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ORIGINAL PAPER

Eutrophication, agriculture and water level control shift aquatic plant communities from floating-leaved to submerged macrophytes in Lake Chini, Malaysia

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Abstract In this study we: (1) present a quantitative spatial analysis of the macrophyte communities in Lake Chini with a focus on the biogeographical distributions of the native *Nelumbo nucifera* and the invasive *Cabomba furcata;* (2) examine the environmental changes that affect plant community composition; and (3) outline a conceptual model of the variation of ecological processes that shape the macrophyte communities. Plant species cover, biomass of *C. furcata* and *N. nucifera,* and water quality and environmental variables were measured before and after monsoonal floods in September 2009 and April 2010. Permutational multivariate analysis was used to examine the significance of the invasion of *C. furcata* at different spatial scales. Relationships between plant species cover and environmental variables before and after flooding were examined using principal coordinates analysis and non-parametric multivariate multiple regressions. Our findings suggest that (1) Variation in plant communities was significant at the lake scale and the distribution of plant species changed after annual floods. (2) Invasion by *C. furcata* significantly affected the overall plant community composition. (3) *C. furcata* biomass increased after the monsoonal season, which indicates that *C. furcata* is adapted to flooding events and that it is becoming increasingly abundant. (4) In addition to the strong monsoonal effect, total depth, nutrient concentration, and sediment type were important environmental variables that significantly affected plant community composition. The macrophyte community in Lake Chini is highly dynamic. The spatial and temporal plant community dynamics are associated with flood regime, water quality, and substrate. Human-induced changes in these parameters are likely shifting the macrophyte dominance from floating-leaved to submerged species.

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Introduction

Floodplain lakes and wetlands are continuously subjected to environmental stressors that affect their plant community composition and structure. Human-induced alterations such as eutrophication have been reported to result in change of dominance from rooted and floating-leaved plants [which typically characterise undeveloped wetlands (Lougheed et al. 2008) and natural environments (Radomski 2006)] to assemblages made up of floating plants and more tolerant emergent species (Lougheed et al. 2008), from submerged plants to emergent species (Egertson et al. 2004) or from submerged plants to floating plants (Bini et al. 1999). Changes in the hydrological regime have also been responsible for transition in wetland macrophyte communities. Van Geest et al. (2005) and Whyte et al. (2008) reported that floodplain lakes along the Lower Rhine and Lake Erie coastal wetlands switched from floating-leaved dominance to emergent-dominance following decline of the water level. In the Murray-Darling Basin, Australia, regulation and damming of the river changed the hydrology of fringing floodplain wetlands and subsequently altered ecological processes that affected macrophyte diversity and species composition (Kingsford 2000).

Infestation of non-native species in such changing environments alters community structure and ecosystem function (Ehrenfeld 2003; MacDougall and Turkington 2005; Farrer and Goldberg 2009) and patterns of succession. The dynamic patterns of vegetation and community succession following transition from a native species assemblage to an invaded community are influenced by site availability and the species differential availability and performance (Pickett and McDonnell 1989). Multiple perturbations, such as nutrient enrichment and alteration of food-web structure, reduce ecological resilience, alter feedback mechanisms, and may subsequently induce a sudden shift of dominance (Carpenter and Cottingham 1997; Folke et al. 2004). Understanding the key mechanisms that drive shifts of plant community dominance is crucial to facilitate management and restoration success.

This study reports the plant community alteration that has occurred in a tropical floodplain wetland system, Lake Chini, Malaysia, in response to a shift in plant species dominance from a floating-leaved species (*Nelumbo nucifera*) to a submerged species (*Cabomba furcata*), as previously observed by Shuhaimi-Othman et al. (2007). The appearance of *C. furcata*, a non-native species, was first reported in 1998 (Wetland International 1998) and its abundance was noted to have spread to other lakes within the wetland basin in 1999 (Gan and Bidin 2005). It has currently reached infestation proportions (Chew and Siti-Munirah 2009) and is severely impacting on the natural and cultural heritage values of the wetland. What has triggered this infestation and shift of plant community dominance away from the once stable *Nelumbo* community is not known. Unfortunately, past studies of the plant communities in Lake Chini were not based on quantitative data, which hinders the understanding of how the changes in the macrophyte community composition and structure relate to variability in environmental properties. This is compounded by limited hydrological and water quality data available from which to build a baseline understanding of the system. To the authors' knowledge, there is also no specific research that has been carried out elsewhere in the world on the change of dominance between *Nelumbo* and *Cabomba* species. Clearly, a thorough understanding of different plant response to ecological changes needs to consider alterations to key environmental attributes that characterise the ecosystem. It is therefore the aim of this paper to: (1) to present a quantitative spatial analysis of the macrophyte communities in Lake Chini with a focus on the biogeographical distributions of *N. nucifera* and *C. furcata;* (2) to examine the environmental changes in Lake Chini that may affect the plant community composition; and (3) to outline a conceptual model of the variation of the ecological processes that shape macrophyte distribution to assist in management of Lake Chini to meet conservation goals. The work is based on review of data from the available literature and a comparative analysis of baseline ecological survey work conducted in September 2009 and April 2010.

Study area

Lake Chini is the second largest freshwater lake in Malaysia. It is a small ($\sim$2 km^2) alluvial riparian

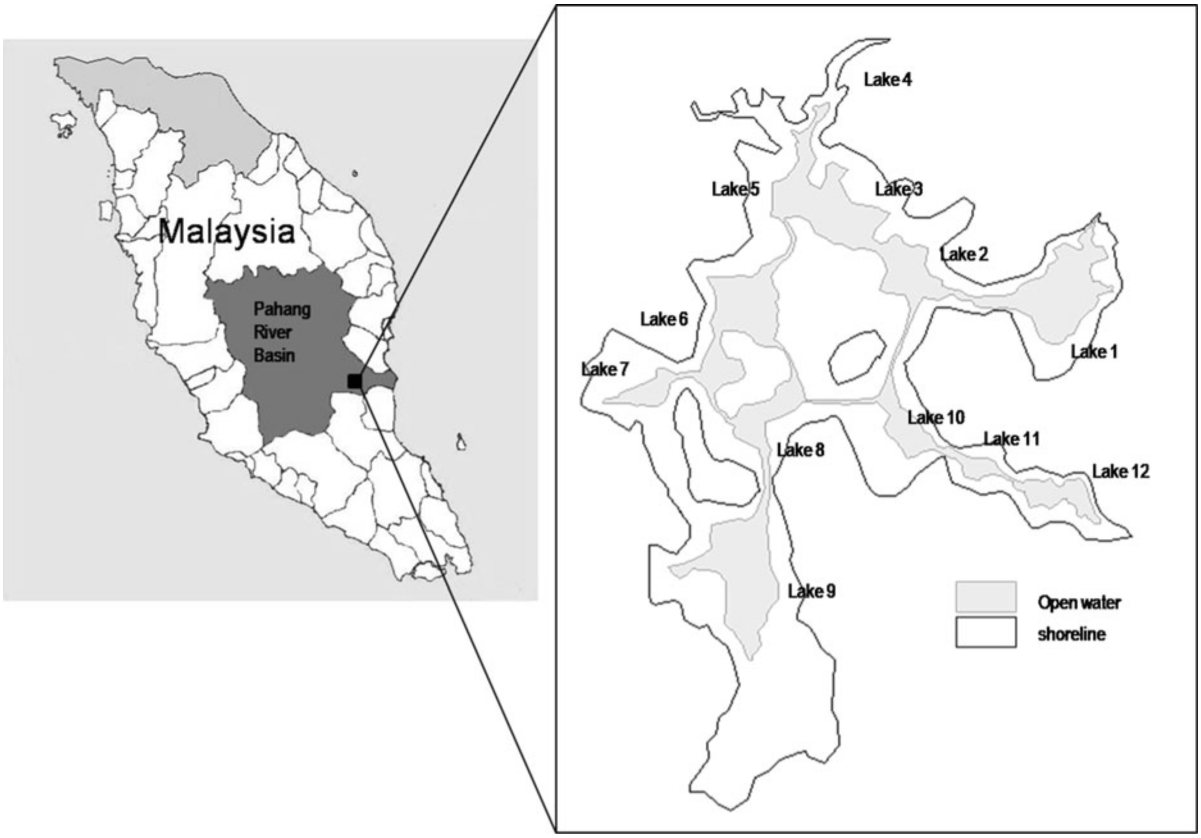

Fig. 1 Location of Lake Chini in peninsular Malaysia with inset showing the lake system. Lake outlet is located between Lakes 4 and 5

swamp system that is located within the Pahang River floodplain (Fig. 1). The lake is comprised of 12 small lakes that are inter-connected by natural channels. Due to its close proximity to the main river, the lake's size and depth changes significantly seasonally, remaining shallow (mean depth around 2 m) during the dry period throughout most of the year and expanding to double its normal size during the monsoon months (Nov–Jan). Extensive beds of floating-leaved and emergent macrophytes form an important feature of the lake, and similar to other wetlands, account for a large proportion of the total primary production (Ikusima and Furtado 1982). *N. nucifera* once covered a substantial part of the surface water and large blooms of its lotus flower led to the lake becoming a tourist attraction. Due to its ecological importance and ecotourism value, Lake Chini was designated as a UNESCO Biosphere reserve in 2009. However, the extensive presence of *C. furcata* in Lake Chini in 2007 disrupted navigation and has since diminished its tourism potential (Chew and Siti-Munirah 2009). There is a need to understand the factors that influence the differences in macrophyte dominance in order to rehabilitate and manage Lake Chini's environment for eco-tourism purposes, and concomitantly retaining its ecological diversity.

Alteration of the land use in both the catchment and the lake environment, facilitated by socio-economic pressure over the past 20 years, has affected the lake ecosystem. Logging and conversion of forested area to agricultural land has increased (Shuhaimi-Othman et al. 2007), and such practices are known to affect hydrological processes (Bruijnzeel 1991). In 1995, a weir was constructed at the downstream end of Chini River, at the confluence of the Chini and Pahang Rivers, in order to maintain higher lake water levels for year-round navigability (Shuhaimi-Othman et al. 2007). This altered the natural flood pulse and pattern of water level fluctuation and may affect the macrophyte community structure.

Study organisms

Nelumbo spp. and *Cabomba* spp. come from different life form groups which differ in structure, morphology, physiology, and habitat (Schulthorpe 1967; Cooke et al. 2005), and subsequently their adaptation to the environment. *N. nucifera* is an Asiatic floating-leaved plant that is native to Malaysia (Schulthorpe 1967). *N. nucifera* and its American relative, *Nelumbo lutea*, comprise the only two species in the family Nelumbonaceae. They have roots and rhizomes in the sediment, connected by petioles to floating and emergent leaves (Cronk and Fennessy 2001). Rapidly growing petioles, attached in the middle of the leaf blade, allow the leaves to rise with increasing water levels (Nohara and Tsuchiya 1990). *Nelumbo* spp. grows well at depths of 1.5–2 m (Schulthorpe 1967; Baldina et al. 1999) up to a maximum depth of approximately 3 m (Unni 1971; Kunii and Maeda 1982). They can grow in both acidic and alkaline water (Meyer 1930). They absorb nutrients from sediment and propagate by seeds and rhizomes. The preferred substrate is benthic soil comprised of mainly gray, loamy mud (Kunii and Maeda 1982).

In contrast, *Cabomba* is a genus of submerged macrophytes consisting of five species that originate from the Americas (Orgaard 1991). Several species in the genus have been introduced to water bodies around the world and the distribution exhibits a wide latitudinal range from cold temperate to tropical waters (Schooler et al. 2009). As for most introduced *Cabomba* populations, *C. furcata* was probably introduced to Malaysia through the aquarium trade (Orgaard 1991) and has become naturalised in Lake Chini within the last decade (Chew and Siti-Munirah 2009). *C. furcata*, in its native range, grows in an environment that experiences fluctuating water levels, from dry periods to periods of high water levels (Orgaard 1991). It commonly grows rooted at 2–3 m water depth (Orgaard 1991), although *Cabomba caroliniana* has been found rooted at depths up to 6 m (Schooler and Julien 2006). It grows well in acidic water, preferably at pH 4-6 (Sanders 1979; Orgaard 1991). *Cabomba* spp. uptake nutrients directly from the water through shoots, leaves, and stems (Wilson et al. 2007) and have been observed to grow well in nutrient rich water (Oki 1994). *Cabomba* spp. can also exist in turbid water (Sanders 1979), prefer fine and soft substrates, and primarily propagate through vegetative reproduction by means of stem fragmentation (Schooler et al. 2009).

Methods

Overview

In order to assess changes within the Lake Chini catchment, data on land use and surface phosphate concentration were collected from the available literature (Division of Agriculture 1966; DARA 1992 unpublished data; Shuhaimi-Othman et al. 2007). Data on adjacent land use were available in the literature from 1966 to 2007 while data on surface phosphate concentration were available from 1998 to 2007. Water level data were obtained from the Drainage and Irrigation Department of Malaysia and the National Hydraulic Research Institute of Malaysia. Hydrological records were available from 2007 to 2010. Field measurements were carried out at Lake Chini on 26–28 September 2009 involving a survey of plant community abundance and composition and measurement of water quality and sediment properties. Twelve main stations were selected at each lake for intensive water quality and sediment sampling. Similar plant abundance and water quality surveys were undertaken on 12–14 April 2010 to examine the after-effect of the monsoonal flood on the abiotic variables and biotic communities.

Plant community sampling

The abundance of aquatic plant species within the lakes was assessed as plant cover. Plant cover was visually estimated from a boat by an experienced observer within 1 m^2 quadrats at each site along 2–4 transects within each lake. Two quadrats were recorded at each site. Three to five sites were assessed in each transect, depending on the transect length which ranged between 70–500 m. Transect positions were randomly selected, beginning in the centre of each lake, and arranged perpendicular to the shoreline. The coordinates for each site were marked using Garmin GPSMap 60 model CSx (Garmin International, Kansas, USA) and downloaded into the Garmin MapSource® mapping software version 6.13.7. The surveyed positions were overlaid on a satellite image (IKONOS 2006) using GIS software (Arcview ver.

3.3, ESRI, Redlands, CA, USA). Specimens of plant samples were sent to the local herbarium (Forest Research Institute of Malaysia and UKMB) for taxonomic identification.

Biomass measurements of *C. furcata* and *N. nucifera* were carried out where dense beds of the respective plants grew along gradual slopes. One transect was selected at each aquatic plant bed, where the quadrats were haphazardly positioned through these beds, beginning at the shoreline and extending to the centre of the lakes. Using SCUBA, three samples were taken, first at 0.25 m, then at each successive 0.5 m depth increment, from 0.5 m to either: (a) the depth where the plants no longer grew or (b) the deepest point in the lake. Plant samples were collected using a quadrat (0.25 m^2), then washed and coiled, and placed into individual plastic bags. The plants were then stored in cool container, and transported to the laboratory within 24 h. Plant samples were dried to constant weight in a drying oven at 103°C and the dry weights were recorded to 0.01 g.

Environmental variables

In situ profiles of temperature, pH, dissolved oxygen (DO), turbidity, specific conductivity and depth were taken at all surveyed sampling points using a YSI 6600 multi-parameter sonde. Water samples were collected using a Van Dorn sampler at 12 main stations located around the centre of each lake at 2-depths (surface and bottom levels). Additional samples were taken near the surface at selected sites having dense macrophyte beds, mainly either *C. furcata* or *N. nucifera*. Water samples were analysed for phosphate (PO_4^{3-}), ammonium (NH_4^+) and nitrate (NO_3^-) in accordance with standard methods (APHA 1992). All the water samples were placed in a cooler box (temperature $\leq$ 4°C) and transported to the laboratory within 24 h. Sediment samples were collected using a Van Veen Grabber, stored in a transportation box, and sent to the laboratory for sediment texture analysis (British Standards Institution 1990). An additional distance measure, the distance from the centre of each lake to the weir, was obtained from the coordinates and the satellite image. Distance from the weir was ranked prior to analyses.

Statistical analysis

To provide a quantitative spatial analysis of the macrophyte communities in Lake Chini, we first used non-metric multidimensional scaling (NMDS), based on the Bray–Curtis dissimilarity matrix (Clarke 1993) to visualise multivariate patterns among the plant species cover within the 12 lakes, across the two seasons. To extract meaning from the axes produced in NMDS, we performed principal coordinates analysis (PCoA) in PERMANOVA to correlate environmental variables with the ordination axes (Anderson and Willis 2003; Anderson et al. 2008). In this analysis, we used Pearson correlation to highlight linear relationships between individual variables across the plot. Principal component analysis (PCA), which projected samples to maximise their variance, was applied to reduce the number of observed variables and summarize the pattern of the correlation between total depth, temperature, pH, dissolved oxygen, turbidity, conductivity, phosphate, nitrate, ammonium, %silt/clay content and rank distance from weir. NMDS and PCA were based on lake averages. We then used linear regression to illustrate the relationship between *C. furcata* cover and diversity. The Shannon–Weiner Index of Diversity, calculated from mean lake abundance (cover) in September and April, was used as the measure of plant diversity.

A hierarchical experimental design composed of three factors, i.e. Lake (L: fixed), transect (T: random, nested in L) and site (S: random, nested in L and T) and percent *C. furcata* cover as covariate was used to characterize the effects of invasion by *C. furcata* on the macrophyte community composition in Lake Chini. Permutational multivariate analysis of variance, PERMANOVA (Anderson 2001a; Anderson et al. 2008) was performed on a basis of zero adjusted Bray–Curtis dissimilarity matrix (Clarke et al. 2006) for the rest of the other species cover dataset to test whether invasion by *C. furcata* significantly affected plant community composition at the spatial scale of lake, transect and site. To prevent pseudo-replication, site averages were used for all multivariate analyses. The complex nature of the wetland morphology and the subsequent plant assemblages and hydrological restriction during our study led to an un-balanced replicated study design. All the analyses were performed separately for data collected in September 2009 and April 2010, which characterise the community assemblages before and after the monsoon season, respectively.

Nonparametric multivariate multiple regression, DISTLM was employed to model the relationship between the multivariate species matrix and the 11 environmental variables. The individual variable was initially examined in the marginal test (excluding other variables) and then subjected to a forward selection procedure (BIC selection criterion) with sequential tests to determine the predictor variables that explain the variation in the data. Significance was performed by 9,999 permutations of residuals under the reduced model (Anderson 2001b).

Wilcoxon Signed Rank Tests were performed to determine significant differences between biomass harvested in September and April. Plant cover data were square-root transformed, while biomass values and the water quality variables were natural log transformed to improve normality. All Wilcoxon Signed Rank Tests were performed in SPSS 16.0 (SPSS Inc.). Multivariate methods (NMDS, PCA, PCO, PERMANOVA and DISTLM) were conducted in PRIMER 6 (Plymouth Marine Laboratory, Plymouth, UK) and PERMANOVA + (Plymouth Marine Laboratory, Plymouth, UK).

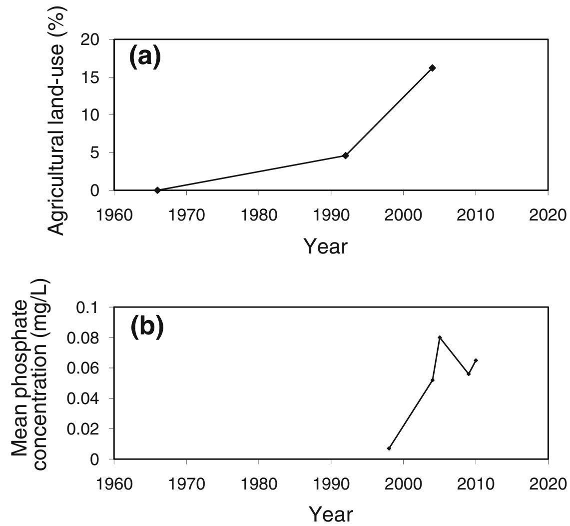

Fig. 2 Historical changes in **a** agriculture land use fraction and **b** mean phosphate concentration (mg/l) at the water's surface. Phosphate concentrations from 2009 and 2010 were taken during the present survey. Historical data sources are listed in the methods

Results

Catchment and hydrological changes

Landscape changes within the Lake Chini catchment were apparent, changing from a forested area in 1966 (Division of Agriculture 1966) to agricultural land with patches of deforestation. Agricultural practices in the form of oil palm plantations and rubber estates accounted for only 280 ha (5.6%) of the catchment area in 1992 (DARA 1992 unpublished data) and this increased to a total of 807 ha (16.2%) in 2004 (Shuhaimi-Othman et al. 2007) (Fig. 2a). Increased water surface phosphate concentration was evident, from average of 0.01 mg/l in 1998 to around 0.06 mg/l in 2010 (Fig. 2b). A decrease in surface phosphate between year 2008–2010 could be associated to flushing of nutrient from the lake by a large flood event in 2007.

Historical data on water levels (Fig. 3) showed the influence of the Pahang River on Lake Chini surface water level during monsoon months. The variability of the lake water level in relation to fluctuation of the river water level was reduced by the weir structure with the lake level increasing slightly with the Pahang River level. Further rise in Pahang River level inundated the wetland and subsequently increased the lake surface level.

Spatial distribution of aquatic plants

A total of 17 plant species, native and non-native, were recorded from the 137 surveyed sites over the 12 lakes (Table 1). We found that *Pandanus helicopus*, *C. furcata*, *N. nucifera*, *Scirpus* spp. and *Lepironia articulata* are the most abundant species in the lake system. Comparison between prior surveys of macrophyte diversity in the literature and the present survey indicate the presence of previously undetected species (see Table S1 in supporting information).

Cabomba furcata and *N. nucifera* coverage differed between the 12 lakes (Figs. 4, 5). *C. furcata* remained widely established in the absence of *N. nucifera* in Lake 12 and Lake 10, and appeared in another lake (Lake 3), where it was previously not found during the September (pre-flood) sampling. The *N. nucifera* population has increased in all lakes where it was present in 2009, and in particular in lakes that were located closer to the Pahang River. Diversity in lakes decreased with increasing *C. furcata* abundance (Fig. 6) in September ($t_{12} = 10.276$, $P < 0.001$).

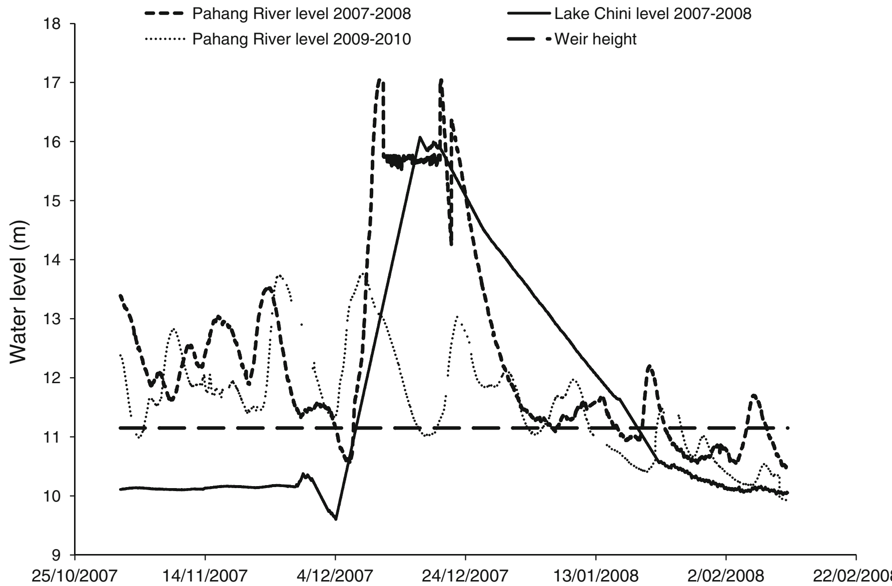

Fig. 3 Comparison between the Pahang River level and Lake Chini water level. Both water levels were approximately referred to mean sea level

Table 1 List of macrophytes recorded in the present survey

Species (scientific name)	Lake											
	1	2	3	4	5	6	7	8	9	10	11	12
Submerged macrophyte												
Cabomba furcata[a]	+		+		+	+	+	+	+	+	+	+
Utricularia gibba				+	+	+	+	+	+	+	+	+
Chara sp.												+
Floating macrophyte												
Salvinia molesta[a]				+								
Rooted, Floating-leaved												
Nymphea pubescens lotus			+		+					+		
Nelumbo nucifera	+	+	+		+	+	+	+	+			
Emergent												
Lepironia articulata	+	+	+			+	+	+	+	+	+	+
Eriocaulon sexangulare				+								
Scirpus grossus	+	+	+	+		+		+			+	
Pandanus helicopus		+	+	+		+	+					+
Eleocharis ochrostachys										+	+	+
Lycopodiella cerniea (cernua)				+								
Cyperus pilosus				+								
Pragmites communis			+		+							
Lygodium microphyllum				+								
Panicum Repens	+		+	+	+	+	+	+	+		+	+

[a] Introduced species

The PERMANOVA detected significant variability at the "lake" spatial scale. The factor "transect" and "site" were pooled since they were the factors with negative estimates for component of variance and a higher *P* value (Anderson 2001b; Anderson et al. 2008). PERMANOVA tests (Table 2) showed that

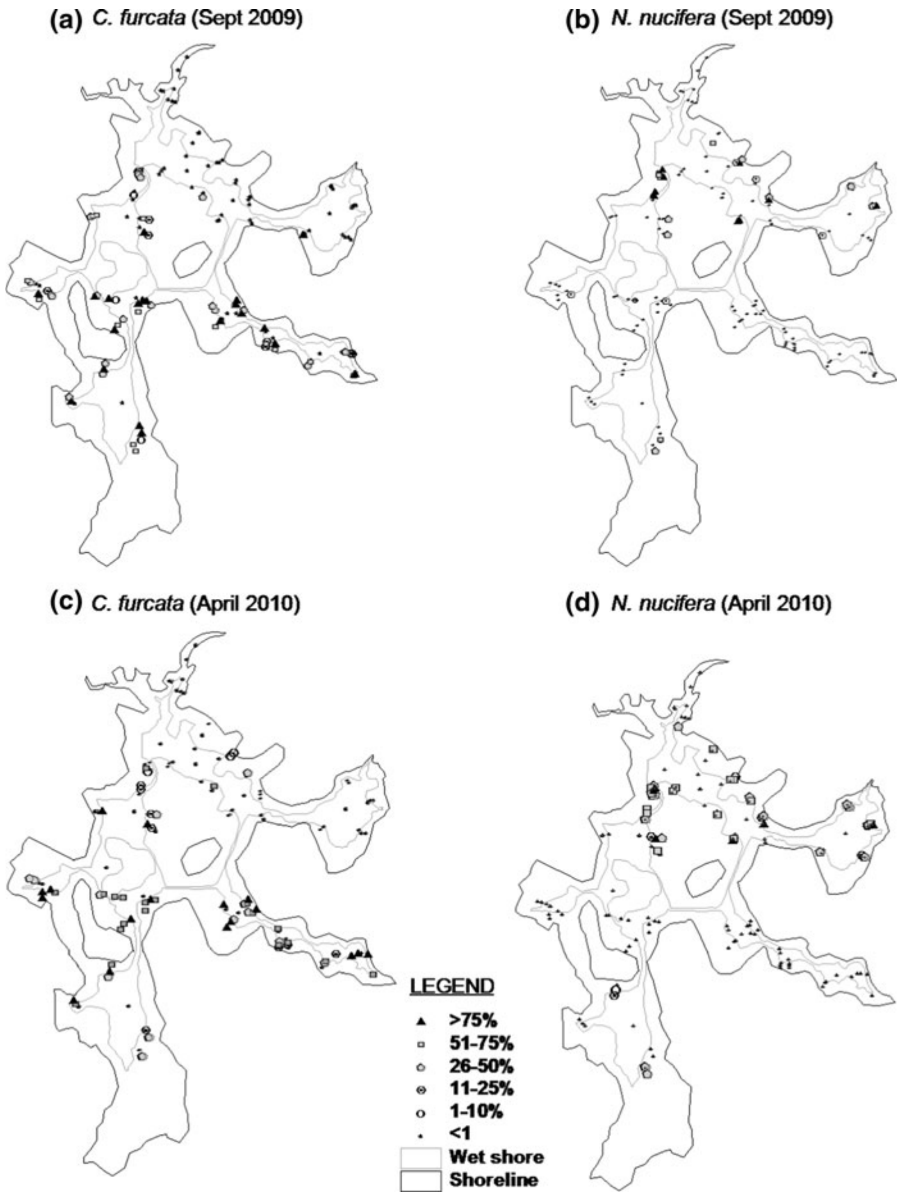

Fig. 4 Comparison of *C. furcata* and *N. nucifera* coverage before and after monsoonal flooding

differences between invaded and un-invaded plant assemblages were highly significant, both in September and April. Differences in the composition of invaded and un-invaded sites were stronger in September compared to April, indicating the effect of the monsoonal flood on the macrophyte community composition.

Mean *C. furcata* biomass from both sampling periods was correlated with depth ($r = -0.773$, $P = 0.042$; Fig. 7). A Wilcoxon Signed Rank Test indicated an increase in biomass from Sept to April; $z = -2.201$, $P = 0.028$ (two-tailed). The magnitude of differences in the means was large and the median score on the biomass increased from Sept (15.1 g/m^2) to April (318 g/m^2). The highest *C. furcata* and *N. nucifera* biomass were sampled in April at depth of 0.5 and 1.5 m with biomass 934.7 g/m^2 and 62.7 g/m^2 respectively.

Environmental variables potentially influencing macrophyte distribution

PCA, employing Euclidean distance, indicated a consistent linear combination of variables making up

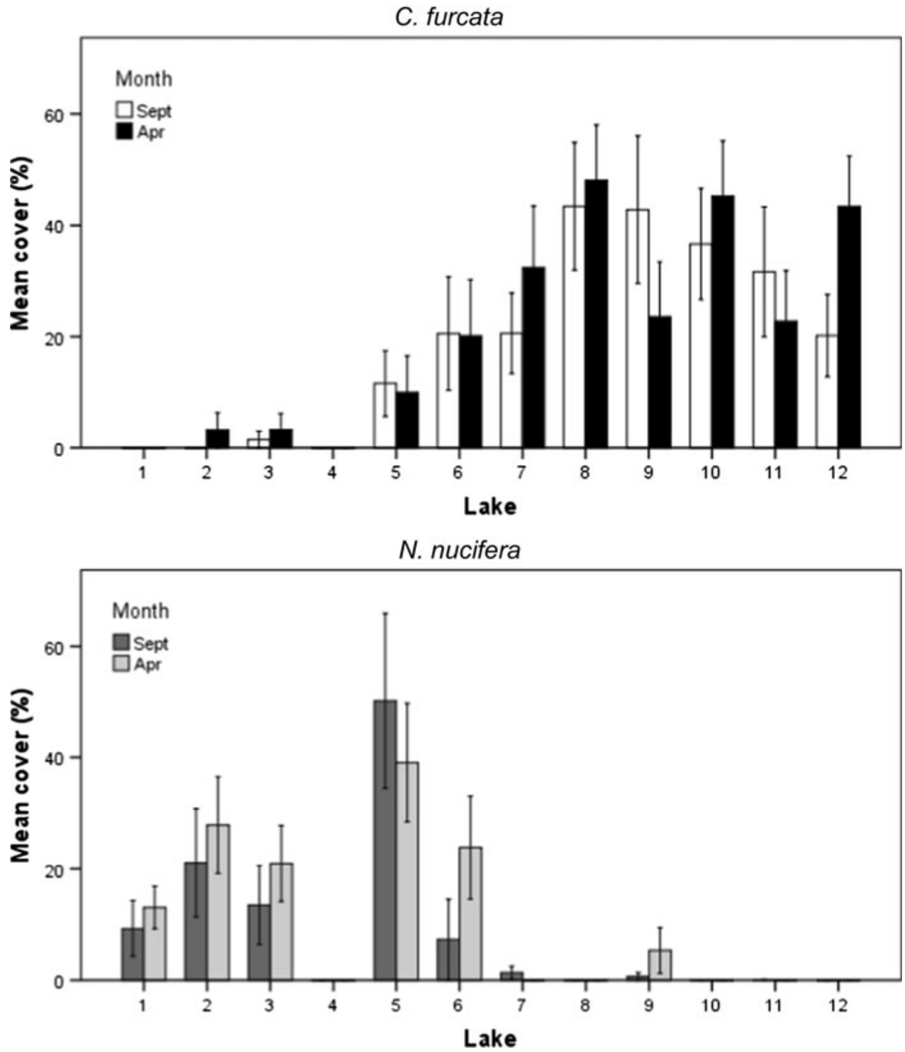

Fig. 5 Mean cover of *C. furcata* and *N. nucifera* by lake and by sampling date. *Error bars* are ±SE

the principal components. The first three eigenvalues explained 69% of the variance; the first component corresponded to 34% variance and second component explained 20% of the variance. Plots of the first two components showed separation of the dataset before monsoon to the dataset after the monsoon, which indicated the influence of flooding on the water quality (Fig. 8). The separation of sites by sampling date along axis 1 was primarily correlated with nitrate concentration and total depth and along axis 2 was correlated to phosphate, turbidity and pH.

The results of DISTLM tests (Table 3) reveal a positive match between the environmental variables and species assemblages in the Lake Chini dataset. Total depth explained ~42.6% of the variation in the composition of the plant assemblages in September 2009 and 26.5% of the community variation in April 2010. Phosphate, temperature, nitrate, %silt/clay and conductivity contributed a further 26.2% of the variance in September 2009, while distance from weir, dissolved oxygen, ammonium and temperature together explained about 24% of the variance in April 2010.

The phosphate concentrations sampled in all areas having dense *C. furcata* and *N. nucifera* beds were very low (non-detectible) in September, while in April, nitrate concentrations were low in the plant beds (Fig. 9). PCoA results indicate sites where *C. furcata* was present were trending toward lakes having a higher silt/clay percentage and increasing distance from the weir, whereas *N. nucifera* was found in lakes having lower silt/clay content (Fig. 10).

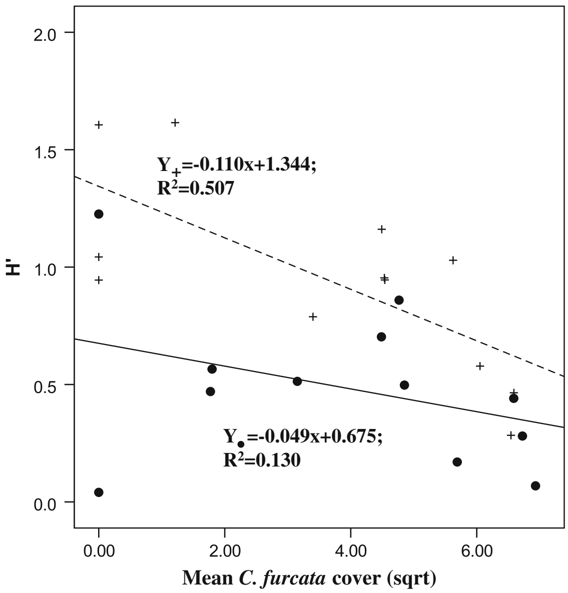

Fig. 6 Regression of *C. furcata* cover against Shannon–Weiner Diversity Index (H'). *Symbols* indicate sampling month: *plus* September, *circle* April

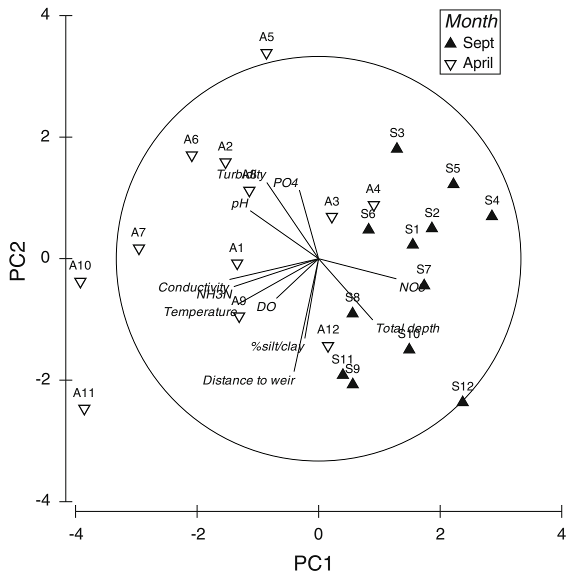

Fig. 8 PCA biplots of the average values of the environmental variables by sampling month. *Number* indicates lake

Table 2 Permutational multivariate analysis of the effects of invasion, lake, transect and site on plant community abundance

PERMANOVA tests					
Source of variation	*df*	SS	MS	F	*P* (perm)
September 2009					
Invasion	1	19,590	19,590	12.475	0.0001***
Lake	11	46,222	4,202	2.676	0.0001***
Pooled	134	210,430	1,570.3		
Total	146	276,240			
April 2010					
Invasion	1	13,991	13,991	11.202	0.0003***
Lake	11	50,843	4,622.1	3.701	0.0001***
Pooled	134	167,370	1,249		
Total	146	232,200			

df degree of freedom, *SS* sum of squares, *MS* mean squares

*** $P < 0.001$

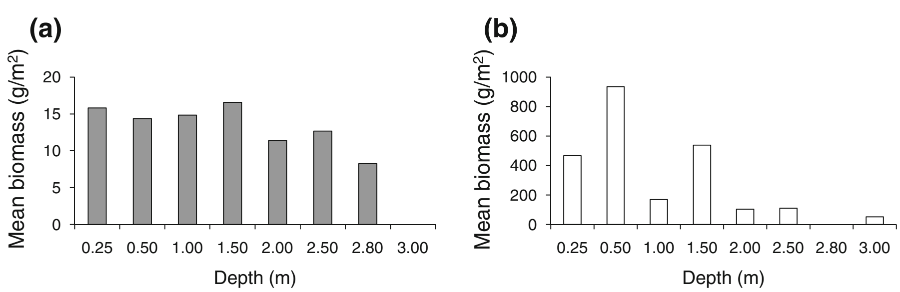

Fig. 7 Relationship between depth and mean *C. furcata* biomass. Biomass is the mean dry weight sampled in all quadrats at that depth. **a** Mean *C. furcata* biomass in Sept 2009. **b** Mean *C. furcata* biomass in April 2010

Table 3 Results of the DISTLM analysis on the Lake Chini dataset in September 2009 and April 2010

Sequential tests					
Variables	BIC	Pseudo-F	*P*	% Var	%Cum
September 2009					
+Log(Total depth + 1)	418.50	42.957	0.0001***	42.55	42.55
+Log(PO_4 + 1)	416.35	6.2481	0.0019**	5.68	48.23
+Log(Temperature + 1)	411.99	8.4811	0.0003***	6.81	55.04
+Log(NO_3 + 1)	410.58	5.2837	0.006**	3.94	58.98
+%silt/clay	408.41	5.9403	0.0039**	4.07	63.04
+Log(Conductivity + 1)	402.51	9.6054	0.0001***	5.67	68.71
April 2010					
+Log(Total depth + 1)	438.49	20.917	0.0001***	26.505	26.51
+Rank distance to weir	435.97	6.6387	0.0008***	7.667	34.17
+Log(DO + 1)	435.90	4.0264	0.0151*	4.416	38.59
+Log(NH_4 + 1)	434.72	5.0482	0.004**	5.163	43.75
+Log(Temperature + 1)	431.25	7.2604	0.0008***	6.667	50.42

BIC Bayesian information criterion, %Var percentage of variance in species data explained, %Cum cumulative percentage of variance explained

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

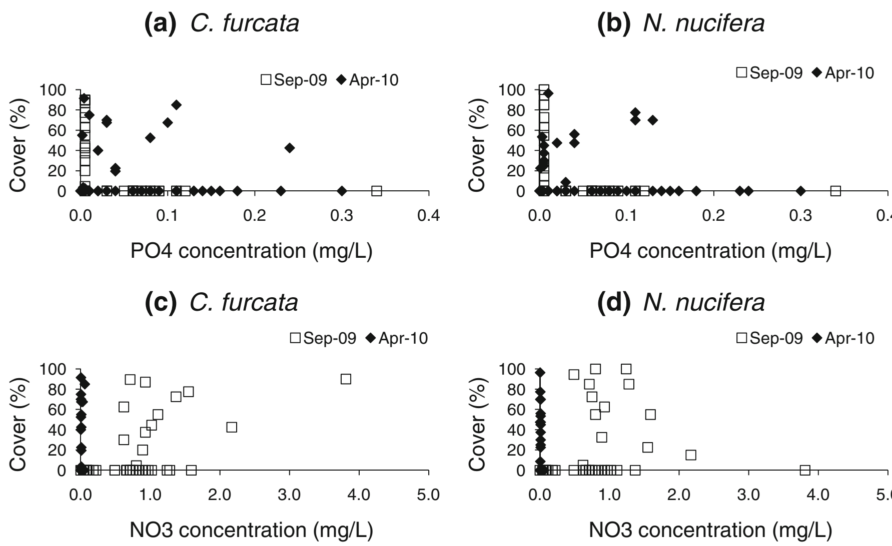

Fig. 9 Relationship between dominant species cover and phosphate and nitrate concentration

Discussion

Similar to other lakes and wetlands around the world, human land-use practices to address socio-economic needs are affecting Lake Chini, resulting in alteration of habitat and biotic communities. The results of this study document landscape and water quality changes in Lake Chini. Change in the surrounding terrestrial landscape from forested areas to agricultural land has altered runoff quantity and quality, and in particular has increased nutrient input into the lake and the suspended sediment load and subsequent deposition. Hydrological alteration further induces ecological changes by stabilising the lake water levels, reducing the flood disturbance regime, and affecting the flood timing and duration (Nilsson and Svedmark 2002).

Spatial variation in the abundance and distribution of the studied plant species between the lakes was

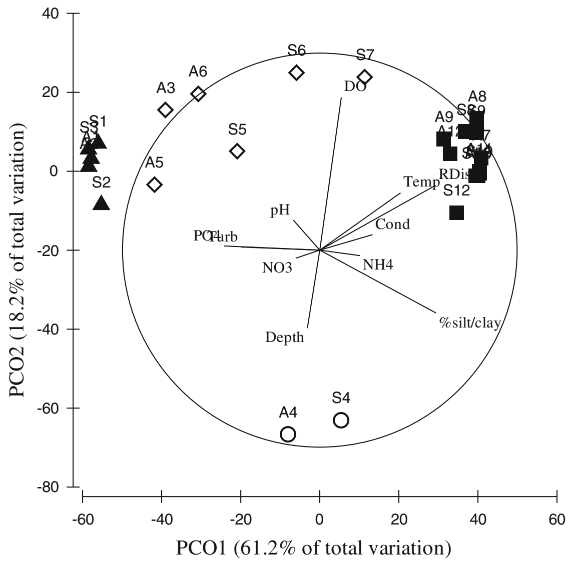

Fig. 10 PCoA plot of plant species abundance and environmental variables. *Symbols* represent main species: *triangles*, *N. nucifera*; *diamonds, N. nucifera and C. furcata*; *squares, C. furcata*; *circles*, other species. *Number* indicates lake; *Letter* indicates sampling month: *S* September, *A* April. Water quality variables were natural log-transformed

apparent. The cover of *C. furcata* observed in September 2009 was lower compared to observations in 2007 (before the intermediate size flood event; Sharip, personal observation; Chew and Siti-Munirah 2009; Sharip and Jusoh 2010). However, both cover and biomass increased from September 2009 to April 2010 which indicated that it may be in the process of re-spreading. Dissimilarities between lakes within invaded and un-invaded sites could result from the complex interaction among different ecological drivers and ecological processes that dominate during the different seasons. This invasion is having a significant impact on the overall plant community diversity. Early growth phase after seasonal disturbance could explain the weak correlation between *C. furcata* abundance (cover) and diversity in April. Increased *C. furcata* biomass after the monsoonal season indicates that the plants survived from the previous year and then grew rapidly, probably due to the availability of resources during and after the floods. The sustained growth of such invasive species could affect the plant community structure and reduce the establishment of other species (Santos et al. 2011).

The spatial and temporal variation of water quality parameters described here are consistent with the results of prior studies that examined the water quality in Lake Chini (Shuhaimi-Othman et al. 2007). The nutrient levels were high, suggesting that nutrient enrichment is a concern and may have a strong impact on the composition of the plant community and the population dynamics of *C. furcata* and *N. nucifera* in Lake Chini. The mean phosphate concentration in Lake Chini was high in both sampling months. (Shuhaimi-Othman et al. 2007) suggest that the increase in phosphate concentration at Lake Chini is attributed to run-off from agriculture areas and settlement (Shuhaimi-Othman et al. 2007). Trace values of phosphate in areas where *C. furcata* was abundant suggest that it may have been consumed by the plants. Studies have shown *Cabomba* spp. absorb nutrients directly from the water through shoots, leaves, and stems (Wilson et al. 2007) and nutrient rich water may have promoted high *C. furcata* abundance in Lake Chini. There was a decreasing trend of phosphate concentration from pelagic to littoral regions in September, while in April, the decreasing trend from pelagic to littoral regions was apparent for nitrate concentration. Physical processes that control the exchange of these constituents from the pelagic to the littoral zone should be further investigated, since differential temperature gradients between the zones were noted and may control nutrient delivery to dense *C. furcata* beds. In addition, the switch from detectable nitrate and undetectable phosphate in September, before the monsoonal floods, to undetectable nitrate and detectable phosphate after the floods in dense macrophyte beds suggests a change in nutrients limiting macrophyte growth.

A change in sediment characteristics in Lake Chini was apparent with increased silt content compared to earlier findings (Abas et al. 2005). Deposition of silty materials is most likely enhanced from run-off and erosion from an increasingly cleared catchment. An increase in silt content in the substrate makes the site more suitable for *Cabomba* spp. growth as it more closely resembles the substrate characteristics of both its native range and areas where it is highly invasive (Schooler et al. 2009). *N. nucifera* preferance for mud loamy substrate (Kunii and Maeda 1982) explains the negative correlation between *N. nucifera* abundance and %silt/clay content. Negative correlation between *N. nucifera* abundance and distance to weir and positive correlation between *N. nucifera* abundance with turbidity may be associated with floods. The

Pahang river, like many tropical rivers, contains high suspended sediment ranging from 1 to 152 mg/l (Sulaiman and Hamid 1997). The suspended solid, derived from erosion of the alluvial and podzolic soil in the river basin (Panton 1964), is composed largely of loamy clay, which is not only suitable for *N. nucifera* growth but also easily resuspended when disturbed. Depending on the timing, duration and flood amplitude, the floating leaves of *N. nucifera* elongate petioles to extend above the turbid water to reduce the impact of flooding (Nohara and Kimura 1997; Nohara and Tsuchiya 1990).

The statistical analysis clearly indicated that water depth was an important environmental variable for both submerged *C. furcata* and floating-leaved *N. nucifera*. The association of depth to variation in *C. furcata* abundance and biomass agrees with the finding of previous studies of another Cabomba species, *C. caroliniana* (Schooler and Julien 2006). High *C. furcata* cover and density were found in shallower areas and abundance decreased with depth. The decrease in lake water level during the dry season (as apparent in April sampling), which happens after the monsoonal flood, coincides with the initial plant growth phase and may contribute to the re-zonation of plant establishment towards the centre of the lake where a more suitable water depth is apparent. Water depth is strongly associated to light penetration (Spence 1982), which is essential for submerged plant growth. A decrease in water level alters the light field across the benthos and can lead to an increase in temperature as more heat is absorbed by smaller volume of water. As the system becomes shallower, the hypolimnion may disappear and result in reduced stratification and increased dissolved oxygen at depth. The high concentration of ammonium in April could be associated with the flood (Shuhaimi-Othman et al. 2007) and result in the observed increases in *C. furcata* biomass. *C. furcata* showed higher primary production in rainy seasons where waters contains high ion, nutrient concentrations and low transparency (M. Pezzato, personal communication).

The change in floristic communities may be the result of the large flood event that occurred in December 2007. The influence of inflow from the Pahang River and the different flooding effect during the monsoon season may have affected the ecological processes and subsequently the composition and distribution of the plant community since significant differences in plant abundance was apparent between the two seasons. Different magnitudes of floods have been reported to exhibit different effects to wetland ecosystems (Hughes 1997; Richardson et al. 2007); intermediate size floods influence plant community distribution while small annual floods affect plant species abundance (Nilsson and Svedmark 2002). The changes in distribution and abundance of *C. furcata* and *N. nucifera* indicates dynamic population shifts which may be largely influenced by the annual flooding cycle. Flooding events may disrupt the substrate and dislodge plants. This could increase the spread of *C. furcata,* which can grow from stem fragments. Results from this study, in conjunction with historical observations, suggests that the distribution and abundance of *N. nucifera* is constantly shifting and is currently expanding, despite recent changes in sediment structure and eutrophication.

Based on our results we have developed a conceptual model of ecological variation in Lake Chini that describes how alteration of the lake ecosystem is associated with the combination of disturbances (Fig. 11), which are known to enhance biological invasion (Hobbs 1991). The installation of the weir structure has changed the biological and physical characteristics of the lake by altering the hydrological processes and disturbance regimes. Together with continuous alteration of the surrounding landscape, and eutrophication and siltation pressures increasing the availability of nutrients in the water and silt content in the sediment, the ecological community is adapting to the new state. Where non-native species are involved, research has shown that disturbance will enhance invasions when it is also associated with an increase in the availability of limiting nutrients (Hobbs 1989). The stabilised water depth, and increasing nutrient availability in water and silt content in the substrate has facilitated the invasion of *C. furcata* in the wetland. The extent of the effects of engineering intervention (damming) in causing a rapid proliferation of the invasive species in Lake Chini is consistent with changes in riparian vegetation (Richardson et al. 2007). In this shallow floodplain wetland, the change of the dominant aquatic vegetation from *N. nucifera* to *C. furcata* has been dramatic and has occurred within a period of less than 10 years.

The occurrence of regime shifts or alternative stable states are acknowledged in different kinds of freshwater ecosystems (Dent et al. 2002; Folke et al. 2004).

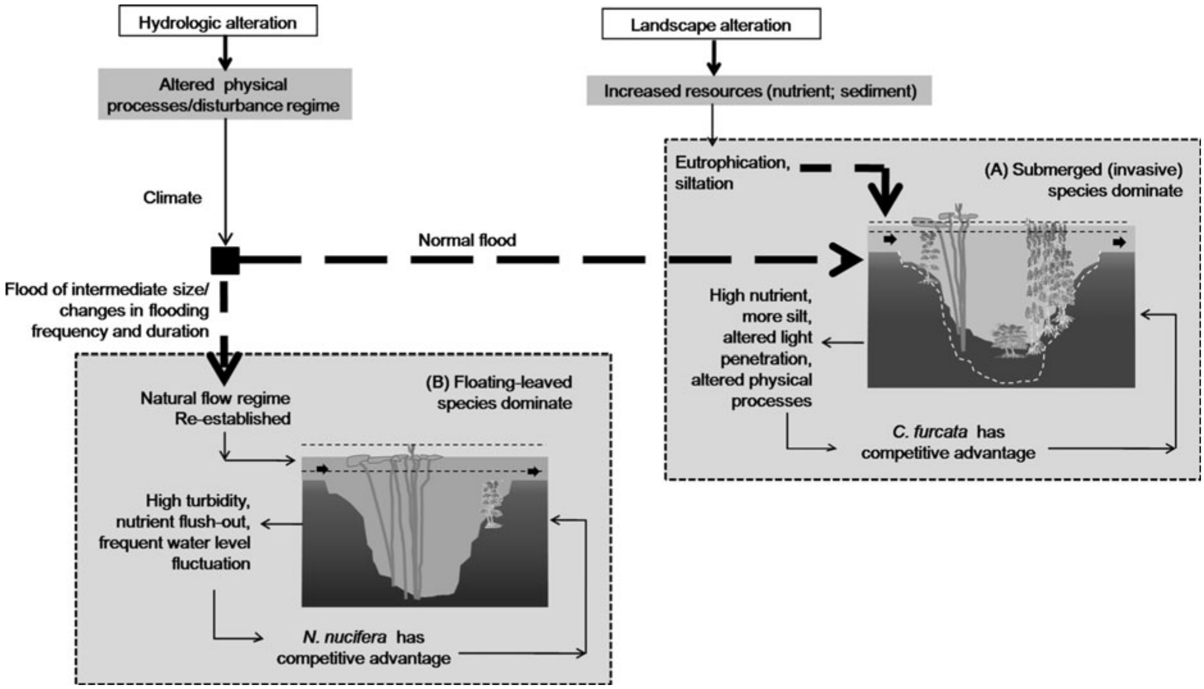

Fig. 11 Conceptual model of ecological changes, feedback mechanisms and multiple states in Lake Chini. *Dotted line* indicates processes that can move the system from one state to the other

Floating plant dominance has been recognised as a new stable state associated with eutrophication over a state characterised by submerged plant in tropical lakes (Scheffer et al. 2003). In contrast to shallow lakes where alternative stable states are primarily between macrophytes and algae, wetland systems where macrophytes dominate primary production exhibit different multiple states. Nutrient enrichment has shifted freshwater marshes in the Everglades from wetlands dominated by sawgrass to cattail marshes (Gunderson 2001). Changing patterns of macrophyte dominance between *N. nucifera* and *C. furcata* implies the possibility of two alternate stable states in Lake Chini. Floating-leaved plants, such as *N. nucifera*, are better competitors for light, carbon and nutrients from the sediment, and once re-established after intermediate size floods, they may have competitive advantage to spread when the natural flow regime is re-established due to flooding by the Pahang River as a results of frequent high intensity rainfall in the Pahang river basin. However, submerged species, such as *C. furcata*, are superior competitors for nutrients in the water column (Gunderson 2001), and continuing eutrophication will likely increase its abundance and spread in the system and eventually could cause a shift of dominance.

Macrophyte occurrence and dominance is characterised by species life history traits and environmental conditions (Pickett and McDonnell 1989). Being able to vegetatively propagate abundantly via fragmentation increases spread rates for *Cabomba* spp., particularly after disturbance events where plants are broken (such as from propellers). This, along with eutrophication and river damming, contributes to making *Cabomba* spp. invasive in many parts of the world (Mackey and Swarbrick 1997; Wilson et al. 2007; Schooler et al. 2009). This study, which based on one seasonal cycle, indicates dynamic patterns of aquatic vegetation with possible multiple states in the Lake Chini ecosystem with the floods and nutrient dynamics as important drivers for shifts in dominance. Continuing observation of the aquatic plant communities and the environmental variables, however, will further illustrate the successional patterns in this lake system. This is particularly relevant to *C. furcata*, as it appears to have the ability to re-colonize and grow rapidly following a flood event, which may be linked to its observed proliferation.

There is no prior knowledge of *C. furcata* being invasive in other countries. The infestation of *C. furcata* in Lake Chini, if not controlled, may disrupt its ecosystem function and impact its natural diversity. Continued research is essential in order to recommend proper management measures. Further research should concentrate on: (1) nutrient cycling and exchange of nutrients between pelagic and littoral zones and between lakes, (2) primary production of the main macrophytes and their relationship to water quality, (3) role of flood variability on plant community structure, and (4) alternative measures for sustainable rehabilitation and management of the lake ecosystem to prevent further loss of plant diversity.

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