Regular pattern formation regulates population dynamics: Logistic growth in cellular automata

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ABSTRACT

Regular pattern formation is common in nature, but its ecological role in population dynamics is not well understood. In this article, we present a logistic probabilistic cellular automata (LPCA) model that combines a basic logistic growth model with two-dimensional spatial dynamics to simulate regular pattern formation. For model generality, only propagation and competition were assumed to occur in LPCA, and their dynamics follow local logistic growth. Simulation outcomes show that the resource scarcity and shape of the neighborhood are the main causes of different regular patterns. We use reference data from an arid ecosystem in Shapotou to parameterize the LPCA model and find that the pattern shifts from spots, labyrinths, to gaps with decreasing resource scarcity and that anisotropic neighborhoods generate banded patterns. The influences of regular patterns on population dynamics were studied by comparing the LPCA model and its mean field approximation (MFA), which discards particular spatial configurations and makes global predictions of population dynamics. The outcomes show that regular patterns can regulate population dynamics and alter equilibrium population size. Furthermore, regular patterns work as optimized spatial configuration to balance space and resource competition.

1. Introduction

Regular pattern formation is very common in real ecosystems (Pringle and Tarnita, 2017), such as arid ecosystems (Klausmeier, 1999; Couteron and Lejeune, 2001; Hillerislambers et al., 2001), savanna ecosystems (Lejeune et al., 2002; Sternberg, 2001), wetland ecosystems (Foster et al., 1983; Rietkerk et al., 2004; Wetzell et al., 2005; Koppel et al., 2015), mussel beds (Koppel et al., 2005, 2008), and coral reefs (Mistr and Bercovici, 2003; Somathilake et al., 2018). Due to self-organization, localized ecological interactions are repeated under homogeneous conditions, spontaneously generating distinct emergent properties at a larger scale, including regular pattern formation (Deutsch and Dormann, 2005). A number of cases of regular spatial patterning have been reported over the past 15 years (Pringle and Tarnita, 2017). The reported regular patterns, including gaps, labyrinths, spots, stripes, and rings (Rietkerk and Koppel, 2008; Pringle and Tarnita, 2017), share similar features and exhibit the same cluster size and grain pattern instead of random configurations. Theoretical ecologists increasingly emphasize that pattern formation has a close relationship with ecological stability, diversity and catastrophic shifts (Rietkerk and Koppel, 2004, 2008; Koppel et al., 2015). However, how self-organized regular patterns affect temporal population dynamics is not well understood (Hart and Marshall, 2009; Crone and Griffith, 2016). An in-depth understanding of the ecological roles of regular patterns is of vital importance for population management and sustainable development (Kauffman et al., 2004).

Previous studies of spatial self-organization were conducted under a well-recognized framework of scale-dependent positive and negative feedbacks (SDFs) (Pringle and Tarnita, 2017; Rietkerk and Koppel, 2004; Deangelis and Yurek, 2017). Models under SDFs couple short-distance positive feedbacks with long-distance negative feedbacks to explain emergent spatial patterning, which is based on the famous activator-inhibitor principle (Rietkerk and Koppel, 2008; Pringle and Tarnita, 2016). With the same theoretical foundation, those ecological mechanisms are diversified and contingent on different types ecosystems or biological groups (Anderson and Neuhauser, 2002; Thompson and Daniels, 2010; Martínez-García et al., 2014). For model generality, we adopt only two most intrinsic population behaviors, propagation and

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competition that are ubiquitous among different sessile or semisessile populations following the minimum ecological requirements for regular pattern formation (Couteron and Lejeune, 2001; Maruva and Shnerb, 2006; Martínez-García et al., 2014). We drew on logistic growth model, one of the most fundamental models in ecology, to describe their dynamics. Then we combined logistic growth model with spatially explicit probabilistic cellular automata (PCA) to get the two-dimensional spatial formulation, since CA as important biological and ecological modeling system serve as important tool for spatial processes, especially the interplay between propagation and competition (Anderson and Neuhauser, 2002; Mendonça and Gevorgyan, 2017). Firstly, individual-based PCA can better describe stochastic and discrete individual behaviors in population, concerning our primary focus on population dynamic (Simpson et al., 2007). And the probabilistic transition rule in CA is representative of stochastic processes in nature (Wang et al., 2003). Secondly, the exclusive space occupation of cell and concept of neighborhoods in CA offers a simpler method for space competition and local interaction than kernel-based integro-differential equations (Deutsch and Dormann, 2005). Allowing for model simplicity and generality, we introduce this logistic probabilistic cellular automata (LPCA) model based previous work to study the growth of sessile organisms competing for space and resources (Boccara and Fuks, 1997; Mendonça and Gevorgyan, 2017).

The primary objective in this article is to study the role of regular patterns in vegetation dynamics. Hence, we used mean field theory to deduce the mean-field approximation (MFA) of LPCA. Mean field theory concerns the behavior of complex stochastic models and simplifies interactions into an averaged effect (Kadanoff, 2009). The mean field theory for CA is based on the assumption that the states of cells in the lattice are independent (Hatzikirou et al., 2010), which means that MFA is able to eliminate the influence of particular spatial configurations and makes global predictions of the population dynamics of LPCA. Therefore, we compared the population dynamics of MFA to those of LPCA to elucidate the role of regular patterns in population dynamics. In summary, we hypothesized that: 1) propagation and competition can generate regular patterns, and these specific spatial configurations cause spatially heterogeneous population dynamics, followed by change in global dynamics, and 2) regular pattern can stabilize population dynamics because of its self-organizing characters.

2. Model definitions

The logistic equation (Eq. (1)), first coined by Verhulst (1838), is one of the most basic equations in ecology (Shnerb, 2004), i.e.,

\[
\frac{dN}{dt} = rN \left( \frac{K - N}{K} \right). 
\]  

(1)

where \( N \) is population size, \( t \) is time, \( r \) is the intrinsic rate of natural increase, and \( K \) is the carrying capacity. However, it is spatially implicit and assume perfect mixing of population. In real ecosystem, the dynamics of a plant is directly affected by its neighborhood, thus, spatial configuration inevitably influences global dynamics. In order to incorporate spatial information, we coined two parameters, namely, \( \alpha \) and \( \beta \), that represent the resource consumption rate and resource supplementation rate to logistic growth model, and get,

\[
\frac{dN}{dt} = rN \left( 1 - \frac{n^*}{\beta n^*} \right) 
\]

(2)

where \( n \) is the number of occupied cells in interaction neighborhood \( V \), and \( n^* \) is the total number of cells in \( V \). \( \Delta t \) is the time step for each iteration, and \( r \) is the intrinsic rate of natural increase. In particular, \( \beta n^* \) is corresponding to carrying capacity \( K \) and \( \alpha n^* \) reflect the influence from neighborhoods. General CA are defined with four tuples: the lattice space, state set, neighborhood, and transition rule (Deutsch and Dormann, 2005). We will detail the four tuples in the following sections.

2.1. Lattice and cells

The LPCA are defined on a two-dimensional lattice \( \mathcal{L} \) with \( I \times I \) cells \((i, j) \in \mathbb{N}\), and the cells are of equal size \( |r_i| \), \( i \) is determined by the mean size of the study objects, e.g., the cell for a tree takes meters as its scale, and the cell for a moss takes centimeters as its scale.

\[
\mathcal{L} \subseteq \mathbb{N}^2 = \{ r : (r_1, r_2), r_1 \in \{1,2, ..., \}, r_2 \in \{1,2, ... \} \}. 
\]

(3)

The small square in a lattice is called a cell and is identified by its position \( r \in \mathcal{L} \). In LPCA, a cell is either vacant or occupied by organisms; thus, we assign the cell a state value \( s(r) \in \varepsilon \), i.e.,

\[
s : \mathcal{L} \rightarrow \varepsilon, \varepsilon = \{0,1\}. 
\]

(4)

The multi-cell configuration \( s \in I^{\mathcal{L}} \) of the lattice is defined by the state value of ordered subset \( \mathcal{M} \), i.e.,

\[
s : = \{ s(r) \}_{r \in \mathcal{L}}, \mathcal{M} \subseteq \mathcal{L}. 
\]

(5)

2.2. Neighborhood and matrix

Due to the spatially implicit form of logistic growth model, its predictions are often divergent from real population dynamics (Jongejans and de Kroon, 2005). Therefore, we incorporate local spatial interaction rules in LPCA, i.e., the temporal dynamics of a cell are only affected by its neighbors in our model. Two types of interaction neighborhoods \( V \) are adopted (Fig. 1). Isotropic neighborhoods cover a round region (the Von Neumann neighborhood is a famous case with radius = 1), which is defined as having a particular radius \( R \), i.e.,

\[ (a) \text{ Isotropic neighborhood} \quad (b) \text{ Anisotropic neighborhood} \]

Fig. 1. Templates of interaction neighborhoods (gray and black cells) for the black cells.
\[ A^{(r)} = \{ c = (c_x, c_y); c_x, c_y \in [-R, \ldots, R] \wedge \sqrt{c_x^2 + c_y^2} \leq R \}. \]

The interaction neighborhood could also be anisotropic. For example, strips in arid ecosystems are closely related to sloped topography and resource flow, and the resources flow alters the range of interactions in different directions (Aguirar and Sala, 1999) For generalization, we introduce an anisotropic neighborhood that is a center-skewed round region to embody the anisotropic local interaction. Resource flow also affects the shape of interaction neighborhood; thus, elliptical shape better matches reality. But preliminary test demonstrated that elliptical shape only stretches patterns produced by round neighborhood, the skewed center is the main cause for bands. For better comparison of two neighborhoods, we abandoned the elliptic shapes. The anisotropic neighborhood \( A^{(r)} \) is defined as

\[
A^{(r, ANU)} = \{ c = (c_x, c_y); c_x, c_y \in [-R, \ldots, R] \wedge \sqrt{(c_x - s_kx)^2 + (c_y - sk_y)^2} \leq R \}
\]

where \( s_kx \) and \( sk_y \) denote the skew of the cell from the center of the round region.

2.3. Transition rules

The dynamics of LPCA are determined by the local transition rule \( \mathcal{R} \); \( \mathcal{R} : \varepsilon \rightarrow \varepsilon \), which follows the definition from Eq. (2). In real ecosystems, ecological events are usually stochastic; thus, the probabilistic transition rule \( \mathcal{R} \) is adopted. The Updated cell state \( s(r, k + 1) \) depends on two values \( n \) and \( s(r, k) \) of cells in the neighborhood. The exact transition probabilities are listed in Table 1. The \( W_0 \) indicates propagation that vacant cells occupied by plant, item \( 1 - \alpha n / \beta n^* \) determines the local density-dependent resource competition. If \( 1 - \alpha n / \beta n^* > 0 \), the vacant cell has the potential to be occupied, and the transition probability can be delineated by total growth \( \Delta t \cdot r \cdot n(1 - \alpha n / \beta n^*) \) divided by the size of the growth region \( n - 1 \) to get growth probability per cell. If \( 1 - \alpha n / \beta n^* < 0 \), over-fierce resource competition leads to competitive exclusion (\( W_0 \)). The \( W_0 \) and \( W_1 \) indicate a cell remain previous state. It is worth noting the transition probability should be between 0 and 1; thus, a small \( \Delta t \) should be used.

3. MFA for LPCA

Mean-field theory assumes that the states of cells in the lattice are independent at all times. Therefore, we upfront give the general mean-field equation for probabilistic CA (Deutsch and Dormann, 2005).

\[
x_{ij}(k + 1) = \sum_{(z_1, \ldots, z_n) \in \varepsilon^*} W((z_1, \ldots, z_n) \rightarrow z^1) \prod_{i = 1}^{n} x_i(t) \delta_{z_i,z_i^1},
\]

where \( x_i(k) \in [0,1] \) is a spatially averaged value denoting the expected density of a cell state \( z_i^1 \) on the lattice at iteration \( k \); \( (z_1, \ldots, z_n) \) denotes the configuration of neighborhood \( \mathcal{A} \), and \( \sum_{(z_1, \ldots, z_n) \in \varepsilon^*} \) traverses every possibility \( (z_1, \ldots, z_n) \in \varepsilon^* \), and \( W \) is its corresponding transition probability to \( z_i^1 \). The \( \prod_{i = 1}^{n} x_i(t) \delta_{z_i,z_i^1} \) is a product of expected density for all cells in neighborhood, \( \delta_{z_i,z_i^1} \) denotes the expected density of state \( z_i^1 \) for cell \( i \); \( \delta_{u,v} \) is the Kronecker delta, i.e., \( \delta_{u,v} = 1 \) if \( u = v \) and \( \delta_{u,v} = 0 \) if \( u \neq v \). In LPCA, there are only two states for a cell (\( \varepsilon = \{0,1\} \)); thus, \( x_i(k) = 0 \). The ergodic transition probability \( W((z_1, \ldots, z_n) \rightarrow z_i^1) \) defined in neighborhood space is more complicated. Therefore, we group all possible states configuration of neighborhoods \( (z_1, \ldots, z_n) \) in LPCA by occupied cell state \( s(r, k) \) and the number of occupied cells \( n \), and obtain

\[
x_i(k + 1) = \sum_{n=0}^{n^*} \left( \sum_{(z_1, \ldots, z_n) \in \varepsilon^*} W_0 \cdot x_0^n \delta_{z_i,z_i^0} + \sum_{t=0}^{t=n^*-1} W_t x_t^n \delta_{z_i,z_i^t} \right).
\]

The contribution of each cell in neighborhood \( \mathcal{A} \) to \( n \) is location independent; thus, the conditional sum can be refined as

\[
\sum_{t=0}^{t=n^*-1} W_t x_t^n \delta_{z_i,z_i^t} = \left\{ \begin{array}{ll} (n^* - 1) & n^* \geq 1, n = n^* \\
0 & n^* = 0 \\
(n^* - 1) & n^* = n, n = n^* \\
0 & n = n^* - 1 \end{array} \right.
\]

Combining Eqs. (9), (10) and (11), the mean-field equations for LPCA are given by

\[
x_i(k + 1) = \sum_{n=0}^{n^*} n + \Delta t \cdot \frac{m}{\beta n^*} \left( n^* \right) x_i(k)^{n^*} / (n - 1) x_i(k) x_i(k)^{n-1} - n^* - 1 \\
\]

When \( n = 0 \) or \( n - 1 = 0 \), the item in \( \sum_{n=0}^{n^*} \) equals to 0. Then we change the lower bound of summation and binomial coefficient and get

\[
x_i(k + 1) = \left( \Delta t \left( \frac{\alpha n^*}{\beta n^*} + \frac{\alpha n^*}{\beta n^*} - \Delta \alpha \right) \right) x_i(k) \sum_{n=0}^{n^*} \left( \begin{array}{c} n^* \\
(n - 1) \end{array} \right) x_i(k)^{n^*} / (n - 1) x_i(k) x_i(k)^{n-1} - n^* - 1 \\
\Delta t \left( \frac{\alpha n^*}{\beta n^*} - \Delta \alpha \right) x_i(k) \sum_{n=2}^{n^*} \left( \begin{array}{c} n^* - 2 \\
(n - 2) \end{array} \right) x_i(k) x_i(k)^{n-2} - n^* - 2 \\
\]

According to binomial theorem, the two summations equal to 1; We put \( \Delta x_i = x_i(k + 1) - x_i(k) \) into Eq. (14) and get,

\[
\Delta x_i / \Delta t = r \cdot x_i(k) \left( 1 - \alpha (1 + x_i(k)) (n^* - 1) / \beta n^* \right)
\]

It clear shows that density dependent \( \Delta x_i \) is influenced by \( n^* \), which suggests size of neighborhood affect dynamics. The MFA can be applied to global scale that \( x_i \) is equal to the number of occupied cells divided by the total cells number, and neighborhood scale with \( x_i = n / n^* \). In neighborhood scale, the third item become \( 1 - q(n - 1)^{n^* - 1} / n^* + 1 / \beta n^* \), which is approximately equal to \( 1 - \alpha n / \beta n^* \) with big \( n^* \).
4. Parameterization and initiation

We use a typical case of an arid ecosystem to parameterize the LPCA model, where water limitation is the main source of stress for vegetation. $\beta$ and $\alpha$ are the water supplementation rate in bare soil and water consumption rate of vegetation. The reference ranges for parameters were based on water balance data from the Shapotou Desert Experimental Research Station, Chinese Academy of Sciences (list in Table 2). The research station borders the Tengger Desert, located in the central part of western China ($N 37.27^\circ, E 104.57^\circ$). The climate at the site is characterized by abundant sunshine and a low relative humidity. The mean annual precipitation is 188.2 mm (1952–2009), and the mean annual temperature is $9.6^\circ$C. The potential evapotranspiration during the growing season (May–September) is 2300 mm–2500 mm.

The windy season lasts from September to April, with an average wind velocity of 2.6 ms$^{-1}$. The dominant plants include Caragana korshinskii, Artemisia ordosica and some herbaceous plants. The setting of $\alpha$ and $\beta$ are based on water balance, i.e.,

$$P = E + T + R + D + \Delta S,$$

where $P$, $E$, $T$, $R$, $D$ and $\Delta S$ are precipitation, evaporation, transpiration, surface runoff, soil water recharge and soil water change, respectively, with millimeters (mm) as the units. For simplicity, we assume that $R$ and $\Delta S$ equal 0. $\Delta S = 0$ means that the water budget of vegetation is balanced. $R = 0$ is common in drylands because such zones are dominated by small precipitation events (Li et al., 2009). Thus, $\beta$ is depicted by $P - E - D$, which represents the net water supply without vegetation. $\alpha$ is depicted by $T$ because the assimilated water is negligible. $T$ uses the mean value of transpiration of Caragana korshinskii and Artemisia ordosica. In principle, this approximate parameterization is incorrect, because these indexes are interdependent and context dependent (Li et al., 2009, 2014; Zhang et al., 2016). However, the approximations capture the main concepts for water consumption ($\alpha$) and water supplementation ($\beta$); thus, they are useful and acceptable for LPCA.

To initialize the LPCA, a randomly distributed lattice with a global density of 1% was set, i.e., each cell in the initial lattice was assigned an equal probability ($P = 0.01$) of being occupied. The boundary of real habitat is usually unlimited or fuzzy; therefore, we impose a periodic boundary condition for digital simulation. The simulation time was set to 50 years (100 iterations). Then, we set three levels of $\beta$ (Table 2) combined with two kinds of neighborhoods (Fig. 1) for simulations. Notably, striped patterns are frequently related to resource flow or slope topography (Rietkerk and Koppel, 2008; Pringle and Tarnita, 2008).

Table 2

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Units</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\lambda$</td>
<td>1 m$^2$</td>
<td></td>
<td>Cell size</td>
</tr>
<tr>
<td>$l$</td>
<td>50</td>
<td></td>
<td>Side length</td>
</tr>
<tr>
<td>$r$</td>
<td>2 year$^{-1}$</td>
<td></td>
<td>Intrinsic growth rate</td>
</tr>
<tr>
<td>$\Delta t$</td>
<td>0.5 year</td>
<td></td>
<td>Time step</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>63.7 mm year$^{-1}$</td>
<td></td>
<td>Resource consumption rate</td>
</tr>
<tr>
<td>$\beta$</td>
<td>15, 35, 55 mm year$^{-1}$</td>
<td></td>
<td>Resource supplementation rate</td>
</tr>
<tr>
<td>$R$</td>
<td>6</td>
<td></td>
<td>Radius of round neighborhood</td>
</tr>
<tr>
<td>$\delta_x$</td>
<td>$-2$, $2$</td>
<td></td>
<td>Skew of neighborhood on the x axis</td>
</tr>
<tr>
<td>$\delta_y$</td>
<td>1</td>
<td></td>
<td>Skew of neighborhood on the y axis</td>
</tr>
</tbody>
</table>

The parameter values are set to represent vegetation in arid ecosystem, based on (Zhang et al., 2016, 2006; Huang et al., 2015).

Fig. 2. Patterns generated by LPCA with three parameter values and two kinds of neighborhoods. (a–c) refer to isotropic neighborhoods with different resource supplementation rate ($\beta = 15, 35, 55$); (d–f) refer to anisotropic neighborhoods with different resource supplementation rate ($\beta = 15, 35, 55$) and upward refers to upslope. The iteration number is 100, which equals 50 years.
5. Results

The spatial pattern of an assemblage can be described by scale and grain. Pattern scale describes the mean size between patches and gaps. It is easy to imagine that pattern size is closely related to the size of the neighborhood (N*) and cell (ir) in LPCA. Preliminary computation illustrated that even the smallest neighborhood (e.g. the Von Neumann neighborhood) could generate regular patterns. Pattern grain is this article is descriptive (spots, labyrinths, gaps and stripes). Fig. 3 displays the simulation process with 100 iterations (50 years), where regular patterns gradually form and present sharpened edges. When \( \beta = 15 \), spots emerge in the pattern, but the edges are noisy because of the probabilistic characters of LPCA (Fig. 2a); when \( \beta = 35 \), labyrinths emerge, where isolated patches intertwine with each other, forming labyrinthine structure (Fig. 2b); and when \( \beta = 55 \), gaps emerge that resembles the “opposite version” of spots, with the highest density among the three (Fig. 2c). In general, spots, labyrinths and gaps share certain intrinsic similarities: 1) they have the same pattern scales, even with differences in density; and 2) the shape and distribution of regular structures in patterns are isotropic in that they demonstrate uniformity in all orientations. By contrast, an anisotropic neighborhood generates stripes in the vegetation pattern. The stripes broaden with increasing \( \beta \), but the scales remain the same.

The comparison between the LPCA and MFA is shown in Fig. 3, where we ran the LPCA model 1000 times to obtain the density distribution. The confidence interval was set to 95 %. The MFA (eq. (15)) is in the “difference form”. To obtain a smoothed curve, we transferred the MFA to the “differential form” and used a numerical solver for integration. In general, the shape of the neighborhood does not affect the outcome of MFA. Based on Eq. (15), the dynamics are only affected by the total number of the neighborhoods (N*). In addition, the growth rate in the MFA is slightly slower than that in the LPCA in the early iterations (t < 5) because the spatial configuration dampens the global growth rate through uneven propagation and competition. In latter iterations, the trajectories are divergent among different values of \( \beta \). When resource supplementation is low (\( \beta = 15 \)), final population size is higher in LPCA than in MFA; when resource supplementation is moderate (\( \beta = 35 \)), the growth trajectories are generally the same; and when resource supplementation is high (\( \beta = 55 \)), vegetation density in the LPCA increases to the same level as that in MFA and then gradually decrease. In sum, the simulation results suggest that regular patterning could regulate population size, which complies with our first hypothesis.

6. Discussion

In the simulation of LPCA, spots, labyrinths, and gaps emerge on the lattices (Fig. 3), indicating that propagation and competition alone can generate regular patterns, in line with Couteron and Lejeune (2001). Previous studies basically followed a similar scenario, in which neighboring individuals facilitating each other by resources concentration or stress amelioration produce short-range positive feedbacks, while distant individuals at a high density generate long-range negative feedbacks by resource competition (Pringle and Tarnita, 2017; Gilad et al., 2004; Kletter et al., 2009). However, mechanisms of facilitation are disputable in many cases and not ubiquitous among ecosystems (Brooker et al., 2008; Couteron and Lejeune, 2001; Martinez-Garcia et al., 2013). Thus, we used propagation instead, in order to release the prerequisite of regular pattern formation from facilitation, given that propagation and competition are generally thought to be intrinsically density dependent and scale dependent in nature (Couteron and Lejeune, 2001; Koppel et al., 2015). The propagation adopted in LPCA is significantly different from that in Fisher’s reaction-diffusion equation (Fisher, 1937) with two-order Laplacian operator for dispersal. By contrast, our propagation and death are coupled in transition rules (Table 1) and reflect scale dependence, where \( n \) couples the spatial scale and feedback because \( n \) reflect the size of regular structures and transition probability (\( W_{i,j} \), \( W_{i,j} \)) altogether in a neighborhood. Taking spots structure as an example, small size of a spot (small \( n \)) relates positive feedback for local population, while big spot (large \( n \)) causes senescence and shrinkage of spots from competition. By these means, the pattern formation of LPCA is still under the framework of SDs.

The simulation also demonstrates that regular patterns emerge when \( 0 < \beta / \alpha < 1 \), which suggests that resource scarcity is the main driver of regular spatial patterns. This finding was also reported by Lejeune et al. (2002), in which an interaction-redistribution model was proposed to study vegetation dynamics. As in this article, the interaction-redistribution model also abstracted different kinds of resources. In general, the patterns shift from spots and labyrinths to gaps as resource scarcity diminishes (Fig. 2). Under extreme condition, stable homogeneity in spatial pattern occurs when \( \beta \leq \alpha \) or \( \beta \rightarrow 0 \). In addition to resource scarcity, the shape of the neighborhood also affects pattern grains. Fig. 2 (a–c) shows that patterns generated by isotropic neighborhoods have no preference in direction. This finding accords with earlier observations in the Patagonian steppe (Soriano et al., 1994), where shrubs can establish in any location with spotted vegetation patches. By contrast, anisotropic neighborhoods generate stripes on the lattice (Fig. 2d–i), and the stripes broaden with decreased resource scarcity. This finding is in line with previous evidences that the establishment of shrubs in banded vegetation on slopes exhibits anisotropy (Thiery et al., 1995). That is, the building phase of shrubs occurs upslope of the vegetation bands, and the degenerative phase occurs downslope (Thiery et al., 1995; Aguiar and Sala, 1999). In addition, the simulation shows that stripes move upward opposite to resource flow, which accords with observations of Deblauwe et al. (2012). This finding further strengthens our confidence in LPCA.

Mean field theory is commonly used to predict the global behavior of complex systems, and this bottom-up method provides a useful, spatially implicit approximation irrespective of spatial variation (Kadanoff, 2009). Based on the comparison between the LPCA and the MFA, we conclude that there are two different phases in spatial explicit population growth: the logistic growth phase (t < 5) and the pattern formation phase (t > 5). The logistic growth phase is characterized by local density dependence in which local density and particular spatial configurations affect global growth. The results show that the MFA increases slightly faster than the LPCA, which suggests that nonuniform distributions may dampen population growth, and the logistic growth model may overestimate the overall growth. In addition, we perform 1000 simulations with different initial lattices and find more variation (e.g., the width of the confidence interval) in the logistic growth phase, which further emphasizes the influence of spatial configuration on population dynamics. By contrast, in pattern formation phase the pattern changes from being random to aggregated, and clear edges for localized structures form in about 50 years (Fig. 3). Besides, the propagation-based positive feedback in LPCA is relatively weak compared to the one resulting from resource concentration (Couteron and Lejeune, 2001); thus, we expected that the pattern formation phase would be shorter with these mechanisms. Spatially implicit models (SIMs) usually aim to develop ecological theory or reveal ecological generality; however, top-down methods are often subject to “contingencies” in nature, which affect their predictions (Deangelis and
Yurek, 2017; Lawton, 1999). By contrast, spatially explicit models (SEMs) try to use small-scale collective rules to cope with practical problems at larger scales (Calabrese et al., 2010). There is a major gap between SIMs and SEMs need to bridge, since these two types of models often produce discrepant results and predictions (Deangelis and Yurek, 2017). From this point of view, the comparison between LPCA and MFA can supplement the logistic growth model.

The main concept of MFA is to replace all local interactions with an average interaction (Kadanoff, 2009). Therefore, it is supposed that if the lattice has a random distribution, then all local interactions are equal; thus, MFA is accurate for LPCA. Generally, the trajectories of LPCA and MFA are same, and the linear stability analysis in terms of MFA (Appendix A) shows that the final density \( x_1 = (\beta n^* - \alpha) / (\alpha (n^* - 1)) \) is globally stable to disturbances, which also imply the regular patterns as the indicator sable state for arid system. Simulation also reveals that when populations are randomly distributed \((t = 5, \text{Fig. 3})\), the densities are equal between LPCA and MFA. Given this result, the comparison between LPCA and MFA in the pattern formation phase becomes a comparison between a regular pattern and a random pattern. Fig. 3 shows that in the pattern formation phase, regular patterns alter population size. Under harsh conditions \((\beta = 15)\), the equilibrium density predicted from MFA is significantly lower than that from LPCA. Spatial self-organization may be an underappreciated means to maximize resource utilization in the formation of isolated spots. Under milder conditions \((\beta = 35)\), labyrinth patterns exhibit the same equilibrium density in both the LPCA and MFA, and the growth trajectories are nearly identical. When \(\beta = 55\), the population reaches a climax equal to the equilibrium density of MFA and then declines, which suggests that the formation of gaps may cause self-thinning.

These findings are rather encouraging; thus, we plotted the relationships between the equilibrium population densities of LPCA and MFA along a gradient of resource supplementation rate (Fig. 4b). The discrepancy between the two lines points to the role of regular patterns on equilibrium density that regular patterns help maintain a more stable community size. In order to investigate this discrepancy, we define \(\beta n^* - \alpha n^*\) as potential resource (PR) that is negatively related to

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**Fig. 3.** The comparison of growth trajectories between logistic probabilistic cellular automata (LPCA) and mean field approximation (MFA) under different resource supplementation rate \((\beta)\). Dashed red lines indicate the density of occupied cells predicted by MFA. Blue areas delineate the possible range of densities that were simulated 1000 times by LPCA with 95 % confidence intervals, and black lines are the corresponding mean values. Shaded parts represent logistic growth phase, and unshaded parts represent pattern formation phase. The snapshots under curves reveal the transition of spatial patterns along iterations. Population growth is depicted with a stochastic distribution in space \((t < 5)\), and regular patterns gradually after growth \((t > 5)\) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).
competition and plot it for spots case. Then we plot the rank potential resource distribution of cells in lattice for different resource supplementation rates ($\beta$) (Fig. 4a). Results show that occupied cells happen to be on the spots with positive PR, while the vacant cells locate on spots with negative PR, which forms a counter-intuitive spatial pattern that the patches occupied by plants have higher PR, while vacant place underdoes fierce resource competition. In addition, frequent population dynamics occur in edges of occupied patches where $\text{PR} < 0$, which means that the regular pattern confines the population dynamics to the edge parts of plant patches and guarantee redundant potential resource for occupied cells. As a result, regular patterns systematically regulate the population dynamics in a stable manner and maintains stability for population compared to that in random distribution. This result also explains the wider variation of density in logistic growth phase than in pattern formation phase (Fig. 3). Fig. 5 is the schematic plot for spots patterns that black circles are shrub patches and the circles around them are their neighborhoods. It is easy to imagine the strong competition from adjacent spots that intersectional regions suffer, thus, with increasing $\beta$, plants gradually occupy the place from the highest PR to lower PR, accompanying the pattern transferring form spots to labyrinths to gaps. To sum up, when patterns form, the distribution of cells form this particular distribution of PR, in return, this distribution of PR strengthens the distribution of cells. In addition, LPCA simulation in long time showed hexagonal combination support that as well because this arrangement provides best coverage of two-dimensional space (Pringle and Tarnita, 2016). In summation, the results highly suggest regular pattern as optimized spatial configuration to balance space and resource competition.

**Declaration of Competing Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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**Fig. 4.** (a) The rank potential resource distribution of cells in lattice for different resource supplementation rates ($\beta$). The colored points indicate occupied cells, while the grey points indicate vacant cells. The data comes from one snapshot of spots pattern after 100 iterations. (b) Density of occupied cells for different resource supplementation rates ($\beta$) after 100 iterations, when the density in both LPCA and MFA is steady.

**Fig. 5.** The schematic plot for the formation of spots, where black areas indicate vegetation patches and the circles around them are their neighborhoods. Hexagonal arrangement is optimal to fully utilize resource and to balance space and resource competition. Plant patches take the highest PR; The grey parts locate in intersections of two neighborhoods with mediate PR; The dark grey parts locate in intersections of three circles with low PR. With increasing $\beta$, plants gradually occupied the cells from the highest PR to lower PR, forming spot, labyrinth, and gap patterns.
Appendix A. Linear stability analysis

In order to gain insight into pattern formation phenomena in the LPCA, we perform linear stability analysis of the discrete nonlinear MFA from eq. (15),

\[ x_i(k+1) = H_i(x_i(k)) = \alpha (x_i(k)(1-x_i(k)), \quad x_i(k) \in (0,1) \]

\[ x_i(k+1) = H_0(x_i(k)) = 1 - H_1(x_i(k)) \]

(1)

We analyze the steady-state solutions \( x = (x_0, x) \) which makes \( x(k+1) = x(k) \), with respect to small spatially heterogeneous local perturbations \( \Delta x(k) = x(k) - x \) close to fixed point \( x \). Then we take first-order Taylor expansion of \( H(x + \Delta x(k)) \) to obtain linear approximation of \( \Delta x(k+1) \),

\[ \Delta x(k+1) \approx J \Delta x(k), \quad J = \left[ \begin{array}{c|c}
\frac{\partial H_0}{\partial x_0} & \frac{\partial H_0}{\partial x_1} \\
\frac{\partial H_1}{\partial x_0} & \frac{\partial H_1}{\partial x_1}
\end{array} \right] \]

Hence, \( \Delta x(k) = J \Delta x(0) \), and the dynamics of the perturbation \( \Delta x(k) \) are determined by the Jacobi matrix \( J \), especially by the spectral radius,

\[ \mu = \max \{ |\lambda| : \lambda \in \text{eigenvalues of } J \} \]

(2)

From Eq. (1), \( x_i \) gets two steady-state solutions 0 and \( x_i^* = \frac{x_i + \alpha}{\alpha x_i} \). Accordingly, we get the spectral radius,

\[ \mu = \left\{ \begin{array}{ll}
\frac{1 + \Delta t - \frac{\partial H_0}{\partial x_k}}{\frac{\partial H_1}{\partial x_k}}, & \text{if } x_i = 0 \\
\frac{1 - \Delta t + \frac{\partial H_0}{\partial x_k}}{\frac{\partial H_1}{\partial x_k}}, & \text{if } x_i = \frac{x_i + \alpha}{\alpha x_i}
\end{array} \right. \]

(3)

If \( \mu < 1 \), then perturbations \( \Delta x(k) \) converge \( (\lim k \Delta x(k) = 0) \), which means the steady-state solutions \( x \) is locally stable. If \( \mu \geq 1 \), then perturbations are divergent. In particular, if \( \mu = 1 \), there exists a constant \( C \) that makes \( |\Delta x(k)| \leq C |\Delta x(0)| \) for all times \( k \), which all perturbations are bounded. We put the values (Table 2) in Shapotou region to eq. (19), and find that \( \mu > 1 \), \( x_i = \frac{x_i + \alpha}{\alpha x_i} \). This result indicate that the regular pattern is the stable spatial configuration for arid system, other spatial patterns will eventually evolve to regular patterns.

References


