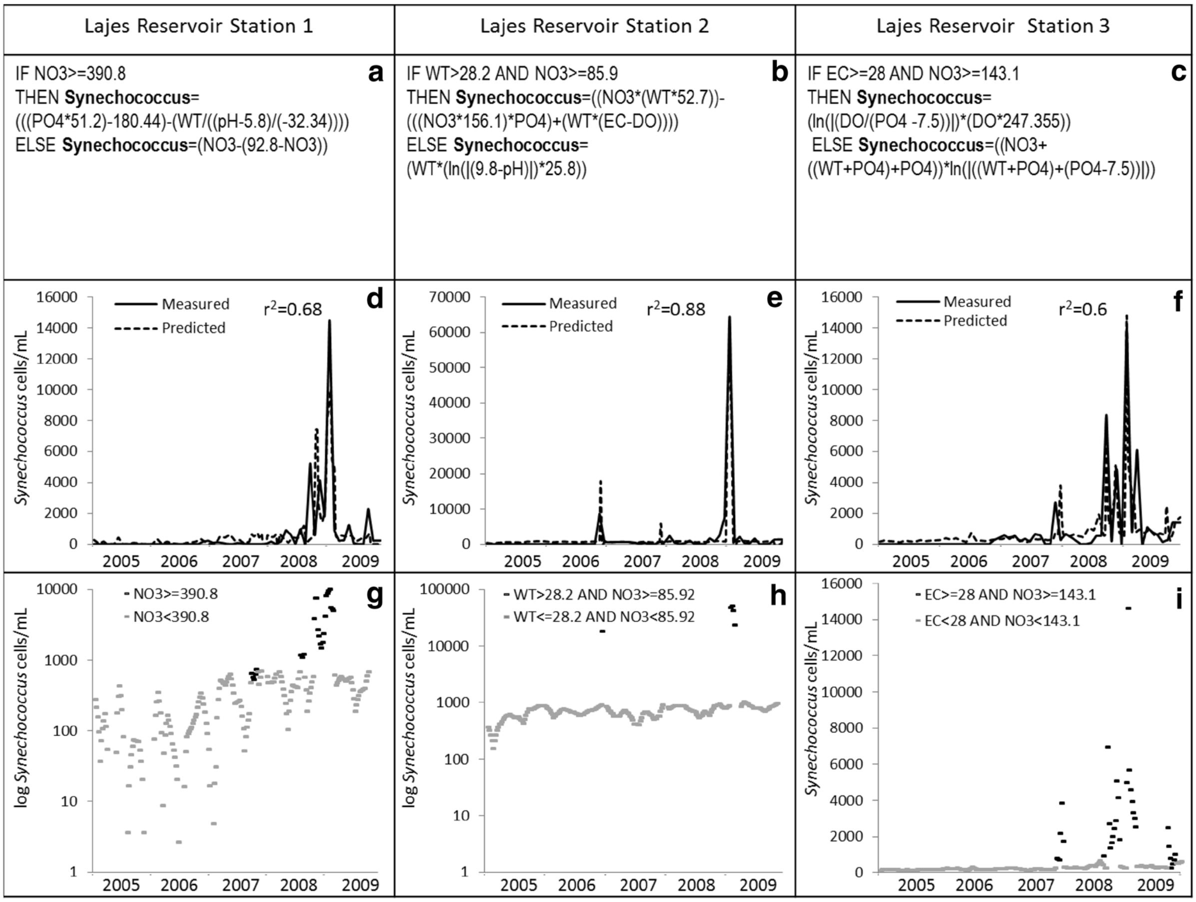


Fig. 7 Seven-Day ahead forecasting models and ecological thresholds for *Synechococcus* at station 1 (**a**, **d**, **g**), station 2 (**b**, **e**, **h**) and station 3 (**c**, **f**, **i**)

oligotrophic lakes. Nutrient uptake rates of picocyanobacteria are high due to their small size, resulting in relative fast growth with doubling times of 1 day in warm lakes (Padisák et al., 1997; Stockner et al., 2000; Schallenberg and Burns, 2001). Population dynamics of picocyanobacteria are also affected by selective grazing by protozoans and rotifers (Callieri & Stockner, 2000, 2002; Callieri, 2007; Callieri et al., 2012), which may explain rapid changes of cell numbers observed for *C. imperfectum, C. ferruginea* and *Synechococcus* sp. in Lajes Reservoir. Therefore, future research will aim at top-down mechanisms of population dynamics of picocyanobacteria by including zooplankton data in predictive and explanatory modelling of Lajes Reservoir by means of evolutionary computation.

Conclusions

The results of this research have shown that

(1) heterogeneously distributed picocyanobacteria in oligomictic tropical lakes with extended water retention times require spatially explicit forecasting models;
(2) 7-day ahead forecasting models induced from limnological data of Lajes Reservoir by the hybrid evolutionary algorithm HEA identified local hotspots for fast growth events of the three picocyanobacteria with good accuracy. Spatially explicit forecasting of fast growth and dispersal of picocyanobacteria will inform the Water Authority responsible for domestic water

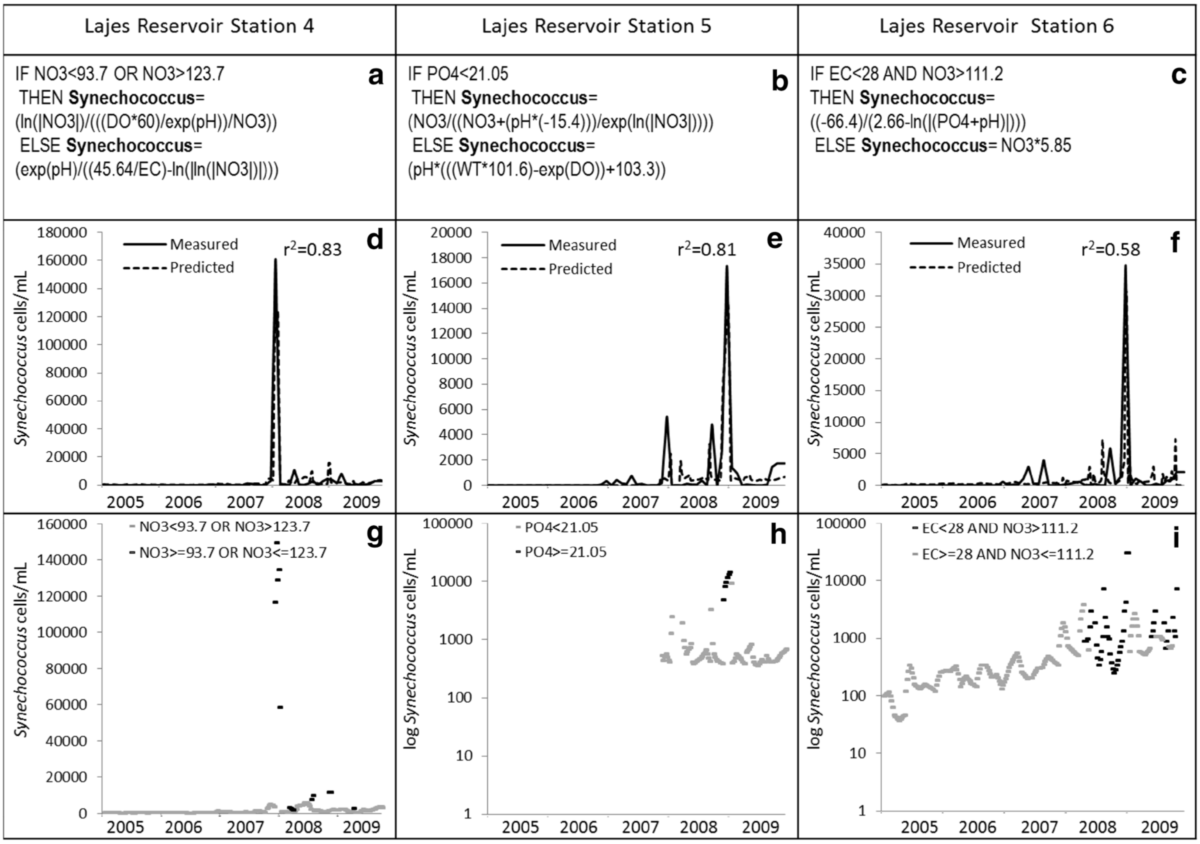


Fig. 8 Seven-day ahead forecasting models and ecological thresholds for *Synechococcus* at station 4 (**a**, **d**, **g**), station 5 (**b**, **e**, **h**) and station 6 (**c**, **f**, **i**)

supply from Lajes Reservoir, since only chlorination is applied prior to human consumption;

(3) the models determined following environmental thresholds and relationships for fast growth events of the three piccocyanobacteria:

(a) nitrate is the main driving force for fast growth of *Cyanodictyon imperfectum, Cyanogranis ferruginea* and *Synechococcus* sp. throughout Lajes Reservoir

(b) the picocyanobacteria showed low sensitivity to changes in phosphate concentrations in the mesotrophic Lajes Reservoir that may suggest that cyanobacteria adopted the sulphur-for-phosphorus strategy by substituting phosphate by sulfolipids at low phosphorus concentrations (Van Mooy et al., 2006)

(c) *Cyanogranis ferruginea* displayed a negative correlation with increasing water temperature possibly indicating its reliance on nutrient supply from lake turnovers and higher competitiveness at low light levels during mixing

(d) *Synechococcus* spp. seemed to be favoured by habitat conditions at site 5 where fish farming release nitrogen compounds and cause phosphorus limitation. It is known for its high affinity for orthophosphate and competitively superior to other algae and bacteria under pulsing supply (Vadstein, 2000; Moutin et al., 2002).

Future research will apply HEA for modelling the impact of inter-specific competition and predation as well as of zooplankton grazing on population dynamics of picocyanobacteria, and will test the newly developed MOHEA (multi-objective hybrid evolutionary algorithm) for spatially explicit forecasting of

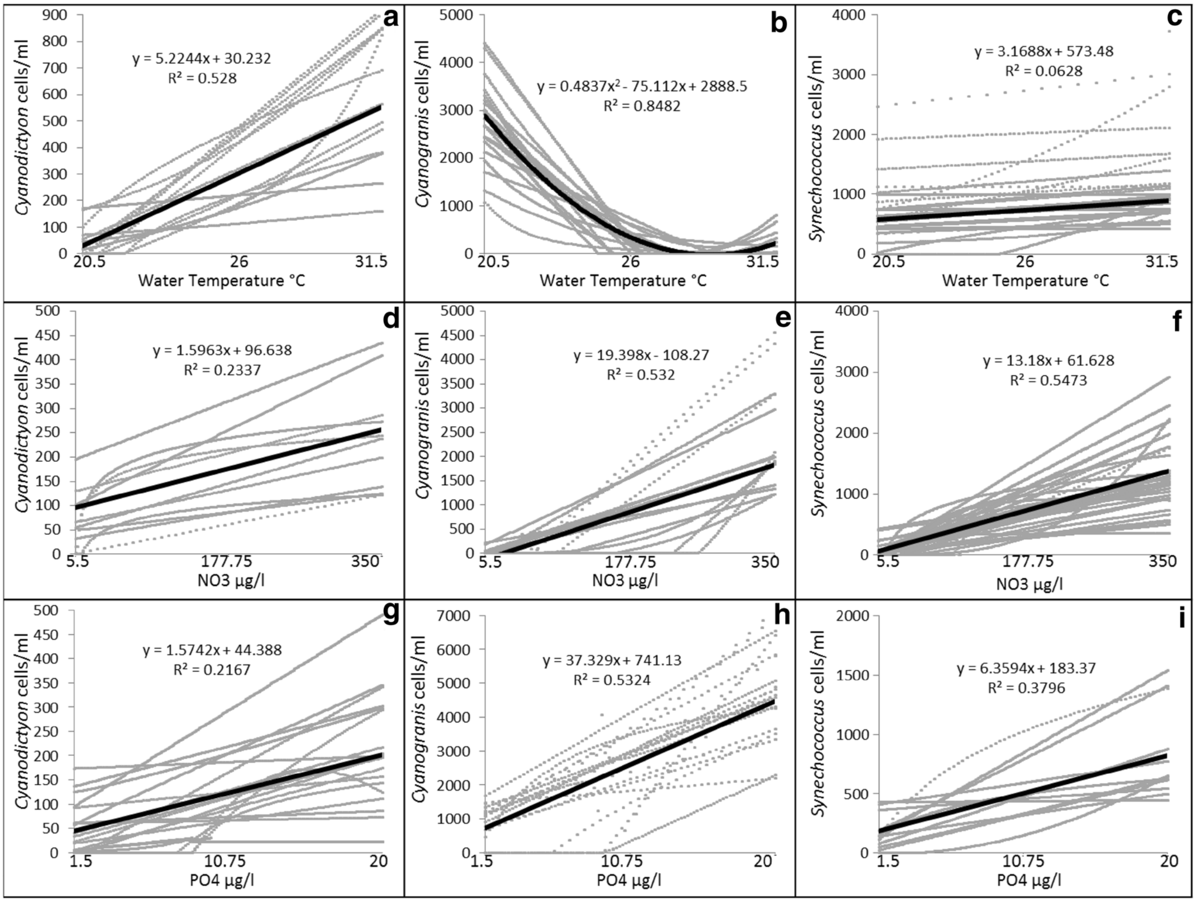


Fig. 9 Relationships between *Cyanodictyon* and water temperature WT (**a**), nitrate NO_3 (**d**) and phosphate PO_4 (**g**), between *Cyanogranis* and WT (**b**), NO_3 (**e**) and PO_4 (**h**) and between *Synechococcus* and WT (**c**), NO_3 (**f**) and PO_4 (**i**) revealed by sensitivity analyses of ten best models of six sites for each cyanobacterium

population dynamics of picocyanobacteria by one model with six outputs for the six sampling sites.

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