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Research Article

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Spatial patterns as long transients in submersed-floating plant competition with biocontrol

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Abstract

A cellular automata model was developed and parameterized to test the effectiveness of application of biological control insects to water hyacinth (*Pontederia crassipes*), which is an invasive floating plant species in many parts of the world and outcompetes many submersed native aquatic species in southern Florida. In the model, *P. crassipes* is allowed to compete with Nuttall's waterweed (*Elodea nuttallii*). In the absence of biocontrol acting on the *P. crassipes*, *E. nuttallii* excluded *P. crassipes* at low concentrations of the limiting nutrient (nitrogen), and the reverse occurred at high nutrient concentrations. At intermediate values, alternative stable states could occur; either *P. crassipes* alone or a mixture of the two species. When the biocontrol agent, the weevil *Neochetina eichhorniae*, was applied in the model, there was initially a rapid reduction of the *P. crassipes*, However, over time a regular striped pattern emerged of moving spatially alternating stripes of *P. crassipes* and *E. nuttallii*. This pattern of moving stripes persisted over thousands of days, but in some simulations the pattern was suddenly replaced by an irregular temporally varying pattern that lasted indefinitely. Thus, the striped patterns is an example of a long transient. The irregular spatio-temporal pattern that replaces it appears to be permanent, though that has not yet been established. Model parameters were varied to study effects of plant growth rate, nutrient concentration and nutrient diffusion rate on the dynamics of the system.

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Highlights

CA simulates competition of invasive floating and submersed native plants.

Insect biological control agent is added to CA model of the competing species.

The invading floating species is first drastically reduced by the biocontrol agent.

Regular spatial patterning of the two plant species emerges, then disappears.

Introduction

Spatial self-organization into regular patterns has been observed in numerous ecosystems around the world, and self-organizing mechanisms behind the pattern formation have been incorporated in models in some cases (e.g., Rietkerk and van de Koppel 2008). A famous example is the so-called 'tiger bush' first reported by MacFadyen (1950) in parts of Africa, where stripes of vegetation alternate with stripes of bare ground along parallel elevation contours. Vegetation stripes form under conditions of low rainfall, gentle slope, and on soil that is a hard enough surface for water to flow on, but where the occurrence of plants increases water infiltration. The striped pattern has been explained in terms of precipitation falling evenly along the gentle slope and accumulating as it flows downhill. If a small patch of vegetation happens to develop at some point along the slope, it will intercept some water, which will soak in and support further growth of the plant biomass. The plant biomass at that point will ultimately reach a point, through transpiration, that it exhausts the water flowing from upslope and will grow no further. Spreading horizontally, the vegetation forms a line along that elevation, below which there is no vegetation until enough water accumulates from the precipitation downhill of that equi-elevation line. This process can be modeled with simple reaction-advective-diffusion equations (Klausmeier 1999). Extensions of this model, describing striped or other types of regular patterns, have been developed (e.g., HillRisLambers et al 2001; Lefever and Lejeune 1997; Guttal and Jayaprakash 2007; Saco et al. 2007). Although most cases of self-organized pattern formation have been in terrestrial systems, self-organized patchiness has been observed in aquatic vegetation (e.g., Schoelynck et al. 2012) and mathematically modeled (Cornacchia et al. 2018).

It has been recognized that spatial patterns can change dramatically at some time. Such switches can occur rapidly in systems that have more than one state (Solé 2011; Kefi et al. 2014). Sudden changes can occur due to gradual changes in an environmental variable or from a large disturbance. It has been noted, for example, that a semi-arid ecosystem consisting of patches of vegetation spaces can switch rapidly to bare soil with slight decreases in rainfall (von Hardenberg et al. 2001; Rietkerk et al. 2002; Kefi et al. 2007). Such systems may exhibit hysteresis, as conversion back to patchy vegetation may require a higher rate of precipitation than the rate below which the switch to bare soil occurred. Therefore, there is a range of precipitation conditions under which either state may occur, depending on initial conditions, and disturbances could cause switches between these alternative states (Rietkerk et al., 2004). Either

of these states may persist over a long period of time and appear stable, but might actually be examples of what are called 'long transients', as one state could switch rapidly to another. Many empirical examples of long transients have been identified in a variety of ecosystems; see Hastings et al. (2018) for a review. While the examples listed appear to require some change in an external driver or some stochasticity, there are mathematical examples of sudden switches that are due to inherent processes within deterministic equations. An active area of theoretical ecology is understanding the causal pathways that can lead to drastic switches in patterns that have been long-lasting (Hastings et al. 2018; Morozov et al. 2019).

Here we present a case in which both spatial pattern formation and the sudden switching between two types of patterns emerges from a model that was developed to simulate biological control of an invasive floating aquatic species. The emergence of both the spatial patterns involved and the long transient behavior of a pattern appear to be due to characteristics of the system along with spatially local stochasticity. The invasive species motivating the model, *Pontederia* (syn *Eichhornia*) *crassipes* (Mart.) Solms (Pontederiaceae), or water hyacinth, native to South America, is considered invasive in over 50 countries (e.g., Villamagna and Murphy 2010; Lu et al. 2007). *P. crassipes* is a strong competitor for space with native submersed aquatic vegetation (SAV) (Ewel 1986). Therefore, biocontrol agents, including the mottled water hyacinth weevil, *N. eichhorniae* Warner (Coleoptera: Curculionidae) have been introduced to as part of an integrated control effort (e.g., Tipping et al. 2017). A model of integrated biocontrol of *N. eichhorniae* on *P. crassipes* was developed and applied to controlled experiments (Xu et al., in review).

Xu et al. (2023) developed a non-spatial model involving only the invasive floating species, *P. crassipes* and its main biocontrol agent. In order to extend the model to include competition of the floating species with a species of submersed aquatic vegetation (SAV), we adapted the spatial model of McCann (2016). McCann's model does not include biocontrol, only competition between floating aquatic vegetation (FAV) and SAV, duckweed, *Lemna gibba*, and Nuttall's waterweed, *Elodea nuttallii*, respectively. McCann's competition model is identical to that of Scheffer et al. (2003), except that it is extended to space in the form of a cellular automata (CA) model. We used *P. crassipies* instead of *L. gibba* as the FAV and added biological control, in the form of the weevil *N. eichhorniae*, to the model of McCann (2016). Later, although *N. eichhorniae* is not a biocontrol agent of other FAV, we changed parameter values of the FAV to

obtain more general results of broader theoretical interest. Therefore, although the modeling was based on an empirical example, the model demonstrates a more general phenomenon.

Methods

The model simulates competition between a submersed aquatic vegetation (SAV) and floating aquatic vegetation (FAV), where a biological control agent, a weevil, is used to attempt to control the FAV, which is assumed to be an undesired invasive species that can outcompete the native SAV in the absence of biocontrol. The nutrient nitrogen is assumed to be limiting to FAV, while either nitrogen or light can be limiting to SAV (Fig. 1).

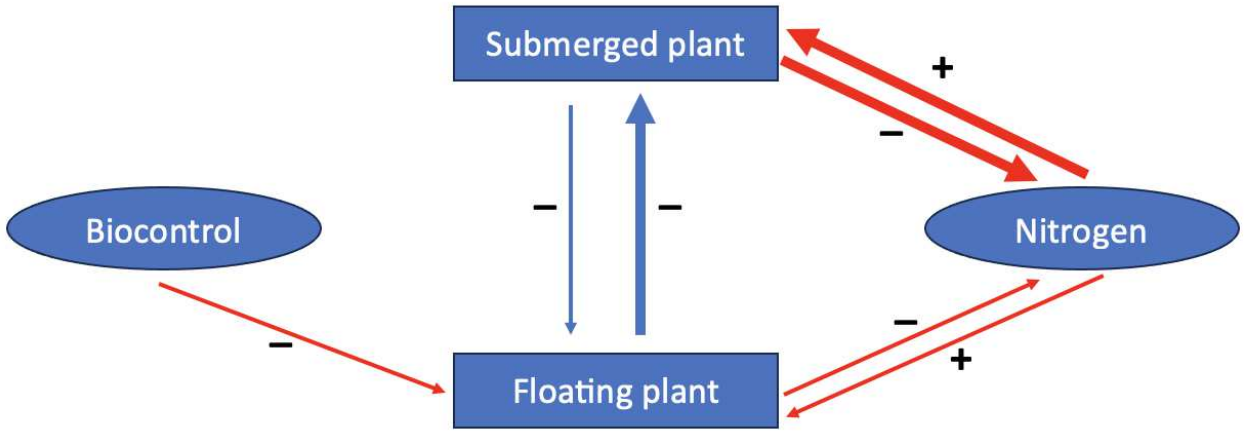


Fig. 1. Competition between FAV and SAV. The SAV is a better competitor for limiting nutrient (nitrogen), but the floating plant can shade the submerged plant.

Equations for competition of SAV and FAV

The equations of competition between the SAV and FAV are identical to those used by Scheffer et al. (2003) and McCann (2016).

Growth of SAV is described by the equation,

$$\frac{dS}{dt} = r_s * \mathrm{S} * \frac{n}{n+h_s} * \frac{1}{1+a_s S+bF+W} - l_s * S. \quad (1)$$

while growth of FAV is described by the equation:

$$\frac{dF}{dt} = r_f * F * \frac{n}{n+h_f} * \frac{1}{1+a_f*F} - l_f * F), \quad (2)$$

where S and F are dry weight biomass, r_s and r_f are the maximum growth rates, and l_s and l_f are the loss rates from respiration and mortality, of SAV and FAV, respectively. Nutrient concentration in mg liter^{-1} is given by n and h_s and h_f are the half-saturation values for nutrient uptake of SAV and FAV. Parameters a_s and a_f are the intraspecific competitive effect of SAV and FAV, respectively, while b is the effect of shading of the FAV on the SAV, and W is the effect of light absorption on submersed plant growth. As in Scheffer et al. (2003) and McCann (2016), it is assumed here that the water is shallow and clear enough that $W = 0$.

Total limiting nutrient concentration in the system, N, which is divided among the vegetation and soluble form in the water column, is assumed fixed in the models of Scheffer et al. (2003) and McCann (2016);

$$N = n + nq_sS + nq_fF. \quad (3)$$

Here q_s and q_f are coefficients of the effect of submerged and floating plants on the nitrogen concentration in the water column; that is, they represent the fractions of nutrient tied up in the vegetation per unit dry weight biomass. Therefore, the concentration of nutrient in the water column is

$$n = \frac{N}{1 + q_sS + q_FF} \quad (4)$$

Extension to spatial dynamics

McCann (2016) used the equations of Scheffer et al. (2003) to simulate competition of SAV and FAV in a spatial arena, using a cellular automata (CA) model composed of a block of contiguous spatial cells. The model of Scheffer et al. produced a bifurcation diagram in which only SAV existed at low nutrient (nitrogen, N) concentrations, only FAV existed at high N concentrations, and alternative stable states existed at intermediate N levels. McCann's (2016) spatial model produced results consistent with those of Scheffer et al. (2003). We adopted McCann's model with some modifications. Unlike McCann (2016), who simulates various spatial configurations of cells, we considered only a 50 x 50 square of 1 x 1 m cells.

Both vegetation types are capable of spreading in the model. We simulated spread such that, at each time step, if the biomass in a given spatial cell was greater than an assumed threshold

level, *neigh*, it could spread a certain fraction, *col*, to any of eight adjacent cells that have current biomass levels less than a value, *focal*. Vegetation could not spread beyond the limits of the 50 x 50 arena, as the boundaries are reflecting.

Nutrient was allowed to spread by symmetric two-dimensional diffusion between adjacent cells, but the concentration at any point is also assumed to be influenced by the local vegetation biomasses. If there were no diffusion, local nutrient concentration in each cell would be given by Eq. 4. If diffusion were very large, nutrient concentration would be evenly spread across the spatial arena. In the absence of specific knowledge, we consider a variety of nutrient diffusion rates.

Inclusion of biocontrol agents

The goal of including biocontrol agents in the model was to provide a simulation model to describe the integrated management experiment performed at the Department of Agriculture's Invasive Plant Research Laboratory (IPRL) at Davie, Florida. The model of the biocontrol agent was motivated by that of van Schalkwyk's model of the interaction of and the weevil *N. eichhorniae* but differs in mathematical form. van Schalkwyk (2016) and van Schalkwyk et al. (2017) used differential equations for the invasive plant, water hyacinth (*P. crassipes*) biomass and numbers for three stages of the weevil, adults and first and second stage larvae. The application of the model of *P. crassipes* with biocontrol by *N. eichhorniae* is described in Xu et al. (in review).

Our model uses a Leslie matrix with time steps of a day for numbers in four pre-adult stages of the weevil; eggs, first stage larvae, second stage larvae, and pupae, while *P. crassipes* biomass and adult weevils are modeled using difference equations with daily time steps. The lengths of the pre-adult stages are as follows: eggs (12 days), young larvae (29 days), old larvae (14 days), and pupae (20) days, based on averages of data from van Schalkwyk (2016). The structure of the model with details of the biocontrol agents, is shown in Fig. 2, and van Schalkwyk's parameters for differential equations were adapted to parameters for the Leslie matrix description used here. The Leslie matrix equation can be written in general form as $\boldsymbol{M}$;

$$\boldsymbol{M} = \begin{vmatrix} E_{12,12} & 0 & 0 & 0 \\ T_{E,L1} & L1_{29,29} & 0 & 0 \\ 0 & T_{L1,L2} & L2_{14,14} & 0 \\ 0 & 0 & T_{L2,P} & P_{20.20} \end{vmatrix} \quad (5)$$

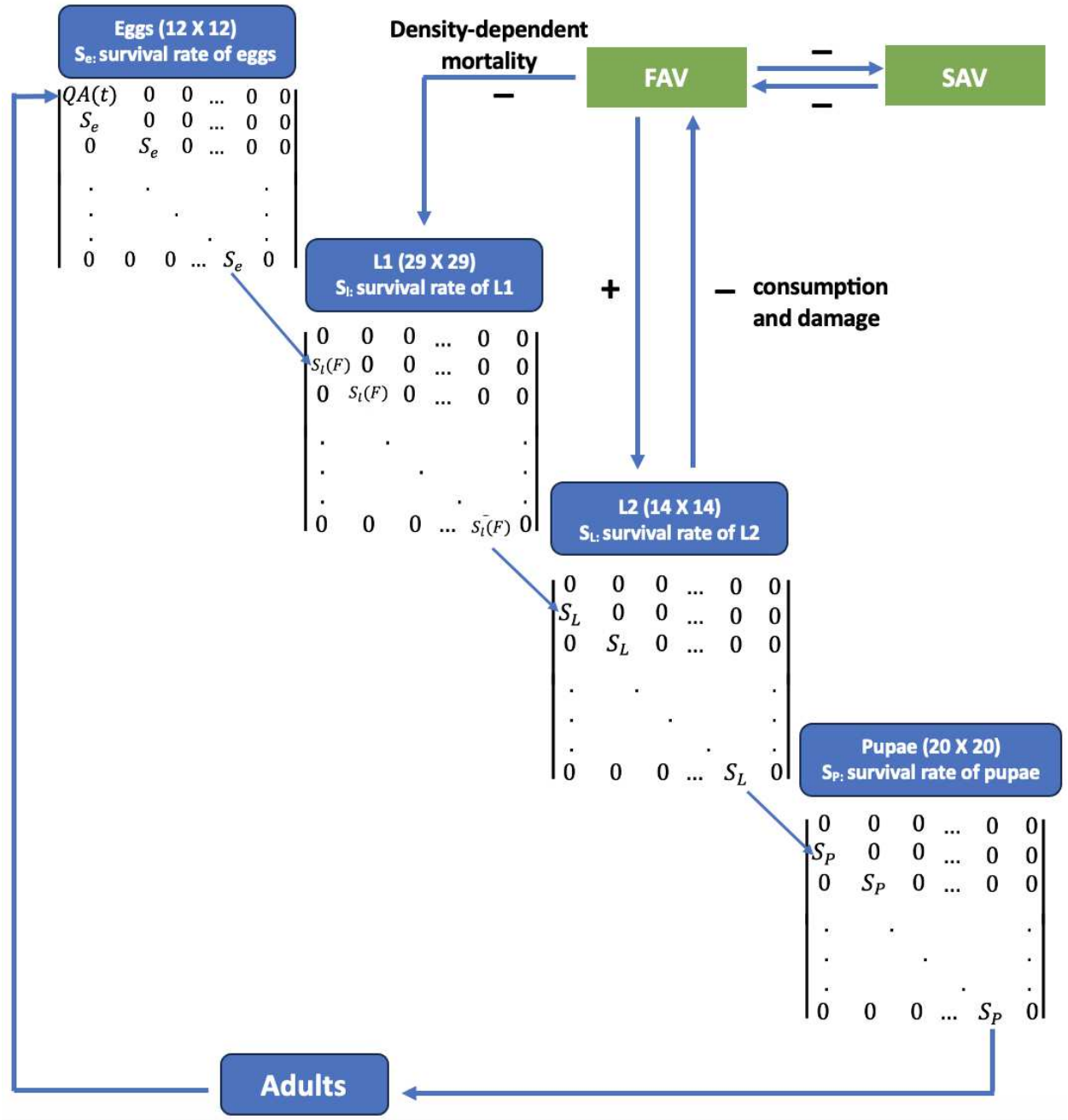


Fig. 2. Depiction of the basic structure of the model in which the life cycle of the weevil, *N. eichhorniae*, interacts with the *P. crassipes*, which competes with SAV (*E. nuttallii*). The daily survivals S_e, S_l, S_L, and S_P differ between stages but are identical within stages. The young (L1) larvae are subject to density-dependent survival (Eq. 6) is due to the density of larvae per unit water hyacinth biomass. Old (L2) larvae cause damage to *P. crassipes* biomass by consumption.

where the breakdown into submatrices is shown in Figure 2. Submatrices $T_{E,L1}$, $T_{L1,L2}$, and $T_{L2,P}$ describe the transitions among life stages. The submatrices $T_{E,L1}$, $T_{L1,L2}$, and $T_{L2,P}$ each only have

one non-zero element in the upper right-hand location, representing transitions from the oldest day-class of one life-stage to youngest day-class of the next.

Survival rates from day to day were assumed uniform within each life stage, as constants along the sub-diagonals. The matrix $E_{12,12}$ also includes a term *QA(t)* in the ($i = 1, j = 1$) location that represents oviposition of new eggs by adults *A(t)* at time *t*, where *Q* is fertility (eggs per adult per day). As in van Schalkwyk (2016), first stage larvae experience density-dependent mortality, which is represented in the matrix elements in the submatrix for first stage larvae, $L1_{29,29}$. These include, along with constant survival parameters, a function representing the effects of crowding on survival. The survival for each day-stage in the first stage larvae then is,

$$S_l(F) \equiv surv_{L1} = 1 - \mu_{L1} - J_{L1} * TotalL1(t)/(F(t) + k) \quad (6)$$

where μ_{L1} is density-independent mortality, J_{L1} is the coefficient of density-dependent mortality, *TotalL1* is the total number of first stage larvae ($TotalL1 = \sum_{i=1}^{29} LarvaeL1_i$), *F(t)* is *P. crassipes* biomass (grams dry weight, or g dW), and where *k* is a very small number to keep the denominator from being zero. The larger *TotalL1(t)*/*F(t)* is, the less available plant biomass there is per larva. The eggs, second stage larvae, and pupae have only density-independent mortalities, denoted $\mu_{eggs,}$ μ_{L2}, and μ_{pupae}. Matrix *M* operates on the vector

$B(t) = \lfloor Eggs(t)\ \ Larvae1(t)\ \ Larvae2(t)\ \ Pupae(t) \rfloor'$ as $B(t+1) = \boldsymbol{M}B(t)$, (*B* for biocontrol agent) where each of the four parts of *B(t)* is a sub-vector of 12, 29, 14, and 20 elements, respectively. The prime represents transpose.

The difference equation for adult weevils of population size, *A(t)*, is,

$$A(t+1) = \mu_{adult} * A(t) + (1 - \mu_{pupae}) Pupae_{20}(t), \quad (7)$$

where μ_{adult} is the daily survival of adults and $1 - \mu_{pupae} \equiv P$ in Figure 1 is the survival from the day-20 pupae to an adult, the same as the survival from one pupal day-class to the next. No upper limit on adult age is imposed.

Only the adult biocontrol insects are assumed to disperse, and they are assumed to disperse from cells existing agent-occupied water hyacinth to adjacent cells in which a certain minimum biomass of FAV, *neigh.* All eight cells surrounding a cell occupied by adults are censused, and those having a minimum number of adults, $Adult_{threshold,}$ can donate a random

number of adults to a neighboring cell in which the water hyacinth biomass exceeds a number, $F_{attract}$.

Parameterization of model

Scheffer et al. (2003) and McCann (2016) parameterized their models of competition between SAV and FAV based on the submersed plant *Elodea nuttallii* and the floating duckweed *Lemna gibba*. We changed the parameters from *L. gibba* to *P. crassipes* by using a lower growth rate, r_f and greater negative effect, b, on the submersed vegetation. Later, to obtain more general results, we used different parameter values for these and other parameters. These parameters are shown in Table 1.

In order to impose biocontrol, we first used the model and parameters that had been applied to *N. eichhorniae.* The resultant simulation model produced results that motivated further study. To obtain results beyond the system of primary interest, after initial simulations with *P. crassipes*, to be consistent with McCann's model, we next used parameters for a fast-growing FAV, *L. gibba* in McCann (2016), maintaining the parameters of the biocontrol agent *N. eichhornia*. Although we don't know of empirical interactions of *N. eichhornia* with fast growing species, this combination allowed us to obtain broader range of results at least of theoretical interest. The parameters for *N. eichhorniae* are shown in Table 2.

Initial conditions

In the model, initial conditions could be set at a variety of ways. Each species could be initiated with any starting biomasses in any of the spatial cells. Adult biocontrol agents could be introduced in any numbers to any of the cells containing FAV. This flexibility allowed an enormous number of possibilities for starting a simulation. The model was first used to show that our coding of the model in the absence of biological control agents was completely consistent with the results of McCann (2016). In particular, when our model was spatially homogeneous in the sense that each spatial are occupied by the same initial numbers of SAV and by the same numbers of FAV, the results of the competition are the same as in Scheffer et al. (2003). When biocontrol was added, a number of different initial conditions were used, a few of which are explored here. In general, simulations were started with initial amounts of SAV and FAV

randomly established in the 50 x 50 cell arena, and small numbers of adult biocontrol insects, $Adults_{added}$, added once, 300 days after start of the simulation, or periodically (every 300 days) to cells with FAV scattered randomly near the center of the plot, only to cells with FAV biomass greater than $F_{threshold}$. (Whether adults were added every 300 days or not after the

Table 1. Variables and parameters for the vegetation components used in the model.

Variable	Description	Units	
F	Floating plant biomass	g dW m^{-2}	
S	Submerged plant biomass	g dW m^{-2}	
n	Nutrient concentration in water column	mg nitrogen $liter^{-1}$	
Parameter	Description	Values: McCann FAV, SAV	Values: *P. crassipes* vs Submersed
r	Maximum relative growth rate	r_f=0.5 r_s=0.5	r_f=0.1 r_s=0.1
h	Half-saturation concentration for n	h_f=0.2 h_s=0	h_f=0.2 h_s=0
a	self (light) limitation	a_f=0.01 a_s=0.01	a_f=0.0065 a_s=0.01
l	losses	l_f=0.05 l_s=0.05	l_f=0.01 l_s=0.025
q	The effect of submerged and floating plants on the nitrogen concentration in the water column	q_f = 0.005 q_s = 0.025	q_f = 0.005 q_s = 0.025
b	Negative effect of floating plants on submerged vegetation	0.02	0.04
W	Light attenuation in the water column	0	0
N	Total nitrogen in system (mg nitrogen $liter^{-1}$)	2 or 4	4
N_{diff}	*Low N diffusion rate* *Medium N diffusion rate* *High N diffusion rate*	0.03† 0.1† 0.2†	/ / /
col	Biomass to colonize focal cell	1 g dW	1 g dW
focal	Biomass, above which, focal cell will not be colonized	1 g dW	1 g dW
neigh	Neighbor biomass, above which, focal cell is colonized	20 g dW	20 g dW
T_{adult}	Time interval between additions of insects	300 d	300 d
$F_{threshold}$	Biomass threshold above which insects will be added to floating plants	20 g dW	50 g dW

$Adults_{added}$	Number of insects added each time they are added	*2*	*2*
$F_{attract}$	Biomass of FAV for adult to move to	*3 g dW*	*30 g dW*
$Adult_{threshold}$	Number of insects in a cell before one will move	*6*	*6*

*f: floating plants *s: submerged plants

† means the fraction of nutrient that diffuses out of a cell in one time step.

Table 2. Parameter values of *Neochetina* life cycle

Variable	Description	Units
A	Adult insects	Number m^{-2}
E	Insect eggs	"
L1	First stage larvae	"
L2	Second stage larvae	"
P	Pupae	"

Parameter	Definition	Values	Unit
QA	Eggs per day produced by adult *Neochetina*	4 (*L. gibba*) 2 (*P. crassipes*)	
μ_{adult}	Mortality rate of adults	0.03	day^{-1}
μ_{L1}	Mortality rate of first stage larvae	0.04	day^{-1}
μ_{L2}	Mortality rate of second stage larvae	0.06	day^{-1}
μ_{pupae}	Mortality rate of pupae	0.05	day^{-1}
μ_{eggs}	Mortality rate of eggs	0.05	day^{-1}
J	Density-dependent mortality rate of first stage larvae	0.07	(g larvae/g FAV) day^{-1}
c_{L2}	Consumption rate of water hyacinth by second stage larvae	0.02	$(g\ larvae)^{-1}$ day^{-1}

first introduction made no qualitative difference in the results.) The specifics of particular simulations are described in conjunction with the results. All simulations were performed using Matlab R2022a.

Results

The CA model was first tested without biocontrol and with the species and parameters that were used in simulations by McCann (2016), *E. nuttallii* and the floating vegetation, the duckweed species, *L. gibba*. When the two species were started in a homogeneous manner, with the same starting values of *E. nuttallii* and *L. gibba* in every spatial cell, the results were identical to those

of McCann (2016). That is, the bifurcation diagram of Scheffer et al. (2003) was produced, in which only *E. nuttallii* was present at low nutrient concentration, only *L. gibba* at high nutrient concentration, and two alternative states existed at intermediate concnetrations; *L. gibba* alone or coexisting *L. gibba* and *E. nuttallii*. When the initial values of *L. gibba* and *E. nuttallii* were initialized heterogeneously across the lattice, the results were qualitatively similar, but transitions between states for changes in nutrient concentration could be more gradual, with intermediate stages.

The following scenarios all include biological control agents. Different parameter values are used to assess the effects of FAV growth rate, nutrient concentration, and nutrient diffusion rates.

Effects of FAV growth rate

The CA model of McCann (2016) was modified to perform the simulations relevant to the objective of the modeling, to gauge the effect of biocontrol by *N. eichhorniae* on competition with water hyacinth, *P. crassipes*, with a submersed SAV, in this case *E. nuttallii*. This was done by decreasing the growth rate of the FAV used by McCann (*L. gibba*) to a value in the range of known *P. crassipes* values and by increasing the negative effect of the FAV to simulate the strong shading that a species like *P. crassipes*, with high biomass, has on the SAV. We first present a scenario with these results. These results motivated us to explore the effects of other conditions and parameter values in further scenarios, in which FAV growth rate, nutrient concentration, and nutrient diffusion rate were varied.

Scenario 1. E. nuttallii competing with P. crassipes, with biocontrol present, N = 4 mg l^{-1}*, diffusion coefficient* $N_{diff} = 0.1$

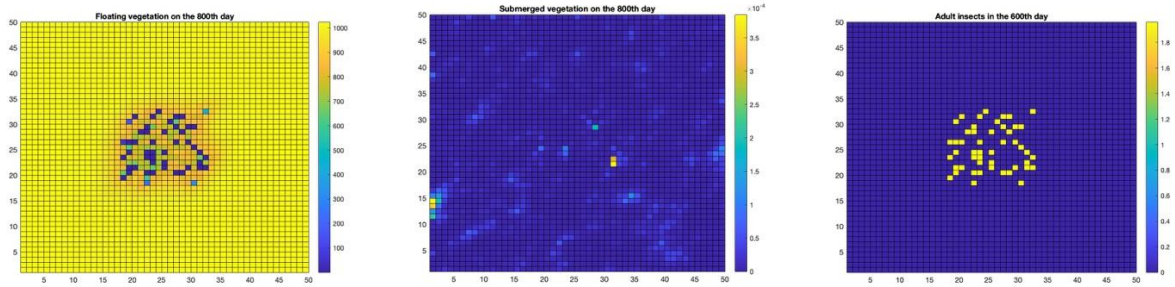
The FAV *P. crassipes* was initiated randomly such that each spatial cell had a 15% chance of receiving 50 g of biomass; similarly for SAV *E. nuttallii*. A cell could be occupied by biomass of both species. Total nutrient (N) concentration per cell (the total of in the two plant types and the water column) was initially set at 4 mg liter^{-1}. An intermediate level of diffusion of nutrient, N_{diff}, was assumed. Starting at time $t = 600$ days, two adult weevils were added to every spatial cell that was within the square bounded by cells 17 and 33 along both the x- and y-axes and which contained > 5 g *P. crassipes* biomass. In most simulations these additions were continued every 300 days for 10,000 days. (However, it was later determined that after the first input of

weevils, they became established, and no further input was needed.) The only stochasticity in the model was in the form of how many adult weevils moved among adjacent spatial cells.

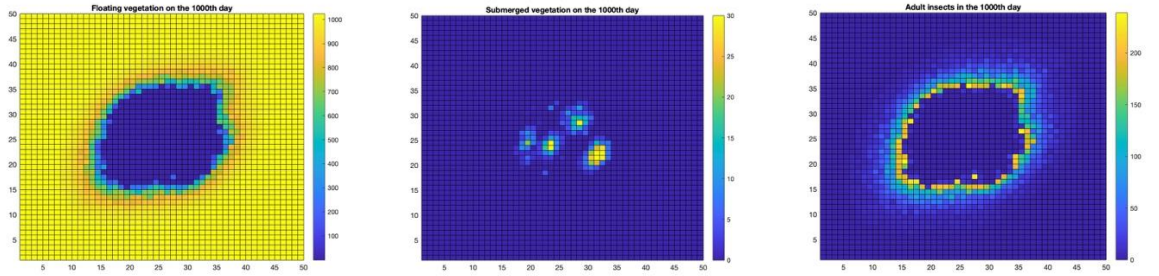
Adults were first introduced to the competition of FAV and SAV at 300 days. By 800 days, the FAV was dominant (Fig. 3a), but the weevils had become established in the center (Fig. 3c) and the SAV was starting to recover (Fig. 3b). By 1000 days, the weevils' range had expanded, reducing FAV, allowing SAV to recover (Figs. 3d, e, f). By day 5000 a striped spatial pattern had become established, shown here at day 11,500 (Figs. 3g, h, i). But between around 15,000 and 16,000 days, the pattern switched to an irregular pattern, shown at day 16,000 (Figs. 3j, k, l).

Time series of the variables S and F are shown in Fig. 4a and of numbers of adult weevils, A, are shown in Fig. 4b. The striped pattern lasts from about day 5000 to day 15,000 and can be considered a long transient. The following irregular pattern seems, based on longer simulations, to persist indefinitely, although it is possible that there are qualitative changes that have not been noted yet.

(a) (b) (c)



(d) (e) (f)



(g) (h) (i)

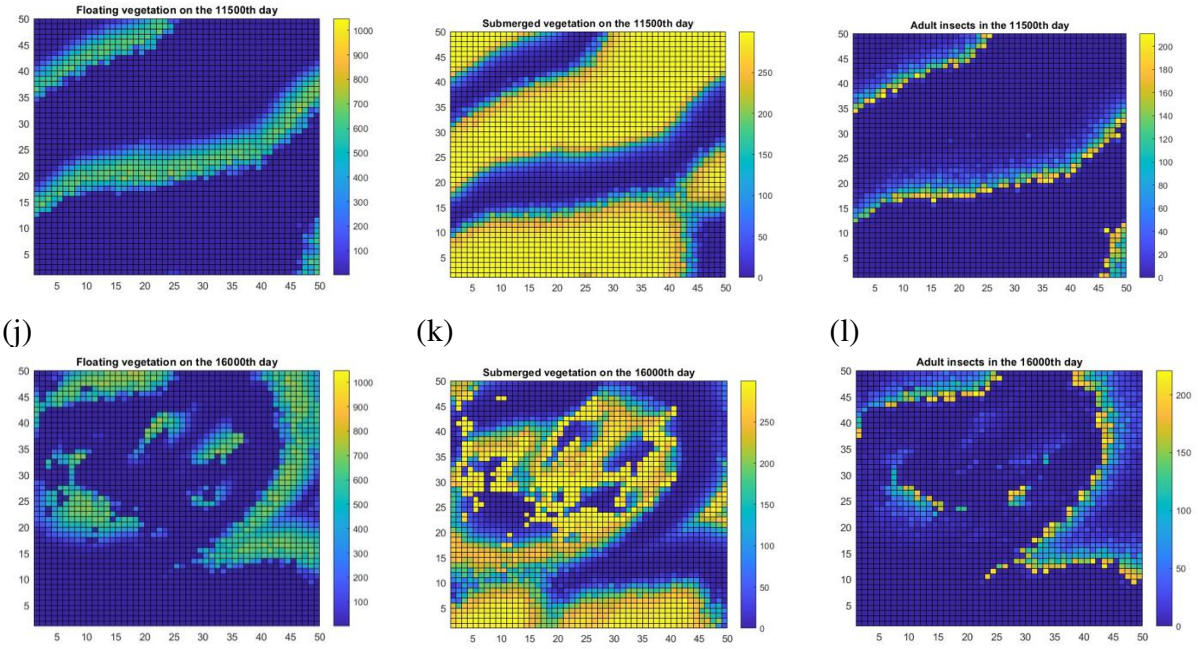


Fig. 3. FAV (left column) and SAV (center column), started from small randomly scattered biomasses and were treated with high nitrogen (N=4) and intermediate nutrient diffusion. (a,b,c) By days 800, 800, and 600, respectively, FAV dominated but adult weevils (right column) occupied some center cells. (d,e,f) By day 1000 the weevils were expanding, reducing FAV and allowing SAV to recover. (g,h,i) A regular striped pattern had emerged by day 5000, shown here on day 11,500. (j,k,l) The regular pattern started to dissipate around day 15,000, leading to an irregular pattern by day 16,000.

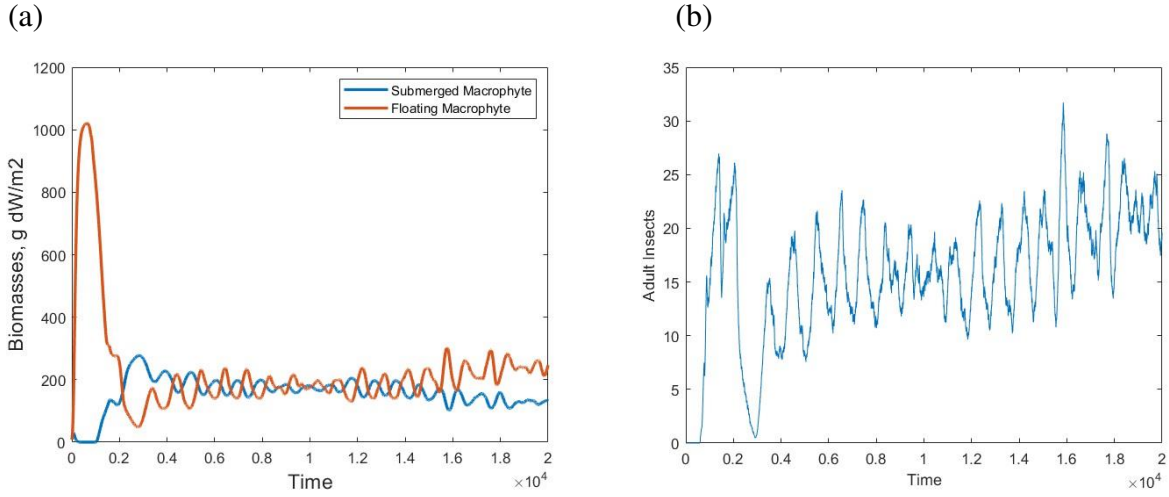


Fig. 4. (a) The mean biomass density (g dW m^{-2}) of FAV and SAV through time, blue line represents submerged macrophyte, red line represents floating macrophyte, (b) the total number of adult weevils per cell (i.e. m^{-2}) over 20,000 days.

The above results of the formation of striped regular pattern, which turned out to be a long transient, motivated more simulations to investigate the properties of the phenomenon. These are all single-simulation results, so only indicate, not prove, possible trends.

Scenario 2. E. nuttallii competing with L. gibba, with biocontrol present, N = 2, N_{diff} =0.1.

Because the results competition of *P. crassipes* and *E. nuttallii* with biocontrol produced interesting results, the model was used to examine other combinations of parameters. We first investigated the effects of a faster growth rate of FAV growth, by increasing the relatively low value of *P. crassipes* to a higher value, that of *L. gibba*, which was simulated in the paper of McCann (2016). Again, the biocontrol agent was the weevil, *N. eichhorniae*. The biocontrol aspect is not realistic, and *N. eichhorniae* does not feed on *L. gibba*, so this combination is only of theoretical interest.

As in Scenario 1, here the amounts of FAV (*L. gibba* here) and SAV (*E. nuttalllii* again) were introduced to spatial cells selected randomly and two adult weevils were added every 300 days to each spatial cell within the central square (as shown in Fig. 3a) and in which floating plant biomass exceeded a threshold of 5 g dW. The total concentration of nitrogen in this case was assumed to be 2 mg liter^{-1}.

After the introduction of adult weevils, the FAV was sharply reduced in the center of the plot, as the weevils expanded, and the SAV returned where FAV was reduced (Figs. 5a, b, c). By day 5000, a regular striped pattern had emerged, as shown in Figs. 5d, e, f for day 13,500. This striped pattern underwent a sharp change at about day 15,000 and was replaced by an irregular time-varying pattern, shown for day 30,000 in Figs. 5g, h, i. The areas in which adult weevil numbers were high correspond to areas where FAV biomass was low and SAV biomass was high.

The time series of mean FAV and SAV biomass per cell are shown in Fig. 6a, while that of adult weevils per cell is shown in Fig. 6b. There is a clear rapid shift from the regular striped pattern to the irregular pattern.

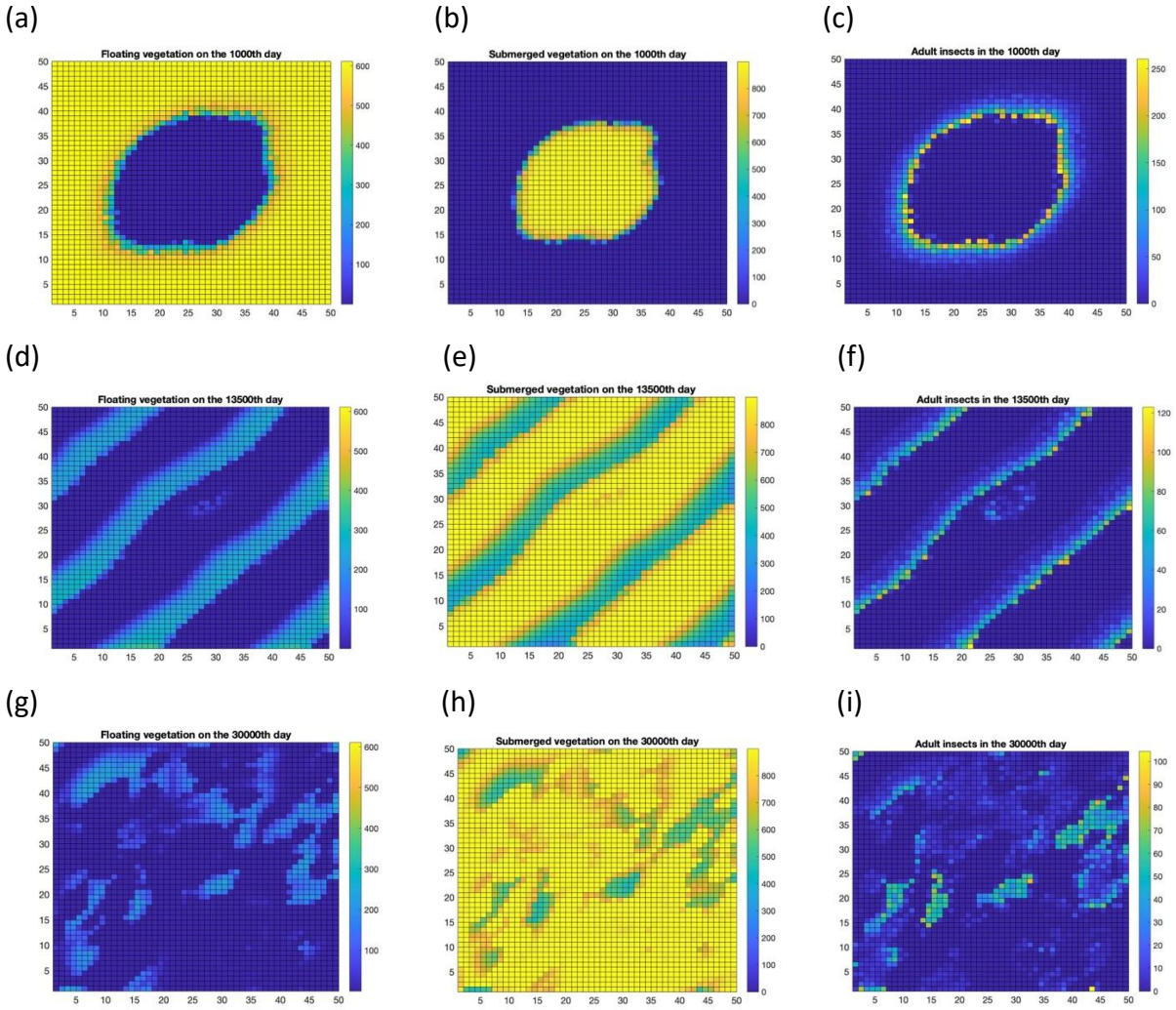


Fig. 5. FAV (left column) and SAV (middle column), started from small randomly scattered biomasses and treated with $N = 2$. The adult weevils (right column) started from a square of number in the center. (a, b, c) By day 1000 the weevils had expanded in the center of the lattice, reducing FAV, so that SAV recovered. (d, e, f) A striped pattern had emerged by day 5000, shown here on day 13,500. (g, h, i) Starting around day 15,000 the striped pattern dissipated and was replaced by a temporally varying irregular pattern, shown on day 30,000.

(a) (b)

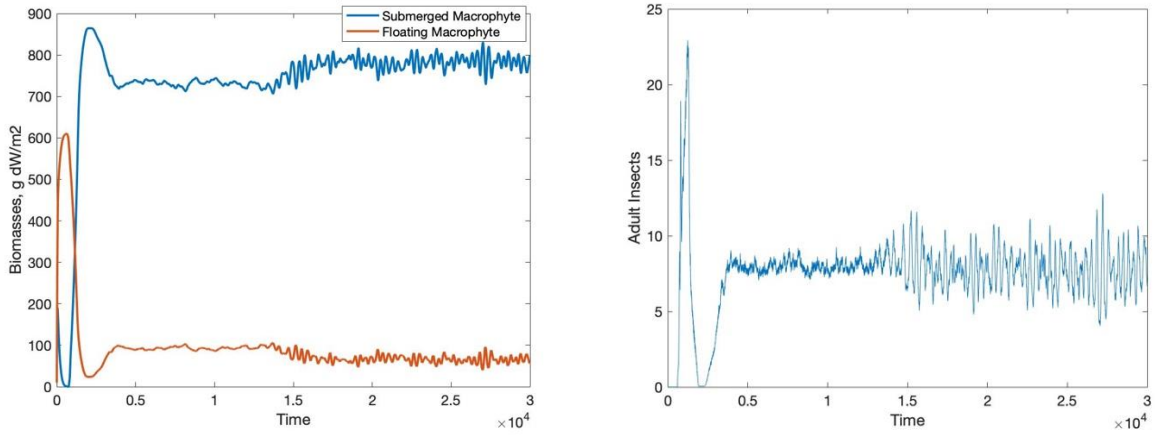


Fig. 6. (a) The mean biomass (g dW m^{-2}) of FAV and SAV through time; the blue line represents the SAV, the red line represents the FAV, (b) the total number of adult weevils over 30,000 days.

These simulations that include biocontrol show the strong negative effect it has on the FAV. However, note that small patches of floating plants are able to persist (Fig. 5g). The size of the model system may allow such patchiness to persist through time, even though the floating plants has basically been suppressed. After the long transient of striped pattern, another long pattern emerged, but it appeared to be persistent. Comparison of Scenarios 1 and 2 shows that the higher growth rate of the FAV, because it is accompanied by smaller shading effect of FAV on SAV, leads to SAV biomass exceeding FAV biomass. The transition from long transient striped pattern to irregular pattern is also sharper.

Effects of nutrient concentration

In Scenario 2 a long transient striped pattern was found under an intermediate nutrient concentration (N=2). To see if nitrogen level makes a difference if only N is changed from Simulation 2, N was next changed to 4.

Scenario 3. E. nuttallii competing with L. gibba, with biocontrol present, $N = 4$, $N_{diff} = 0.1$

We hypothesized that with high nutrient levels (N=4), FAV would be better as resisting competition and biocontrol. Under higher nitrogen levels, the addition of adult weevils as in the previous scenarios does not seem to produce the striped pattern (Figure 7). A time-varying irregular pattern was produced by day 3000 (Figure 7a, b, c) and persisted indefinitely. The time series of mean values per square meter also show that the irregular pattern persisted though the whole simulation once the weevils had become established (Fig. 8).

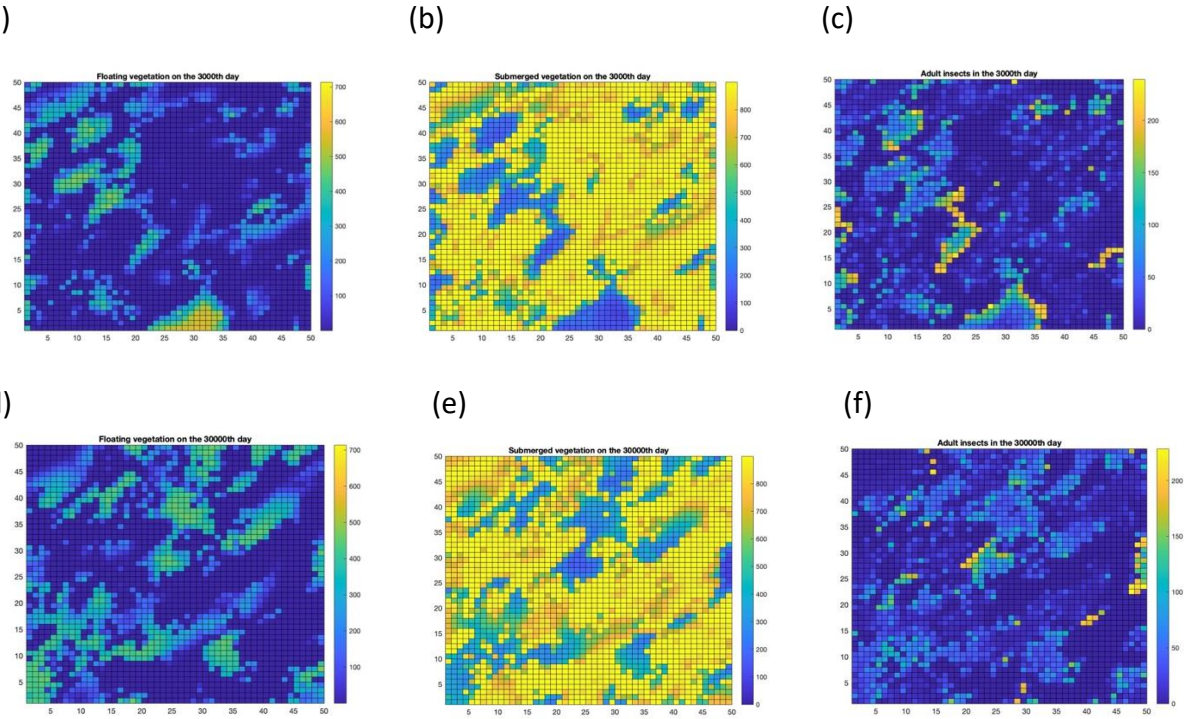


Fig. 7. FAV (left column) and SAV (center column) started from small randomly scattered biomasses and under high nitrogen (N=4). The adult weevils (right column) started from a square in the center on day 600. (a, b, c) irregular patterns of SAV, FAV, and adult weevils on the 3000th day. (d, e, f) The irregular pattern that persisted to day 30,000.

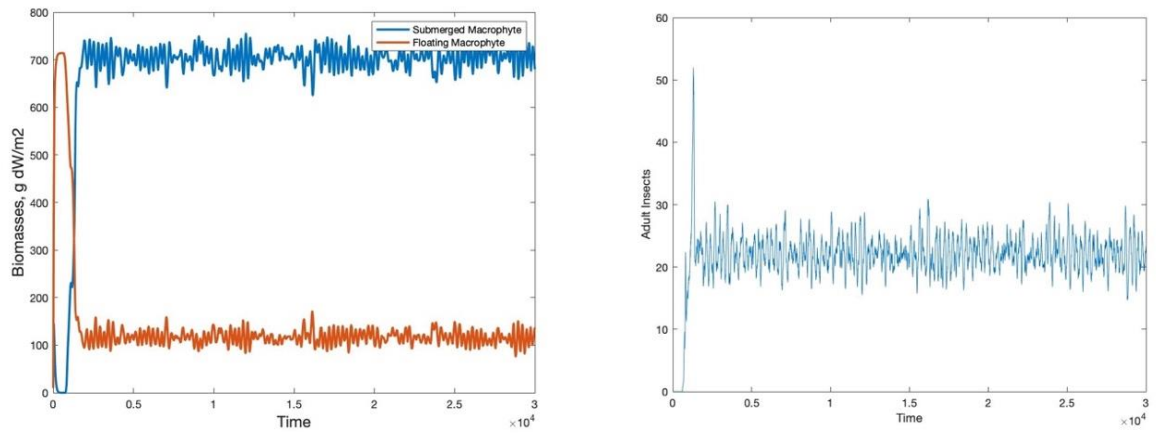


Fig. 8. (a) The mean biomasses (g dW m^{-2}) of FAV and SAV over 30,000 days. (b) The number of adults per square meter over 30,000 days.

Simulations 2 and 3 show that different nitrogen levels can result in different spatial pattern and biomasses of species, as the FAV biomass is higher in Simulation 3.

Effects of nutrient diffusion rates

In order to understand how nutrient diffusion rate, N_{diff}, affects the vegetation striped pattern with biocontrol, we used the high growth rate of *L. gibba* under intermediate nitrogen levels (N=2) as the baseline to do simulations because only $N = 2$ in the *L. gibba* case produced striped long transient pattern. Here, two different N diffusion rates, one very low and the other very high, were used.

Scenario 4. E. nuttallii competing with L. gibba, with biocontrol present, N = 2, N_{diff} = 0.03

For $N_{diff} = 0.03$, each day only 3% of nutrient leaves a cell. For that case, no striped pattern appeared (Fig. 9). Both FAV and adult weevils were reduced to very low values, though greater than zero (Fig. 10).

(a) (b) (c)

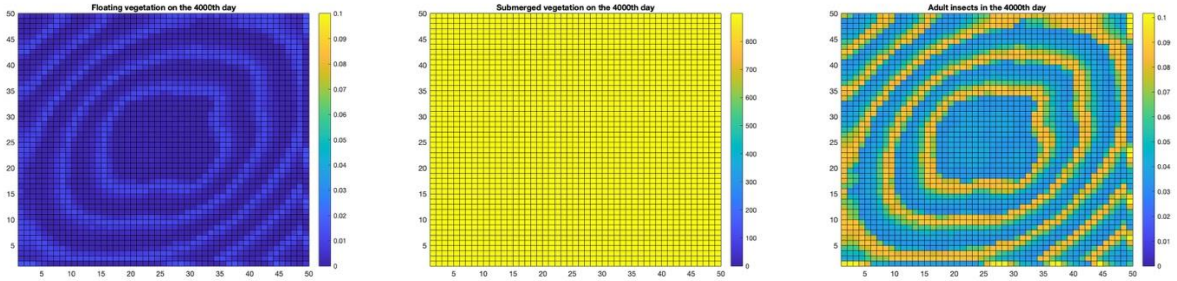


Fig. 9. (a) FAV, (b) SAV, and (c) adult weevils on day 4000. This pattern had persisted in this form through time. The symmetrically expanding pattern of adult weevils is caused by the continued input of adult weevils every 300 days. Adult weevils and FAV are at very low levels.

(a) (b)

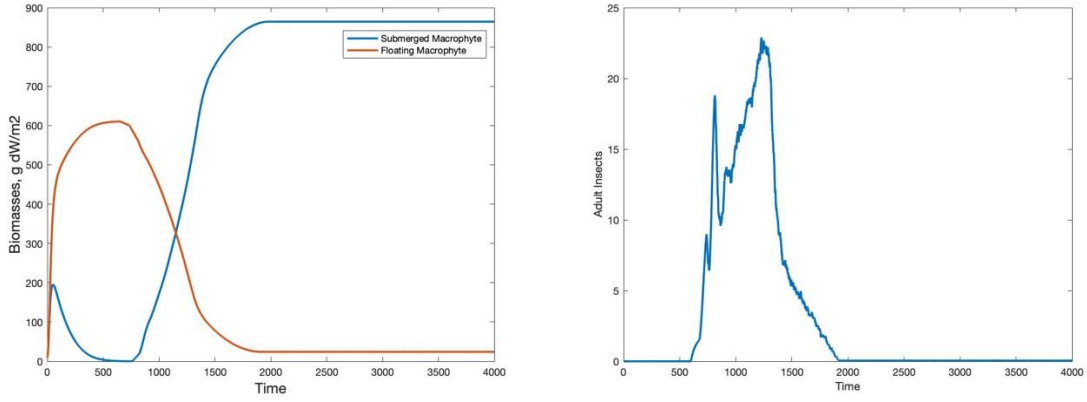


Fig. 10. (a) The mean biomasses of FAV and SAV (g dW m^{-2}) through time. (b) the mean number of adult weevils through time over 4000 days. Adult weevil numbers were small, but greater than zero.

Scenario 5. E. nuttallii competing with L. gibba, with biocontrol present, N = 2, $N_{diff} = 0.2$.

Here, high nutrient diffusion means that every day 20% nutrient leaves cell. Under high N diffusion rate, a striped pattern that is a long transient occurs (Fig. 11). In the time series of mean values, the long transient of striped pattern dissipates rapidly at about 36,000 days (Fig. 12).

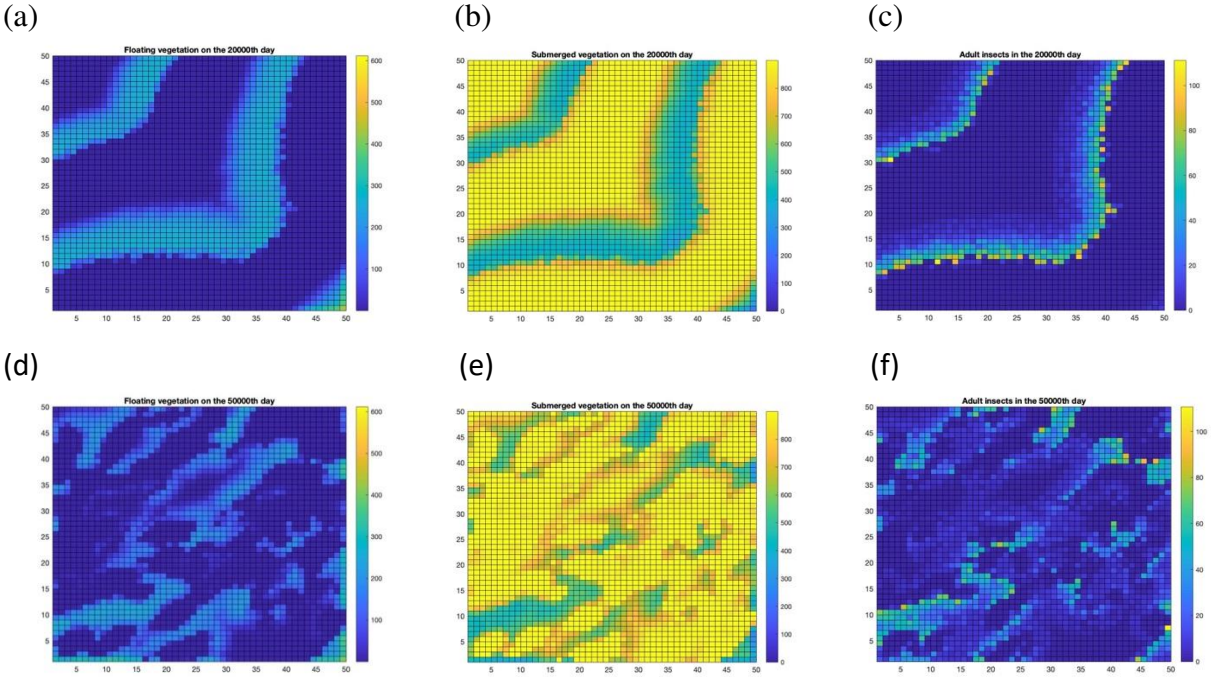


Fig. 11. FAV (left column), SAV (center column) started from small randomly scattered biomasses under intermediate nitrogen (N=2) and high nitrogen diffusion rate (N_{diff} = 0.20). The adult weevils (right column) started from a square of number in the center on day 600. (a, b, c) A regular striped pattern formed by day 5000 and is shown here on day 20,000. (d, e, f) The striped pattern dissipated rapidly starting at about day 36,000.

(a) (b)

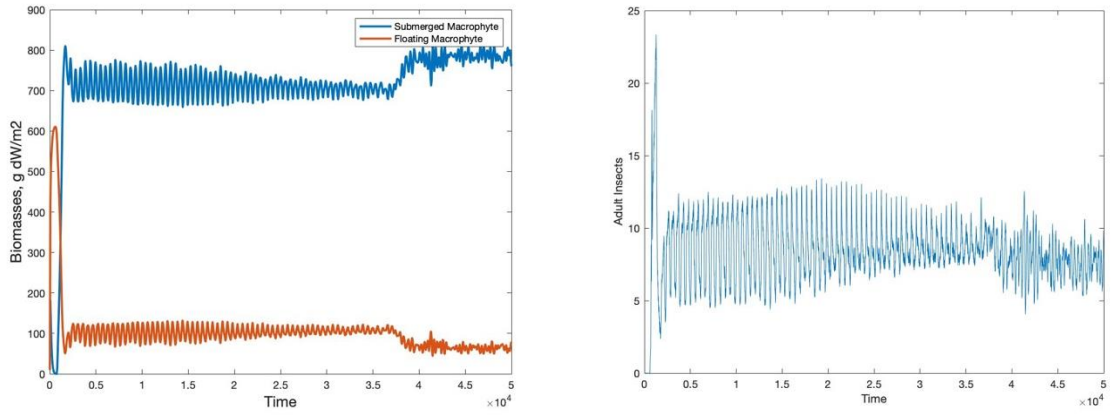


Figure 12. (a) The mean biomasses of FAV and SAV (g dW m^{-2}) through 50,000 days, showing the end of the long transient starting at about day 36,000. (b) the mean number of adult weevils (m^{-2}) through time over 50,000 days.

In the above simulations, adult insects were added every 300 days. Some earlier simulations showed only the first application of adults was needed to establish a persistent weevil population. However, it was still important to show that non-presence of these additions did not affect the transition of the striped pattern to the irregular pattern. That is shown below.

What is the effect of the addition of adult weevils every 300 days?

In some of the scenarios above, including Scenario 2, adult weevils were added at 300-day intervals throughout. We know that once the weevils are established, they remain in the system even if the addition of adults is ceased. There is still a question of whether ceasing to add adults affects whether and when the regular striped pattern is replaced by the irregular pattern. A scenario was performed to check whether cessation of adult weevil addition would cause the switch from the long transient to change.

Scenario 6. E. nuttallii competing with L. gibba, with biocontrol present, N = 2, $N_{diff} = 0.1$. *Addition of adult weevils every 300 days is ceased at day 10,000.*

This simulation is identical to Scenario 2, including that the same Matlab random number intiator, rand('state',8), was used in the simulation, except that periodic input of adult weevils ceased on day10000. The long transient striped pattern still ended at about the same time as in Scenario 2 (Figs. 13 and 14). This shows that the addition of adult weevils every 300 days

subsequent to the initial addition did not make a difference to the dissipation of the striped pattern.

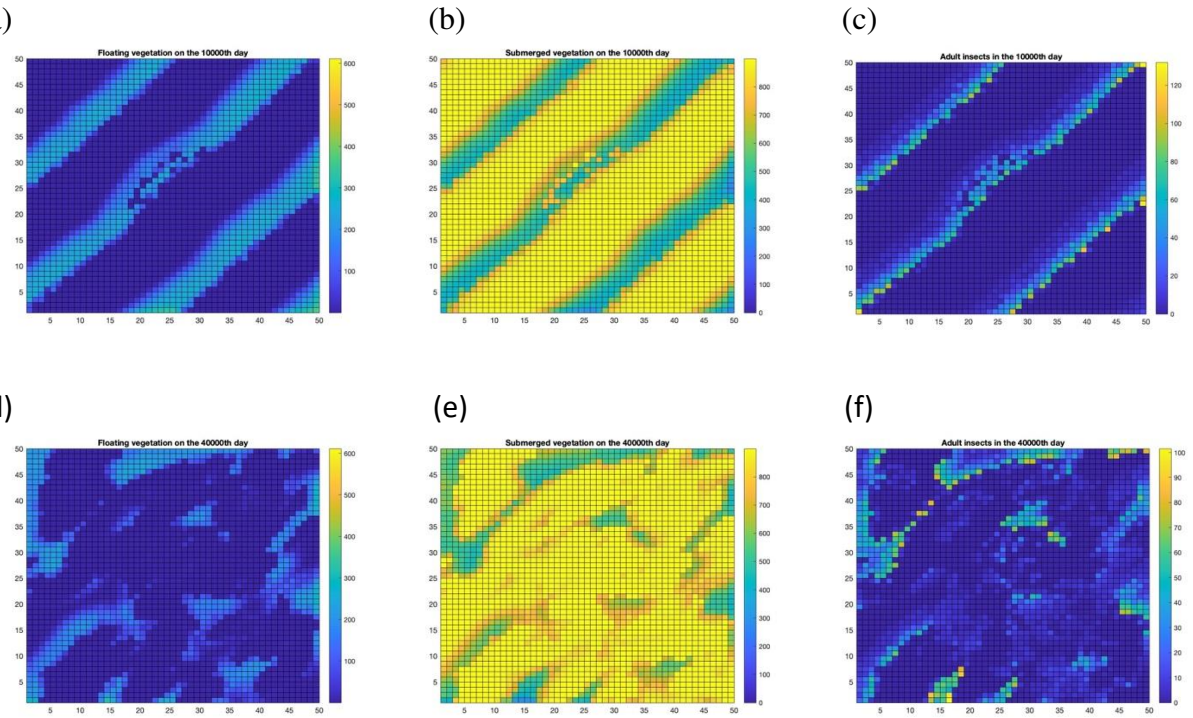


Figure 13. FAV (left column) and SAV (center column) started from small randomly scattered biomasses under intermediate nitrogen (N=2) and intermediate nitrogen diffusion rate, N_{diff}. The adult weevils started from a square of number in the center on day 300. (a, b, c) A regular striped pattern formed by day 5000 and is shown here on day 10,000. (d, e, f) The striped pattern dissipated rapidly starting at about day 15,000, with the resultant time-varying irregular pattern shown at day 40,000.

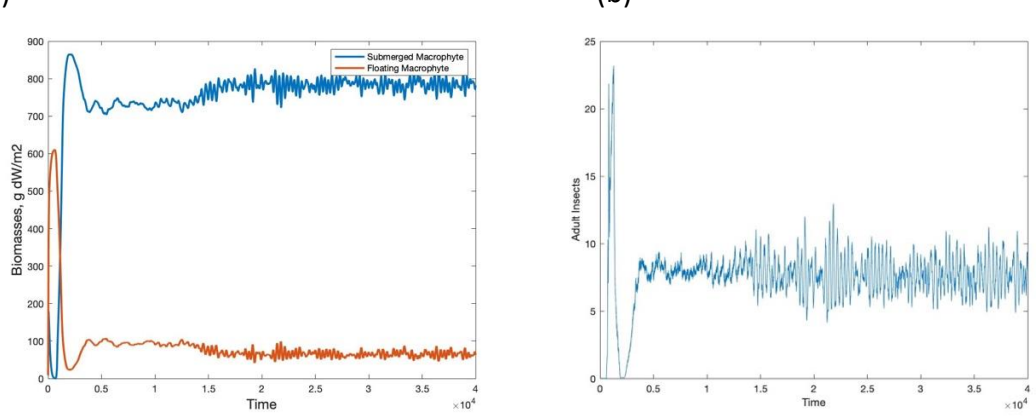


Figure 14. (a) The mean biomasses of FAV and SAV (g dW m^{-2}) through 40,000 days, showing the end of the long transient starting at about day 15,000. (b) the mean number of adult weevils (m^{-2}) through time over 40,000 days.

532
533 It is possible to study the CA simulation in finer time scale, as the simulations run on daily time
534 steps. This can allow the transition from the long transient regular striped pattern to the
535 apparently persistent irregular striped spatial pattern to be studied in great detail, both temporally
536 and at the level of individual spatial cells. In the Supplementary Information, using Simulation 2,
537 we focus on the period 13000-16000days because the transition from the long transient to the
538 irregular pattern occurs over that time period.
539

540 ## Discussion

541 A CA model was used to test the effectiveness of application of biological control insects on
542 water hyacinth (*P. crassipes*) in competition with an SAV (*E. nuttallii* here) to study how
543 biocontrol affects the FAV-SAV competition. The simulation results showed that adding
544 biocontrol would reduce *P. crassipes* to low values, even under high nutrient levels. Simulations
545 also revealed the emergence of a regular striped pattern of alternating FAV biomass, weevil
546 numbers, and SAV biomass, which is a long transient. What is new and interesting is that this
547 pattern emerged unexpectedly in a complex model designed to study biocontrol. Additional
548 simulations using parameters from another FAV showed that these emergent patterns are fairly
549 general.

550 There are four main variables in the model, SAV, FAV, nutrient, and the weevil
551 population, where the weevil population itself consists of five variables, eggs, L1 larvae, L2
552 larvae, pupae, and adults. It is possible that all variables are involved in the emergence of the
553 pattern. The nutrient, N, must be at high enough levels to activate F, the FAV. The FAV inhibits
554 SAV, the weevils inhibit FAV, and SAV inhibits the weevils, as the weevils cannot feed on
555 SAV. Therefore, the FAV, SAV, and weevils undergo a spatio-temporal interaction that is
556 reminiscent of 'rock-paper-scissors' system. Rock-scissors-paper interactions are typically
557 envisioned as competition networks in which species one can outcompete species two, which can
558 outcompete species three, which can outcompete species one, which can result in coexistence of
559 all three in oscillatory dynamics. Although Sigmund (1995) was skeptical that such interactions
560 existed in nature, cases have been noted among marine sessile organisms (Frean and Abraham
561 1975) and there is an extensive theory and modeling literature (e.g., May and Leonard 1975;
562 Frean and Abraham 2001; Károlyi et al. 2005; Ying et al. 2007; Roelke and Eldridge 2010;

563 Galeano et al. 2011; Park 2021). In addition, other types of networks can have analogous non-
564 transitive features. The present case contains only one competitive interaction, that of FAV and
565 SAV, where the former is the better competitor here. The weevil's negative effect on FAV is
566 through exploitation and the negative effect of SAV on the weevil is simply that the weevil
567 cannot be sustained by SAV. The net result has the appearance of being competition for space in
568 the form of a traveling wave with each in pursuit of one of the others.
569 In addition to the rock-scissors-paper analog biological structure, the nutrient diffusion
570 rate may plays a role in the dynamics, although this has only been slightly studied here. It is
571 possible that the time delay in the weevil life cycle, in which there are 75 days from eggs to
572 adults, plays a role as well.
573 Self-organization is important in studying spatial heterogeneity and its consequences in
574 the ecosystem. The sources for 'activation' and 'inhibition' are two basic mechanisms for scale-
575 dependent feedback, one is by resource distribution, the other one is by amelioration of physical
576 stress (Dong and Fisher 2019). Spatial self-organization has been recognized in many other
577 systems caused by some agents, and these agents themselves are components of patches in the
578 self-organized landscape (Dong and Fisher 2019). These agents can be physical or biological.
579 For example, sand grains are produced by regularly spaced dunes and ripples are caused by
580 waves or wind. In our system, the biocontrol weevil is the primary driver of the regular striped
581 pattern, as no such pattern emerges in the system without the weevils. The self-organization on
582 the landscape is driven by biocontrol, and biocontrol itself is also the components of patches and
583 shows the stripped pattern too.
584 A difference in our study from many other studies is that the patterns in our model do not
585 result from observing an empirical pattern and attempting to develop a model to duplicate the
586 pattern in simulations. Instead, the patterns we found emerge from a model based on
587 parameterization of experimental data regarding the components of the model, the SAV, FAV,
588 and weevils. We do not know of any actual empirical patterns of aquatic vegetation that are
589 analogous to the striped patterns in the model. Therefore, the model results are predictions of
590 what could occur in nature or experiment under the right conditions. What are the 'right
591 conditions' also includes starting conditions, such as the spatial patterns of initial input
592 vegetation and adult weevils, including initial and any later inputs of the latter.
593 Exploring the mechanisms resulting in different formation patterns in an ecosystem is a

challenge because of the many parameters that can potentially be involved, requiring substantial numbers of simulations. Roman et al. (2016) developed a theoretical approach to understand spatial organization in food web. Díaz Rodrigues et al. (2012) used analytical methods and computer simulations to study spatiotemporal dynamics of predator-prey system. Our finding is a new step in studying the aquatic vegetation-biocontrol-nitrogen system. Therefore, our next step is to study the factors leading to this pattern phenomena. An advantage of the model is that we can not only predict the possible emergence of a pattern but also investigate how the pattern develops. The simulation provides output on a small time-step (a day is used) and small spatial scale (one square meter resolution). It is possible to study in detail exactly where and when some local stochastic event has occurred, and how it amplifies. An indication of how this can be done is shown for the dissipation of the striped pattern in Fig. S1 in Supplementary Information, along with some discussion, although this is only a start.

The model is limited in a number of ways. Although Scenario 1 was based largely on published model components and parameters, in the subsequent scenarios we used combinations of FAV and biocontrol agents that might not occur in nature. That enabled us to obtain clearer results, but they should only be regarded as theoretical at this point, not specific predictions. The parameter of nutrient diffusion, N_{diff}, was simply guessed, although a range of values was used. The movement rules of adult insects were also assumed. In the model adults only move from one cell to adjacent cells on a daily time step. Although spatial patterns have been observed in aquatic ecosystem, none that we know of approach the precision of patterns in our model. One reason may be that wind and currents, not to mention seasonality, which was ignored, would tend to have a major effect on any self-organized patterns that might emerge. The patterns in our model emerged only on the order of many hundreds of days, which is probably an unrealistic time scale for there to be no disturbances that would prevent such patterns from emerging.

Nonetheless, out model results provide clues to circumstances under which both spatial patterns and long transients could occur, providing a baseline that can be extended to other regions of parameter species. The emergence of regular spatial patterns and of long transients are important areas of study in ecology and other scientific disciplines because they provide valuable insights into the underlying processes and dynamics of complex systems. The emergence of two long spatio-temporal patterns can reveal how a system responds to perturbations and its resilience or adaptability.

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Data availability

The study does not use any data.

Competing interests

The authors declare no competing interests.

Author Contributions

Both authors contributed to the study conception and decline. First draft of the manuscript was written by Linhao Xu and Donald DeAngelis. Both authors commented on the manuscript. Both authors read and approved the final manuscript.

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