

Cellular-automata-based ecological and ecohydraulics modelling

Qiuwen Chen, Fei Ye and Weifeng Li

ABSTRACT

Spatially lumped models may fail to take into account the effects of spatial heterogeneity and local interactions. These properties sometimes are crucial to the dynamics and evolutions of ecosystems. This paper started from the fundamental aspects of CA and focused on the development and application of the approach to ecological and ecohydraulics modelling. Application cases include modelling of prey–predator dynamics by stochastic CA and simulation of riparian vegetation successions in a regulated river by rule-based CA. The results indicated that spatially explicit paradigms such as cellular automata (CA) have a strong capability to bridge the local processes and global patterns.

Key words | cellular automata, ecohydraulics modelling, ecological modelling, spatially explicit

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INTRODUCTION

Limited by computation capacity and available ecological survey data, most of the conventional ecohydraulics models are aggregated and conceptually based (May 1975; Jørgensen 1994). These models are usually based upon Newton's second law of motion and the first and second laws of thermodynamics, and employ partial difference Equations (PDFs) to describe physical processes (Abbott & Minns 1998). The variables of the models are continuous in time and space, and the formulations strictly follow the conservations of mass, momentum and energy. Such model paradigms have been playing important roles in the progress of ecological research and are still fundamental tools (Jørgensen 1994).

However, the aggregated models mostly fail to take into account the effects of individual difference, spatial heterogeneity and local interactions (Chen & Mynett 2006a; Blackwell 2007). They sometimes even contain no spatial information, yet these properties can be crucial to the ecosystem dynamics (De Angelis & Gross 1992; Chen 2004).

Following the rapid development of computational power, in particular high performance computation, detailed simulations have become cheaper and more available. The wide use of advanced survey technologies

makes it possible to collect large scale and high resolution spatial data. Therefore, spatially explicit models have been rapidly developed and applied in broad disciplines (Perry & Enright 2007). These emerging techniques include cellular automata, individual-based and box-based schemes.

Cellular automata schematise the space into a regular lattice according to the principal spatial scale of the system studied (Chen & Mynett 2003). Each cell has some properties and takes a value from finite states. The value is updated in discrete time steps through the predefined local evolution rules that are functions of the current state of the cell itself and its neighbouring cells. Cellular automata are similar to the Eulerian approach in classical fluid mechanics (Abbott & Minns 1998) and are suitable in simulating plant dynamics, where the modelled variables have fixed positions. It is important to clarify that, although in cellular automata the values are updated in discrete time steps, the relevant procedure should not be confused with the recent analysis termed 'natural time analysis'. This, which is based on a new time-domain (natural time), assumes that the time is not continuous, thus greatly differing from the conventional time domain, and has been recently applied to

various complex systems that exhibit high complexity and nonlinearity (Varotsos *et al.* 2003, 2005).

Individual-based model takes each species as the studied object to describe its properties (age, gender and size, etc.) and actions. It is similar to the Lagrangian approach in classical fluid mechanics (Abbott & Minns 1998) and is advantageous in simulating species with spontaneous motions such as fish and animals, where the modelled variables are spatially tracked.

Box-based models divide the studied space into boxes based on their different behaviour or mechanisms. The boxes are usually different in geometry. Within one box the system is considered homogeneous. Each box implements its own dynamical equations. Communication (mass and energy flows) takes place from box to box instead of individual species.

Comparing to conventional model paradigms, they are usually discrete in time, space and model variables. They take each spatial unit or individual species as the target to investigate the evolution in time and the motions in space so as to obtain the global patterns of the system.

Spatially explicit models have been increasingly used in ecohydraulics researches. Chen & Mynett (2003) applied CA to model prey–predator population dynamics and analyzed the related system stabilities. Chen *et al.* (2002) used CA to simulate the competitive growth and colonization of two underwater macrophytes and explained the resulted ecosystem succession in Lake Veluwe, The Netherlands. Morales-Chaves (2004) investigated the growth and spreading of Zebra mussels in the Mississippi River by individual-based model.

This paper started from the fundamental aspects of CA and focused on the development and application of the approach to ecological and ecohydraulics modelling.

CELLULAR AUTOMATA

Cellular automata were proposed by Von Neumann (1949), and the computational theory was established by Wolfram (1984a,b) in the 1980s. It is a discrete mathematical system which consists of a regular lattice of sites (cells or automaton). Each site has some properties and states. The states are updated in discrete time steps according to local

evolution rules ϕ , which are functions of the states of the cell itself and its neighbours. The cell size and time step are determined by the principal time and space scales of the studied systems. Cellular automata often exhibit ‘self-organizational’ behaviour. Even starting from complete disorder, the simple components act together to produce complicated patterns of behaviour.

There are one-, two- and three-dimensional cellular automata, but mostly the one- and two-dimensional CA are studied. Figure 1 illustrates a one-dimensional and a two-dimensional CA system with the nearest neighbours, respectively. The corresponding rules of evolution are expressed as Equations (1) and (2). The rules can be deterministic (Chen *et al.* 2002), stochastic or empirical (Chen & Mynett 2003, 2006b). The neighbourhood schemes (Chen & Mynett 2003; Trunfio 2004) and evolution rules are considered the most important properties that are worth a great deal of attention:

$$a_i^{t+1} = \phi(a_{i-1}^t, a_i^t, a_{i+1}^t) \quad (1)$$

$$a_{i,j}^{t+1} = \phi(a_{i,j}^t, a_{i-1,j-1}^t, a_{i-1,j}^t, a_{i-1,j+1}^t, a_{i,j-1}^t, a_{i,j+1}^t, a_{i+1,j-1}^t, a_{i+1,j}^t, a_{i+1,j+1}^t) \quad (2)$$

According to the definition, a cellular automaton is a combination of data and computing rules that has at least six properties (Chopard & Masselot 1999):

1. *dimensions*, the number of spatial coordinates n ;
2. *width of dimension*, the number of cells in the j th ($j = 1, 2, 3, \dots, n$) coordinate, w_j ;
3. *neighbourhood*, a spatial region for a cell to gather information for updating;
4. *width of neighbourhood*, the number of neighbourhood cells in the j th coordinate, d_j ;

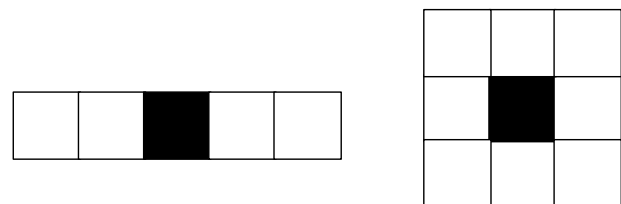


Figure 1 | Cellular automata (left: 1D, right: 2D).

5. *cell state*, the possible values that a cell can take on;
6. *localised evolution rules*, the function f which defines the update of a cell state at each time step.

In addition, a CA system can be characterised by:

1. *parallelism*, which means all cell states are updated simultaneously;
2. *homogeneity*, which states that all cells follow the same evolutionary rules;
3. *locality*, which implies a cell can only gather information from its nearest neighbours and can only affect its direct neighbours.

RULE-BASED STOCHASTIC CELLULAR AUTOMATA TO MODEL POPULATION DYNAMICS

The stability properties of different harvesting strategies are an important aspect of population dynamics systems. Most of the previous studies applied a non-spatial approach such as the Lotka–Volterra model (May 1975; Beddington & May 1980; Beddington & Cooke 1982; Azar *et al.* 1995, 1996). A rule-based stochastic cellular automata model (EcoCA) was developed to simulate the predator–prey system and verified by the classical Lotka–Volterra model. The EcoCA was then used to investigate the statistical stabilities of different harvesting strategies of the predator–prey complex. The simulations showed that constant effort leads to statistically more stable behaviours than constant quota. The joint harvesting of prey and predator with a reasonable constant effort can improve system stability and increase the total yields. These results are important to sustainable management of ecosystems, in particular to many situations of conservation biology and natural resources' exploitation (Qu *et al.* 2008). In addition, it once again confirmed that space plays a significant role in the stability properties of the predation and harvesting system, which indicates the importance of using a spatially explicit model in conservation ecology.

Development of EcoCA model

EcoCA is a two-dimensional cellular automata model which has been developed for simulation of predator–prey

systems (Minns *et al.* 2000; Chen & Mynett 2003). The model has up to three possible cell states: empty, prey and predator; and the state of each cell ($a_{i,j}^t$) is exclusive, namely that at each time step only one of the three states can exist in any one cell. The boundary conditions are fixed in such a way that the neighbourhoods are completed with cells taking the state of empty. The initial conditions are randomly defined, but as uniform as possible, by specifying the densities of prey and predator. The cell size can be subdivided or aggregated for investigating the effects of spatial scale. The neighbourhood configuration can be Von Neumann, Moore or extended Moore (Chen & Mynett 2003; Chen 2004). The evolutions for each cell (i, j) applies stochastic rules that are dependent on the current state of the cell, the number of the neighbouring cells occupied by a predator, N_{pd} , and the number of cells occupied by a prey, N_{py} :

$$P = \phi(a_{i,j}^t, N_{pd}, N_{py}) \quad (3)$$

where ϕ are evolution rules defining the transition probability p that a cell will become either prey- or predator-dominated or empty at the next time step. These evolution rules take into account reproduction, mortality, predation, loneliness and over-crowdedness (Chen & Mynett 2003; Qu *et al.* 2008). The snapshots of a random initial condition as well as the spatial pattern at $t = 600$ of a demonstration run are presented in Figure 2.

Several runs of the system with various starting conditions all led to a very similar pattern of results, as exemplified by the plot of the population dynamics and the phase dynamics (Figure 3).

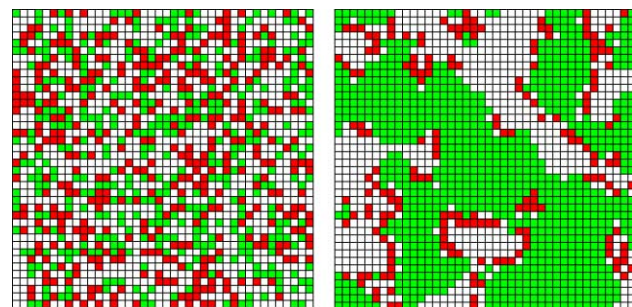


Figure 2 | Snapshots of spatial patterns of prey–predator population dynamics simulated by EcoCA (left: initial condition; right: $t = 600$).

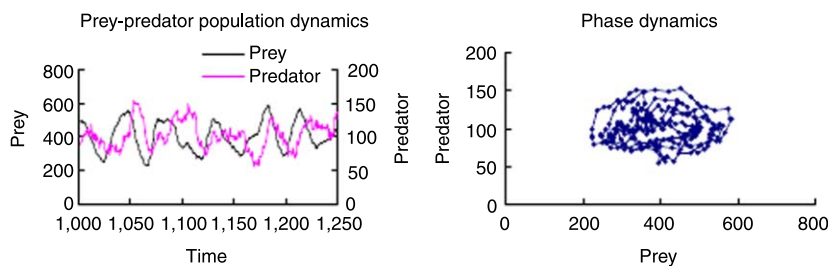


Figure 3 | Population dynamics of prey and predator (top), and phase trajectory (bottom).

It is seen that, although starting from random initial conditions, the system shows strong self-organization properties and produces eminent spatial patches after evolution (Figure 2). The population dynamics is not as strictly periodic as the Lotka–Volterra model, but the cyclic behaviours are well captured. A drifting is constantly induced between orbits, in contrast to the phase trajectories of the Lotka–Volterra model. This is because of the embedded stochastic process in the EcoCA model, which is completely absent in the Lotka–Volterra model. The verification of EcoCA and comparison of statistical descriptors with the Lotka–Volterra model were provided in Minns *et al.* (2000) and Chen (2004), which concluded that the EcoCA model can well reproduce the overall behaviours of the Lotka–Volterra model.

The EcoCA can not only simulate the dynamics of total populations, but also provide their spatial distributions, as shown in Figure 2. Previous research has proved that spatial configuration is important to habitat networks and ecosystem stability (Baptist 2005). Chen & Mynett (2003) had applied the EcoCA to investigate the stability property of the prey–predator system and discovered that it is not only determined by critical population size, but also by their spatial distribution. Even at the same population size, different spatial configurations can lead to coexistence, predator extinction and extinction of both. This kind of feature of structural stability had been acknowledged to be lacking in spatially lumped models (Nicolis & Prigogine 1977; Chen & Mynett 2003) although it has been realised that a more realistic population dynamics model should yield structurally stable focuses and cycles (Thompson & Hunt 1982). For example, the Lotka–Volterra model is hardly possible to study the spatial effects of ecosystems, so that it can only analyse the stability property in line with critical population.

Simulation of harvest strategies

Predation, competition and harvesting are the most factors in population management (Beddington & May 1980; Azar *et al.* 1995). The predation and competition effects reflected by functional response have been substantially studied (Beddington 1975). Much research effort has also been put into investigating the yields of different harvesting strategies (Beddington 1975; Brauer & Soudach 1979; Azar *et al.* 1995) and one of the basic concepts is maximum sustainable yield (Beddington & May 1980). Beddington & Cooke (1982) further studied the stability properties of various management regimes including constant quota versus constant effort, especially the joint harvesting of predators and prey. They found that constant quota cannot be achieved for small population size in order to prevent extinction. They also showed that the maximum stable sustainable yield cannot be fully exploited because any disturbance in that case could lead to system collapse. Costa Duarte (1994) claimed on the basis of numerical simulations that constant quota is more stable than constant effort, which was contrary to what is often believed and was argued by Azar *et al.* (1996).

In this section, the EcoCA was updated and used to investigate the statistical stabilities of different harvesting strategies of the predator–prey complex. The extended functions consist of various options such as constant quota and constant effort, selective harvest and random harvest (Qu *et al.* 2008). In addition, a criterion can be specified so that a pre-scheduled harvesting is suspended when the population density is lower than the threshold.

The results of an exemplified simulation of the updated EcoCA model are presented in Figure 4. In the simulation, a square grid of 20×20 is used. The initial condition is prey = 100 and predator = 100, and the neighbourhood is

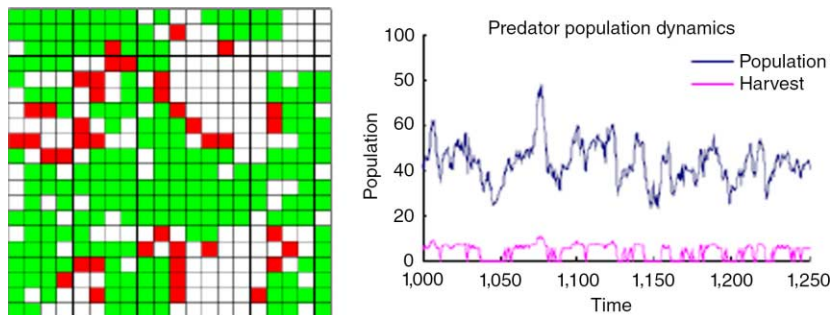


Figure 4 | Snapshot of population dynamics at $t = 1,050$ (left); predator population dynamics and harvest (right). Simulation results of the updated EcoCA model; the square grid is 20×20 ; initial condition is prey = 100 and predator = 100; neighbourhood is Moore scheme; jointly harvesting of prey and predator at the same constant effort 15%; harvesting criterion is 10%.

a Moore scheme. The harvesting strategy is to jointly take prey and predator at the same constant effort of 15% in a random way, and the harvesting criterion is defined as 0.1. It is seen from the results that the updated EcoCA is able to model the harvesting processes.

Four groups of numerical experiments have been conducted: (1) no harvesting, (2) harvesting prey only, (3) harvesting predator only and (4) harvesting prey and predator jointly. Two harvesting methods, constant quota versus constant effort, are examined for each group. The effects of harvesting criterion are studied as well, which imposes a limit of population density when executing a harvest.

The first aspect is to test harvesting on different species that include no harvesting, harvesting of prey only, harvesting of predator only and joint harvesting of prey and predator. For each experiment, constant effort and constant quota are both examined.

The second aspect is to study the difference between constant effort and constant quota. To keep them comparable, the mean harvest of constant effort is used as the constant quota. In addition, the effect of the harvesting

criterion is studied as well. In the present experiments, a threshold population density of 0.15 is selected and then compared with no criterion. However, comparison between selective harvesting and random harvesting is not conducted in this paper although the updated EcoCA model has the capability for such an investigation.

In principal, there are a total of 16 ($4 \times 2 \times 2$) cases to be investigated. But to focus on the key features, only six scenarios are presented here (Table 1). Scenarios 1–4 are to test species effect, scenarios 5 and 6 are to test constant effort versus constant quota and scenarios 4 and 6 are to test criterion effect. The EcoCA used exactly the same initial condition, which is defined by randomly distributing 100 preys and 100 predators in the domain, i.e. a population density of 0.25. The simulation period is 2000 time steps.

The experimental results are analyzed by using similar methods that are applied in previous research (Minns *et al.* 2000; Chen & Mynett 2003). The overall behaviour such as single species extinction, both species extinction and coexistence are examined first. Following that, stationarity (Azar *et al.* 1995) and chaotic dynamics (Hirota *et al.* 1997) are analyzed by using the procedure for screening time

Table 1 | Simulation scenarios of the experiments

Scenarios	Model	Harvest species	Harvest strategy	Harvest ratio	Criterion
1	EcoCA	No harvest			
2	EcoCA	Prey only	Constant effort	0.1	0.15
3	EcoCA	Predator only	Constant effort	0.1	0.15
4	EcoCA	Joint	Constant effort	Both 0.1	Both 0.15
5	EcoCA	Joint	Constant quota	Mean from constant effort	Both 0
6	EcoCA	Joint	Constant effort	Both 0.1	Both 0

series data (Chatfield 1989; Dahmen & Hall 1990). For stationary dynamics, the stability properties will be further quantified in terms of statistical descriptors (Chen & Mynett 2003, 2004) since the EcoCA is a stochastic model. The variance (Var_{prey} and $\text{Var}_{\text{predator}}$) of populations is chosen to be the major indicator of stability in the study.

The dynamics at the beginning are dominated by the effects of random initialisation. However, after sufficient time steps, it is then governed by evolution rules. Therefore, the results of the first 100 time steps are excluded in the time series analyses.

Results and discussions

Several repeated runs of each scenario with the same initial condition lead to very similar statistical behaviours that are summarised in Table 2. The population dynamics and phase trajectory of scenarios 1, 4, 5 and 6 are plotted in Figures 5 and 6. In addition, the harvesting results of scenarios 3–6 are given in Figure 7. Since scenario 5 is unstable, further statistical analysis is unnecessary.

It is seen from the phase trajectories and statistical analyses (Table 2) that joint harvesting leads to the most stationary behaviour, while harvesting on prey alone has the least stationary dynamics. The reason is that the predator's survival depends on the availability of prey. Harvesting on prey alone not only reduces the prey population directly, but also imposes higher predation pressure indirectly. Therefore, the oscillation of populations is increased, which reduces the stationary. The comparison between scenarios 4 and 1 indicates that a reasonable joint harvesting makes the system more stationary than no harvesting because the harvesting can create space (capacity) available for reproduction.

With respect to constant quota versus constant effort, the simulations show that constant quota easily leads to system collapse, while constant effort usually evolves stationary. This result is consistent with the previous findings.

Comparing scenario 6 with 4, it is found that jointly harvesting without restriction led to the system being more stationary and productive. However, it is valid only when the constant efforts are reasonably small, which is 0.22 for predator in these experiments. Otherwise, the system will collapse. Due to the setting of the harvesting criterion, predator yields in scenarios 3 and 4 are sporadic (Figure 7).

Comparisons with the spatially lumped model were investigated under different harvesting strategies. In this study, the modified Lotka–Volterra (MLV) model is applied (Equation (4)), but the analysis is made only for the joint harvesting:

$$\frac{dN}{dt} = aN - bN^2 - \alpha NP - H_1 \quad (4)$$

$$\frac{dP}{dt} = -cP + \beta NP - H_2 \quad (5)$$

where N : population of prey, P : population of predator; a : growth rate of prey; b : loading capacity limits (loading capacity $K = a/b$); c : mortality rate of predator; α : functional response of prey on predator; β : functional response of predator on prey; H_i is the harvesting that is defined as

$$H_i = \begin{cases} C_i, & \text{for constant quota,} \\ r_i N \text{ or } r_i P, & \text{for constant effort,} \end{cases} \quad (6)$$

in which $i = 1, 2$, r_i is the constant effort. The MLV model is numerically resolved through a fourth-order Runge–Kutta

Table 2 | Statistical analyses of each scenario

Scenarios	Dynamics behaviours			M_{prey}	M_{predator}	Var_{prey}	$\text{Var}_{\text{predator}}$
1	Stable	Not stationary	Coexistence	199	45	2,824	149
2	Stable	Stationary	Coexistence	202	38	3,339	157
3	Stable	Stationary	Coexistence	199	45	2,215	164
4	Stable	Stationary	Coexistence	202	41	2,288	116
5	Unstable	–	Prey dominant	–	–	–	–
6	Stable	Stationary	Coexistence	225	45	1,461	102

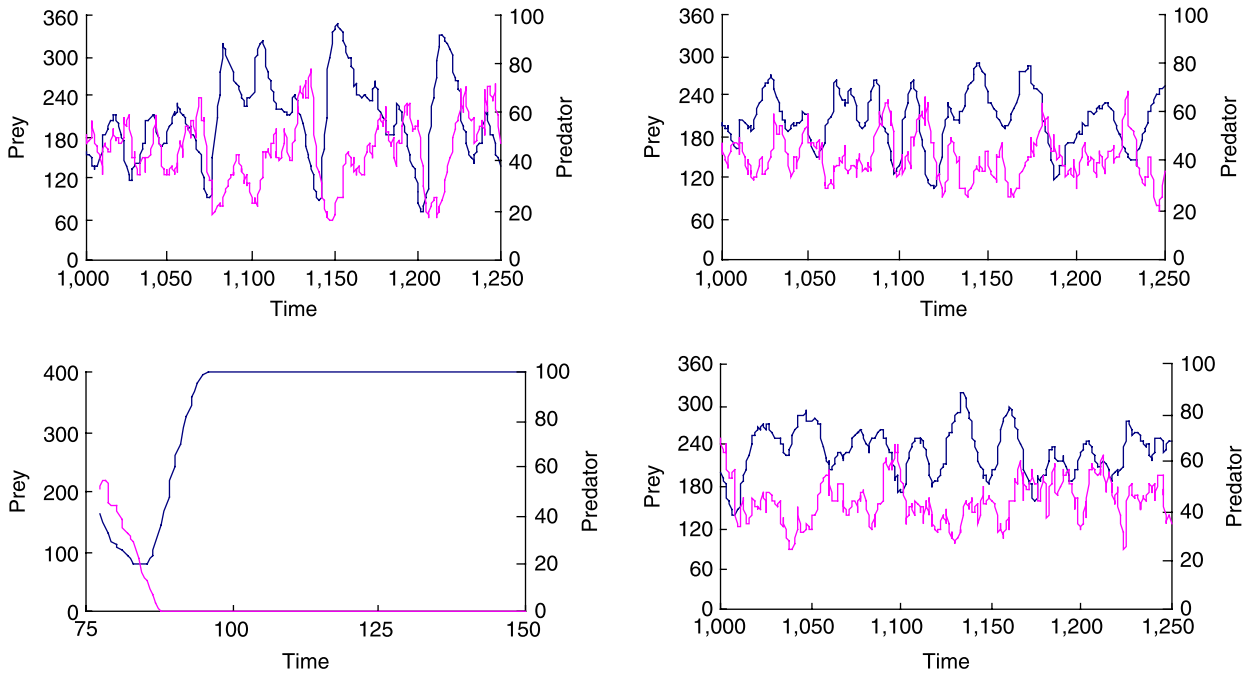


Figure 5 | Population dynamics of scenarios 1, 4, 5 and 6.

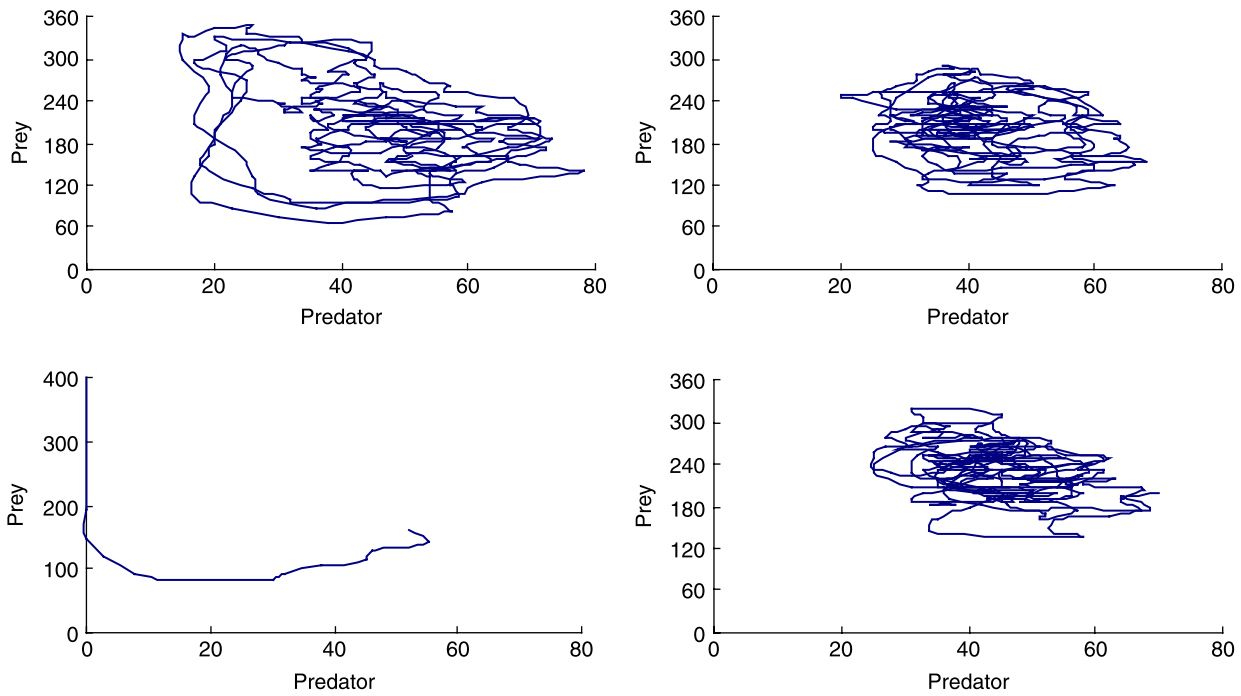


Figure 6 | Phase trajectories of scenarios 1, 4, 5 and 6.

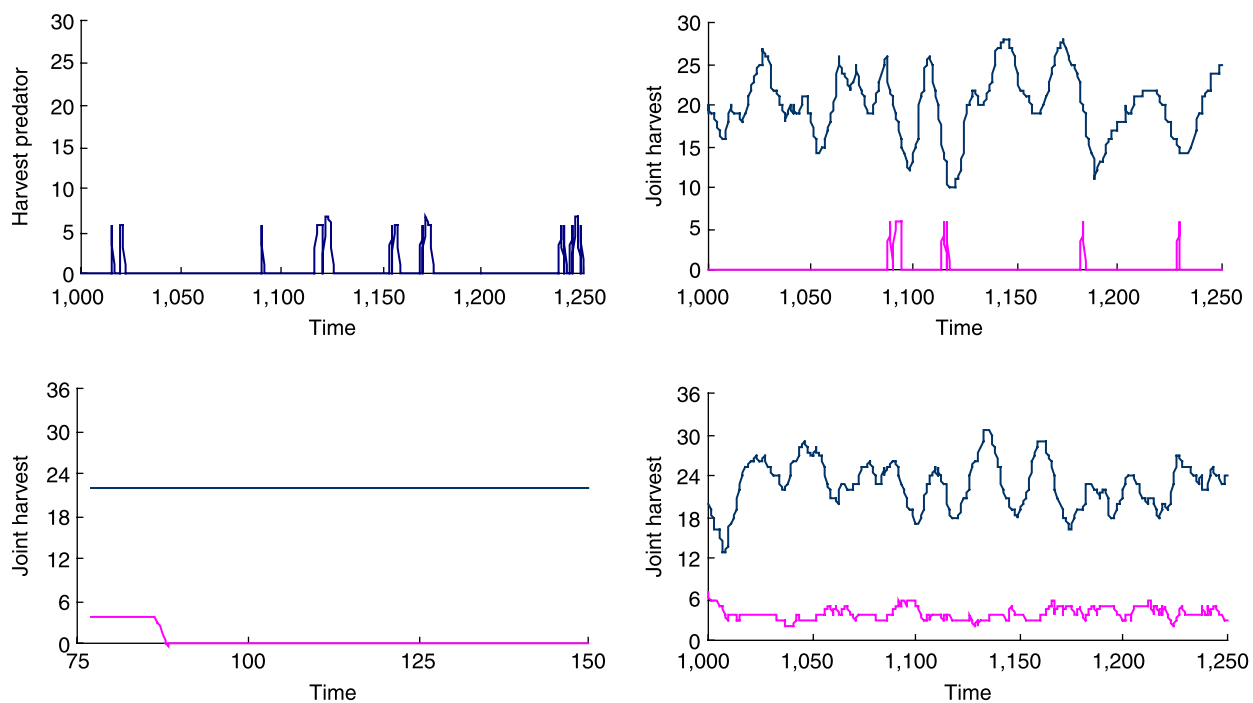


Figure 7 | Harvest of scenarios 3, 4, 5 and 6.

method (Press *et al.* 2007) and the calibrated parameters used in the model are $N_0 = 202$, $P_0 = 41$, $dt = 0.2$, $a = 0.95 \text{ d}^{-1}$, $b = 0$, $c = 0.7 \text{ d}^{-1}$, $\alpha = 0.0085$, $\beta = 0.0018$.

In spatially lumped models, predators can pursue prey globally so that any disturbance such as harvesting would result in large oscillations. In the spatially explicit EcoCA model, predation is limited to the local area and patches emerge (Figure 4). This not only reduces the oscillation, but also increases the probability for the system to recover from one or more patches and thus improve the stability.

It is therefore concluded from the study that (1) joint harvesting on prey and predator with a rational effort can improve the stability and productivity of a predation system; (2) constant effort usually leads to more stable behaviour than constant quota; (3) space places an important role in the stability of a predation and harvesting system that needs to be taken into account in ecosystems conservation. Spatially explicit methods such as cellular automata and individual-based have advantages in understanding such aspects.

UNSTRUCTURED CELLULAR AUTOMATA TO MODEL RIVER RIPARIAN VEGETATION SUCCESSIONS

The dynamics of the EcoCA model is purely dependent on geometric relations between neighbouring cells, and the rules of EcoCA does not account for any physical or biological processes. The case study below demonstrates the application of the rule-based cellular automata (RCA) to model the river riparian vegetation dynamics affected by upstream reservoir operations.

Description of the study area

The Lijiang River is a famous tourism resort in Guangxi province, Southwest China. The flow in the river has dramatic seasonal fluctuations that can reach $12,000 \text{ m}^3/\text{s}$ in the rainy season but down to only $12 \text{ m}^3/\text{s}$ in the dry season. For decades, river regulations have been implemented to ameliorate the flows for tourism cruises. Several reservoirs have been constructed or under construction in the main stem and branches. When all the

reservoirs are in operation, the low flow during the dry season is expected to reach $60 \text{ m}^3/\text{s}$. Since the flow regimes have been, and will be, further modified by reservoir operations, it is important to quantitatively evaluate the influences on the downstream ecosystem.

It is observed that, since operation of the upstream Qingshitan Reservoir in 1958, the downstream riparian and floodplain vegetation structure has been changing gradually (He 2006). Therefore, this research focuses on the downstream riparian vegetation dynamics and successions due to reservoir operations. The study selected a typical compound channel near the Yangshuo hydrological station in the downstream area of the Lijiang River, where the influences of all the upstream reservoirs can be perceived (Figure 8).

A field survey was conducted with concerns on both physical and biological features. The bathymetry and the flow profiles of the studied river section were measured by the Doppler flow measurement device, River Cat, which is manufactured by SonTek/YSI. In total, 15 cross sections were measured and the data for the entire area were obtained by interpolation. About the vegetation condition, 10 sites were surveyed in each side along the river section. In each site, five points that formed an 'S' shape were sampled and each point had a size of $1 \text{ m} \times 1 \text{ m}$. The number and dry weight of three typical species (*Rumex maritimus*, *Polygonum hydropiper* and *Leonurus heterophyllus*) were counted at each point.

The hydrological data during 1958–2004 were collected from the Yangshuo hydrological station, including cross-section geometry, daily averaged discharge, water level and some water quality parameters. In addition, the historical

survey records of the aquatic vegetation were collected as well from the local agency and universities.

Model development

In order to take into account the effects of local riverbed variations and species interactions, the research investigated the application of unstructured cellular automata (UCA) to the vegetation module, which was then integrated with a 2D flow module. The model framework is illustrated in Figure 9. The 'global change' may be caused by either natural or anthropogenic influences (Aassine & Jaï 2002), such as river regulations.

The hydrodynamic model solves the depth-integrated Equations (7)–(9) of fluid mass and momentum conservation in two horizontal directions:

$$h \frac{\partial h}{\partial t} + h \left(\frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} \right) + u \frac{\partial h}{\partial x} + v \frac{\partial h}{\partial y} = 0 \quad (7)$$

$$h \frac{\partial u}{\partial t} + hu \frac{\partial u}{\partial x} + hv \frac{\partial u}{\partial y} - \frac{h}{\rho} \left[E_{xx} \frac{\partial^2 u}{\partial x^2} + E_{xy} \frac{\partial^2 u}{\partial y^2} \right] + gh \left[\frac{\partial a}{\partial x} + \frac{\partial h}{\partial x} \right] + \frac{g \rho u n^2}{h^{1/3}} (u^2 + v^2)^{1/2} = 0 \quad (8)$$

$$h \frac{\partial v}{\partial t} + hu \frac{\partial v}{\partial x} + hv \frac{\partial v}{\partial y} - \frac{h}{\rho} \left[E_{yx} \frac{\partial^2 v}{\partial x^2} + E_{yy} \frac{\partial^2 v}{\partial y^2} \right] + gh \left[\frac{\partial a}{\partial y} + \frac{\partial h}{\partial y} \right] + \frac{g \rho v n^2}{h^{1/3}} (u^2 + v^2)^{1/2} = 0 \quad (9)$$

In which h —water depth (m), u , v —velocities in the Cartesian directions (m/s), x , y , t —Cartesian coordinates and time, ρ —density of fluid (kg/m^3), E —eddy viscosity

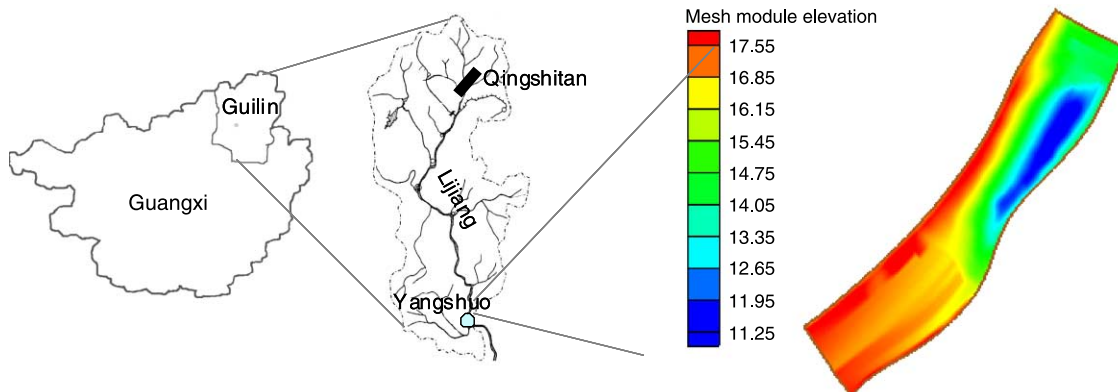


Figure 8 | Study site and the channel bathymetry.

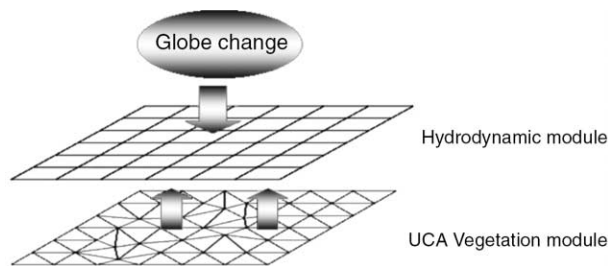


Figure 9 | The framework of the integrated hydrodynamic and UCA model.

coefficient (m^2/s), g —acceleration due to gravity (m/s^2), a —elevation of bottom (m), n —Manning's roughness.

The boundary conditions were defined using the data from the Yangshuo hydrological station. Daily averaged discharge was applied at the upstream boundary and daily averaged water level was applied at the downstream boundary. The finite element method (FEM) was applied to solve the equations numerically. The simulation time step is 15 min and the output data is daily averaged in order to be consistent with the time step in the vegetation module. Six scenarios were simulated that are high, even and low flows for with and without reservoir regulations, respectively.

Three annual herbs that are *Rumex maritimus* (*R. maritimus*), *Polygonum hydropiper* (*P. hydropiper*) and *Leonurus heterophyllus* (*L. heterophyllus*) were investigated on the channel shelf. The annual herbaceous species were selected in the present study because they complete their lifecycle in a relatively short time. Field data were collected to reflect the present distribution patterns of these species.

Table 3 | Empirical values for some model parameters

Water head (m)	<i>R. maritimus</i>	<i>P. hydropiper</i>	<i>L. heterophyllus</i>
Seed weight	0.0002 g	0.0002 g	0.0002 g
Max. growth rate	0.13	0.12	0.13
Max. biomass per plant	2.70 g	1.65 g	3.00 g
Biomass loss rate during inundation	0*	0.02/d	/†
Mortality rate during inundation	0.05/d (i.d. > 40 d)‡	0.025/d (i.d. > 10 d)	0.8/d (i.d. > 5 d)
Growth rate decrease during drought	63% (d.d. > 5 d)§	27% (d.d. > 15 days)	0
Mortality rate during drought	0.05/d (d.d. > 10 d)	0.05/d (d.d. > 20 d)	0

*"0" indicates no biomass loss but not normal growth.

†*L. heterophyllus* suffers large biomass loss during inundation, with an assumed mortality rate of 0.1–0.2/d during short period of inundation.

‡i.d.: inundation duration.

§d.d.: drought duration.

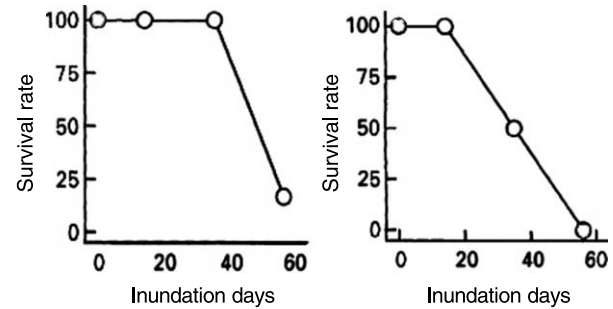


Figure 10 | Response curve of *R. maritimus* and *P. hydropiper* to inundation stress.

The physical template of the riparian zone is represented by a UCA grid, with physical and biological properties specifying bed morphology and vegetation condition. The simulated plants can 'grow' by updating cell properties at each time step. The updating rules are based on several dominant processes of the plant's life cycle. External forcing was introduced by reading the output of the hydrodynamic module. The characteristics of each species are obtained from experiments and existing literature. Table 3 gives the parameters used in the vegetation model. The typical responses of the modelled species to the inundations are shown in Figure 10.

Based on these parameters, the vegetation dynamics were simulated in a UCA grid with the main concerns on the flow disturbances during the growing season. The main CA rules are illustrated below.

- (1) Germination: in the riparian zone, seed germination takes place along with the recession of the first floods after winter dormancy. Due to relatively high dispersal

ability and long dormancy of herbaceous seeds, the compositions of herbaceous seed banks are similar in different areas of a riparian zone and abundant (Schneider & Sharitz 1986). Therefore, the seed availability was not considered as a limiting factor for the herbaceous species. During the initialization of the model, seeds of the three species are scattered evenly in simulation space, and the amount of germinated seeds is equal to the saturated numbers of mature plants.

- (2) Growing period: the juvenile plants are most prone to adverse environment and disturbances. The susceptibility (or tolerance) differs among the species, which contributes to the species differentiation along the water level gradients. *R. maritimus* and *P. hydro-piper* are typical hygrophytes species, while *L. heterophyllus* is not adapted to inundation and mostly presents on the upper land where floods seldom reach.
- (3) Mature period: mature plants of the three species show much more tolerance to adverse environments. They are all able to survive longer inundation or drought stress, and the survival rates are similar. The seeds are produced in this period.
- (4) Winter loss: all the annual herbaceous plants die in the winter, and the seeds have a loss rate.
- (5) The local interactions and species competitions are formulated according to the field survey and lab experiments. Suppose that the resources per unit area is $R = 1$ (resources/m²), and the resources consumption of species i is $c_i = S/(n_i \times M_{\max}^i)$, where S —area of sample site, n_i —the number of species i under optimal conditions in the sample site, M_{\max}^i the maximum biomass of an individual species i under optimal conditions. Taking *R. maritimus* for example, the field survey found that $n_i = 3$ and $M_{\max}^i = 2.7$, so the corresponding $C_i = 1/(3 \times 2.7)$. Therefore, the available resource of the cell k is defined as

$$R_k = S - \sum_{i=1}^n (C_i \times B_i^k) - \sum_{b=1}^3 \sum_{i=1}^n (C_i \times B_i^b) \quad (10)$$

where R_k —available resources in cell k , B_i^k —biomass of species i in cell k , B_i^b —biomass of species i colonizing the cell k from the neighbours. If $R_k > 0$, all species grow

normally. Otherwise, two different options are defined: if *L. heterophyllus* have not reached the saturated biomass, *L. heterophyllus* retains normal growth due to the strong competition capability, while *R. maritimus* and *P. hydro-piper* decrease. If *L. heterophyllus* has reached saturated biomass, it will colonise if there are available resources in the neighbourhood, or it will sustain saturation.

R. maritimus and *P. hydro-piper* follow similar rules as *L. heterophyllus* except that they can only utilise the remaining resources due to their low competition capability. In reality, *R. maritimus* and *P. hydro-piper* hardly reach the saturated level.

The simulation time step of the CA-based vegetation model is 1d. The model reads the output from the hydrodynamic module and calculates its influence on the plant's growth. Although only the water level and flow velocity were taken into account in the present vegetation module, other variables such as water quality could also be incorporated in a similar way.

Results and discussions

Figure 11 is the snapshot of the simulated water depth during low flow and high flow periods within a year. The unsubmerged area of the channel shelf during low flow periods provides the habitat for vegetation establishment.

Figure 12 shows the comparisons of the species distributions without and with reservoir regulations in the typical dry year (2004, post-dam). From the results, the changes in distribution could be perceived. Without flow regulation, the habitat ranges of *R. maritimus* and *P. hydro-piper* were significantly wider than with regulations.

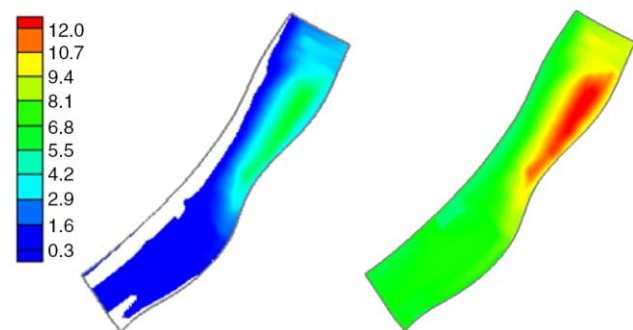


Figure 11 | Snapshot of flow patterns during base flow (left) and high flow (right) seasons.

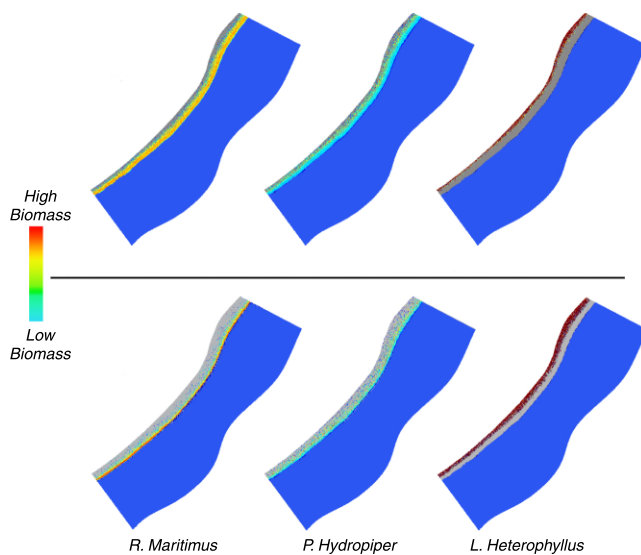


Figure 12 | Species distribution patterns in dry years both without and with reservoir regulations.

When river regulation was implemented, they both largely shrank. At the same time, *L. heterophyllus*, which is more susceptible to flood and tolerant to drought, expanded towards the river side and colonized the habitats that were previously occupied by *R. maritimus* and *P. hydropiper*. The results are, in general, consistent with both the observations and the statistical niche models.

Figure 13 shows the elevation-averaged biomass of each species along the transect. The ‘elevation averaged biomass’ refers to the average biomass of all the plants growing on the same elevation. Because the absolute weights of the species are significantly different, the relative

biomass was used instead. The relative biomass was defined as the proportion of average biomass to maximum biomass of a single mature plant. The values are then in between 0 and 1.

As a typical hygrophytes species, *R. maritimus* mainly grows in the area close to the water line. The peak biomass appears in a strip with an elevation a little higher than the water level under base flow. As the elevation increases, the species disappears gradually due to the drought stress and the competition from terriphytes species. The distribution of *P. hydropiper* has a similar pattern as *R. maritimus*, but the peak biomass appears at a higher elevation because of the difference in flood tolerance. *L. heterophyllus* starts to appear near the peak biomass of *P. hydropiper* and becomes dominant gradually in the zone where floods can seldom reach.

After the reservoir began operation, the distribution of *R. maritimus* shrank, but the peak biomass has not been strongly affected. However, *P. hydropiper* suffered a significant decrease in both the distribution and peak biomass. Compared to *R. maritimus*, *P. hydropiper* is less tolerant to flood inundation and it consumes more stored carbohydrate during inundation. But, on the other hand, it does require frequent flood disturbances to support competition with the terriphytes species *L. heterophyllus*. Therefore, after reservoir operation, less flood frequency and longer flood duration made the riparian habitat less suitable for the growth of *P. hydropiper*. *L. heterophyllus* obviously benefits from the flow modification, with an expanded habitat range and an increased peak biomass.

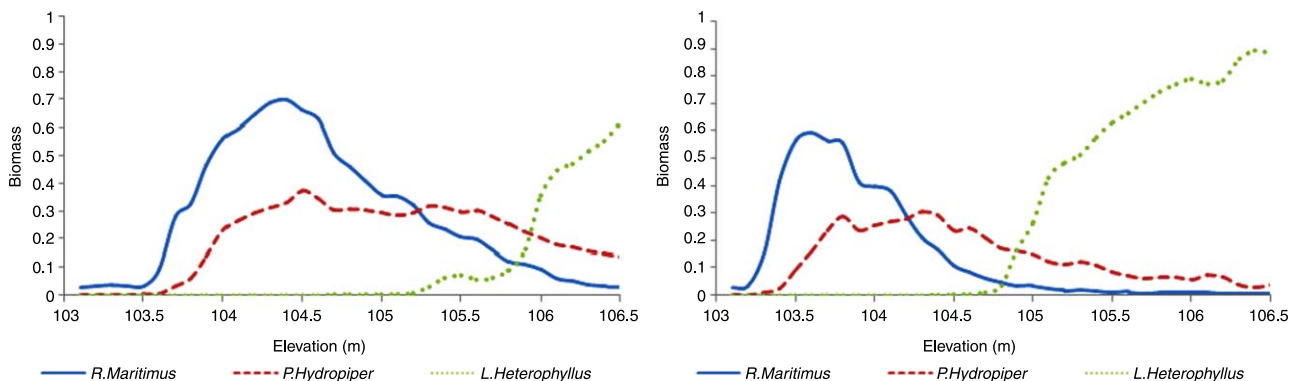


Figure 13 | Species vertical gradients in dry years both without and with reservoir regulations.

CONCLUSIONS

Following the rapid development and widespread use of information technology in ecological research, large scale and high resolution ecosystem data are more easily available. Meanwhile, parallel computation makes detailed spatial simulations realistic. Therefore, spatially explicit models such as CA and IBM are largely facilitated by these developments and have become a promising research field in recent years.

In ecological modelling, cellular automata seem to be more advantageous than PDEs due to the inherent characteristics of ecosystems where (1) some processes are discrete in time such as predation and fecundity; (2) the number of ecological units can often be well approximated by discrete groups of species; (3) species are mainly affected by their local environment and are only affecting their immediate surroundings; (4) inter- and intra-specific interactions between species take place locally; (5) individual properties are different and environmental conditions have spatial variability and anisotropy. The EcoCA model captured well features such as the emerging spatial patterns and the important role of spatial configurations in system stability.

The application of rule-based CA to simulating river riparian vegetation dynamics indicates the great potentials of integrating different model techniques. The strength of the combination consists of (1) the underlying physical processes, such as hydrodynamics, nutrient concentrations and morphological dynamics, can be simulated in detail by numerical modules; (2) the local morphological variations, species interactions and the emergence of patchiness can be captured by cellular automata (Hupp & Osterkamp 1996). Besides, the research attempted to use the unstructured cellular automata to deal with the local variations of riverbed topology. It is necessary to note that the selection of cell size and time step in the coupled model is determined by the governing physical and biological processes.

Although cellular automata already demonstrate certain advantages in ecohydraulics modelling, it does not mean that they can take over from conventional methods that are mainly characterised by physically based description and partial differential equations. The key issue nowadays is to

select the proper methods from a variety of available tools according to the particular problems of interest. In general, the selection of a paradigm or method depends on three main factors: the research objectives, understanding the problem and the availability of data.

The particular interest in spatial patterns evolving from cellular automata models implies that quantification and calibration of CA models should consider spatial information as well, which is often not the case in lumped models. This had hampered the application of cellular automata in modelling practice. However, GIS and RS observations are nowadays more and more widely used in ecological studies. Besides, the fractal analysis and multiple resolution moving windows techniques makes it possible to use raster-formatted GIS/RS data to evaluate CA models (Chen & Mynett 2004).

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