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Yoshida, Hiroshi
Faculty of Mathematics, Kyushu University

Miwa, Yoshihiro
Graduate School of Comprehensive Human Sciences, University of Tsukuba

Kaneko, Masanobu
Faculty of Mathematics, Kyushu University

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H. Yoshida,
Y. Miwa & K. Masanobu

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Faculty of Mathematics
Kyushu University
Fukuoka, JAPAN

Elliptic curves and Fibonacci numbers arising from Lindenmayer system with Symbolic Computation

Hiroshi Youshida ^{a,*}, Yoshihiro Miwa ^b, Masanobu Kaneko ^a

^a*Faculty of Mathematics, Kyushu University, Hakozaki 6-10-1, Higashi-ku, FUKUOKA
812-8581 Japan*

^b*Graduate School of Comprehensive Human Sciences, University of Tsukuba, Tennoudai
1-1-1, Tsukuba-shi, IBARAKI 305-8575 Japan*

Abstract

Starting from an egg, the multicell becomes a set of cells comprising a variety of types to serve functions. This phenomenon brings us a bio-inspired Lindenmayer system. To investigate conditions for a variety of cell types, we have constructed a stochastic model over Lindenmayer systems. This model also considers interactive behaviors among cells, yielding complicated nonlinear polynomials. Using symbolic computation, we have derived the explicit relations between cell-type diversity and cell-type ratio constraint. These relations exhibit elliptic curve- and Fibonacci number-related patterns. This is the first example of elliptic curves to appear in the Lindenmayer context. A survey of the rational points and the quadratic irrational numbers on the derived curves has revealed Fibonacci-related periodic and quasiperiodic patterns. Further, we have found that in some region, there are only two elliptic curve-related periodic patterns.

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Key words: Elliptic curves, Fibonacci numbers, Lindenmayer system, Symbolic computation

* Corresponding author. Faculty of Mathematics, Kyushu University, Hakozaki 6-10-1, Higashi-ku, FUKUOKA 812-8581 Japan. Tel/fax: +81-92-642-7396.
Email address: phiroschi@math.kyushu-u.ac.jp (Hiroshi Youshida).

1 Introduction

The multicell is thought to form according to specific rules, wherein the first cell type transforms into one different cell type or into two or more different cell types. Such cell-type transformation rules can be described by a tree diagram, termed a *cell lineage* diagram, whereas the developmental process of multicells is termed *cell differentiation* [8]. In 1968, such a cell differentiation process was modeled as rewriting rules by Lindenmayer [13, 14].

Here, we analyze a bio-inspired Lindenmayer system (L-system), where the rewriting rules are based on cell lineage diagrams. L-system models for developmental systems with cell lineages and for biological tissues such as blood vessels of the eye have been studied in past decades [10, 21, 22]. In these L-systems, the *interactions* among cells have been ignored because of the complexity or difficulty of the analysis. By contrast, in this paper, we present a symbolic computation, the quantifier elimination method, for the derivation of algebraic equations in an L-system with interactions (“IL-system” hereafter). Further, the stochastic aspects can be introduced into an L-system, termed a stochastic L-system [4, 5]. We studied the IL-system giving nonlinear compositions of extra cellular matrices in green algae [26]. Apart from L-system models, we studied compatible conditions for self-replication and high cell-type diversity by modeling the interaction of cells having chaotic dynamics [24, 25]. Chaotic dynamics yielded stochastic behavior. These previous studies let us know that interactive and stochastic behaviors play an important role in multicells.

In this paper, we extend our previous studies to a stochastic IL-system model (“sIL-system” hereafter) using algebraic equations between cell-type diversity and cell-type ratio constraint on the cell chain. To devise the basic cell differentiation rules, we consider three cell lineage diagrams: (i) the branching cell lineage $A \Rightarrow \{B, C\}$ without the cell-type order conservation rule, (ii) the linear diagram $A \Rightarrow B \Rightarrow C$ with the conservation rule, and (iii) the linear diagram without the rule. Using symbolic computation exhaustively, we have obtained five equations including *elliptic curves* which appears in the Lindenmayer context, for the first time.

Throughout this paper, we present the derived algebraic numbers or equations instead of approximate values. The reason is illustrated by a simple example. Consider the algebraic number $(1 + \sqrt{5})/2$ and its approximate value 1.618. The former is one root of $x^2 - x - 1 = 0$ in x , which can also be expressed as a continued

fraction: $[1; 1, 1, 1, \dots]$. The appearance of only 1 reveals the relationship between $(1 + \sqrt{5})/2$ and self-similarity (quasiperiodicity) of the corresponding sequence [11, 16]. By contrast, from the latter value, 1.618, we cannot submit such a strong proposal. This is why we made the extra effort to obtain the exact algebraic numbers or equations, to allow us to analyze the periodicity and quasiperiodicity of produced patterns.

2 Model: Bio-inspired Lindenmayer System

We study two basic subgraphs extracted from biological cell lineage diagrams: *branching* and *linear* cell differentiation rules of three cell types. This model is described by an sIL system for three cell types, A , B , and C .

We first define the following two basic cell differentiation graphs, *branching* $A \Rightarrow \{B, C\}$ and *linear* $A \Rightarrow B \Rightarrow C$. The proliferation of a type is denoted by $A \rightarrow AA$, $B \rightarrow BB$ or $C \rightarrow CC$, while the transition between types is denoted by $A \rightarrow B$, $A \rightarrow C$ (in the branching diagram), or $A \rightarrow B$, $B \rightarrow C$ (in the linear diagram). We next define the proliferation and transition rates (probabilities) of the branching diagram as follows:

$$A \rightarrow \begin{cases} AA & p_{1,1}, \\ B & p_{1,2}, \\ C & p_{1,3}, \\ A & 1 - p_{1,1} - p_{1,2} - p_{1,3}, \end{cases} \quad B \rightarrow \begin{cases} BB & p_{2,2}, \\ B & 1 - p_{2,2}, \end{cases} \quad C \rightarrow \begin{cases} CC & p_{3,3}, \\ C & 1 - p_{3,3} \end{cases} \quad (1)$$

with $0 < p_{i,j} < 1$ ($1 \leq i \leq j \leq 3$) and $p_{1,1} + p_{1,2} + p_{1,3} < 1$. The rule $A \rightarrow A$, $B \rightarrow B$, or $C \rightarrow C$ shows that the type does not change.

Likewise, the rates of the linear diagram are defined as:

$$A \rightarrow \begin{cases} AA & p_{1,1}, \\ B & p_{1,2}, \\ A & 1 - p_{1,1} - p_{1,2}, \end{cases} \quad B \rightarrow \begin{cases} BB & p_{2,2}, \\ C & p_{2,3}, \\ B & 1 - p_{2,2} - p_{2,3}, \end{cases} \quad C \rightarrow \begin{cases} CC & p_{3,3}, \\ C & 1 - p_{3,3} \end{cases} \quad (2)$$

with $0 < p_{i,j} < 1$ ($1 \leq i \leq j \leq 3$) and $p_{i,i} + p_{i,i+1} < 1$ ($1 \leq i \leq 2$). The one-dimensional cell chain becomes longer as these rules are applied. In addition

to the rewriting rules mentioned above, we adopt another rewriting rule, termed a *cell-type order conservation rule*:

$$AC \rightarrow ABC, CA \rightarrow CBA, \quad (3)$$

which guarantees the contiguity of cell types. When we adopt the above conservation rule, this rule is applied after each application of the branching or linear rewriting rules. This cell-type order conservation rule originates from the “intercalary regeneration” phenomenon in insect legs, as illustrated in Fig. 1. When portions of the legs with noncontiguous positional values are grafted together, new tissue is intercalated to fill the gap so that the noncontiguous positional values disappear [1, 6, 7]. Such a regeneration phenomenon occurs in our previous model of chaotic elements [24, 25] as well as in the actual wound repair in the early stages of the cell lineage diagram [2]. This is why we analyze the effect of the conservation rule. In this paper, we analyze the three diagrams: (i) a branching cell lineage diagram without the cell-type order conservation rule, (ii) a linear cell lineage diagram without the rule, and (iii) a linear diagram with the rule. We have not analyzed a branching diagram with the rule because we have not found a corresponding phenomenon in the actual cell-lineage diagrams.

Using these three models, we calculate the following composition in the cell chain:

$$AA, AB, BA, (AC, CA), BB, BC, CB, CC, \quad (4)$$

where (AC, CA) does not exist when the cell-type order conservation rule is adopted and applied during the elongation of a cell chain. In this paper, we adopt the above “two” contiguous composition instead of the “one” composition A, B, C because we do not aim to regard, for instance, $AAAAABBBBBCCCCC = A^5B^5C^5$ as a sequence with high cell-type diversity. In other words, we aim to evaluate the pattern-dependent diversity. Of course, we could adopt a more than two contiguous composition, but such composition gives an intractable calculation. For this reason, we have adopted the two contiguous composition (4).

Further, we assume the following constraint:

$$gN(AA) = N(BB) = N(CC) \wedge gN(AB) = N(BC), \quad (5)$$

where \wedge denotes “And,” g designates the parameter in this constraint, and $N(XY)$ denotes the number of the two contiguous cell types XY in the cell chain. $N(AB) = N(BA)$ and $N(BC) = N(CB)$ hold always because of the mirror symmetry of the

rewriting rules.

Under the constraint (5), we have calculated the maximum value of $N(AB)/N(AA)(= N(BC)/N(BB))$, which represents the ratio of junctions to nonjunctions between different cell types. Here, we have adopted this maximum as the measure of *cell-type diversity* in the sense that the appearance frequencies of two contiguous cell types become uniform as the ratio $N(AB)/N(AA)$ approaches 1 under the constraint (5). Notice that the large value of $N(AB)/N(AA)$ prevents us from regarding $A^n B^n C^n$ as a high-diversity pattern.

3 Method

3.1 Estimation of cell-type composition

We calculate the *growth matrix* of the two contiguous cell types based on [17, 23]. This matrix enables us to estimate its composition after n applications of the branching or linear rewriting rules (and the cell-type order conservation rule). In this paper, we have calculated three growth matrices for the branching cell lineage without the cell-type order conservation rule, and the linear diagram with and without the conservation rule, as shown in Table 1.

Let M be the growth matrix of the two contiguous cell types under some condition. Here, we start with AA ; that is, the axiom is AA , therefore, the composition at step n can be calculated by $(1, 0, 0, \dots)M^n$. We study the composition as n approaches infinity—in other words, for a sufficiently long cell chain. First, we derive the conditions for coexistence of the two contiguous cell types from the eigenvalues and the eigenvectors of the growth matrices. Second, under the constraint (5) and the coexistence condition, we estimate the composition using the growth matrix. Last, we derive the equation between the maximum value of $N(AB)/N(AA)(= N(BC)/N(BB))$ and the constraint parameter g in (5) using the quantifier elimination method.

3.2 Quantifier Elimination Method

In this paper, we investigate the maximum value of $N(AB)/N(AA)(= N(BC)/N(BB))$. For this purpose, we have used the quantifier elimination (QE) method. QE is one

of the main subjects in computer algebra [3, 15]. QE deals with first-order formulas comprising polynomial equations, inequalities, quantifiers (\exists, \forall), and boolean operators such as \wedge (And), \vee (Or), and \neg (Negation). QE computes an equivalent quantifier-free formula for a given first-order formula over the real field. For instance, for the input $\forall x(x^2 + bx + c > 0)$, QE outputs the equivalent quantifier-free formula $b^2 - 4c < 0$. QE obtains the relations between the unquantified variables that make the input formula true. We obtain the maximum value of an objective polynomial under some constraints by adding one extra variable, which is assigned to the objective polynomial [23]. For instance, to calculate the maximum value of $x/(p + y)$ under the constraints $x^2 + py^2 \leq 1 \wedge y \leq x^2$, we provide QE with the following input, adding an extra variable h :

$$\exists y \exists x (x^2 + py^2 \leq 1 \wedge y \leq x^2 \wedge h(p + y) == x).$$

For this formula, the QE output is $p < 0 \vee h^2 p^3 - p - h^2 < 0$, which indicates that the maximum value of $x/(p + y)$ is $\sqrt{p/(p^3 - 1)}$ when $p > 1$ and that this value does not exist ($+\infty$) when $p \leq 1$. Thus, even when parameters exist, we can obtain the maximum value; in other words, QE gives the equation between the maximum value and parameters. We can use QEPCAD-B or Mathematica Ver. 6/7 as QE-implemented software.

4 Results

4.1 Equations derived by QE

We first derive the coexistence condition of two contiguous cell types for the branching cell-lineage diagram. Analysis of the eigenvalues and their corresponding eigenvectors of the growth matrix reveals the coexistence condition: $2p_{1,1} - p_{1,2} - p_{1,3} > 0 \wedge 2p_{1,1} - p_{1,2} - p_{1,3} > 2p_{2,2} \wedge 2p_{1,1} - p_{1,2} - p_{1,3} > 2p_{3,3}$ ¹. Under this condition and the constraint (5), the following relations hold:

$$\frac{N(AB)}{N(AA)} = \frac{p_{1,2}(g(1 - p_{1,2} - p_{1,3}) - p_{1,3})}{2p_{1,3} + g(p_{1,2} + p_{1,3})},$$

$$p_{1,1} = \frac{-(1 - p_{1,2} - p_{1,3})(2p_{1,3} + g(p_{1,2} + p_{1,3}))}{2(p_{1,3} - g(1 - p_{1,2} - p_{1,3}))},$$

¹ See also [23, Section 5.2] for details.

$$\begin{aligned}
p_{2,2} &= (g(-2 + p_{1,2} + p_{1,3})(p_{1,3}(p_{1,2}^2 + 2p_{1,3}) + g(p_{1,2}^3 + p_{1,2}^2(-1 + p_{1,3}) + p_{1,2}(6 \\
&\quad p_{1,3} + p_{1,3}^2)))/(2(p_{1,3} + g(-1 + p_{1,2} + p_{1,3}))(g^2(p_{1,2}^2 + p_{1,2}(-2 + \\
&\quad p_{1,3}) - p_{1,3}) + p_{1,2}p_{1,3} + g(-1 + p_{1,2})(p_{1,2} + 2p_{1,3}))), \\
p_{3,3} &= (gp_{1,3}(-2 + p_{1,2} + p_{1,3})(p_{1,3}(2 + p_{1,3}) + g(p_{1,2} + p_{1,2}p_{1,3} + p_{1,3}^2)))/ \\
&\quad (2(p_{1,3} + g(-1 + p_{1,2} + p_{1,3}))(g^2(p_{1,2}^2 + p_{1,2}(-2 + p_{1,3}) - p_{1,3}) + p_{1,3}^2 \\
&\quad + gp_{1,3}(-3 + 2p_{1,2} + p_{1,3}))). \tag{7}
\end{aligned}$$

To obtain the maximum value of $N(AB)/N(AA)$ by QE, the following input is used:

$$\begin{aligned}
\exists p_{1,3} \exists p_{1,2} \left(\psi(p_{1,2}, p_{1,3}, g) \wedge h == N(AB)/N(AA) \wedge p_{1,2} > 0 \wedge \right. \\
\left. p_{1,3} > 0 \wedge p_{1,1} > 0 \wedge p_{2,2} > 0 \wedge p_{3,3} > 0 \wedge p_{1,1} + p_{1,2} + p_{1,3} < 1 \right),
\end{aligned}$$

where $\psi(p_{1,2}, p_{1,3}, g)$ is a formula derived by combining conjunctively all equations and inequalities appearing in the coexistence condition and the constraint (5). However, one cannot obtain the maximum if one provides the QE command of QEPCAD-B 1.48 or Mathematica 6.0.1 with the above formula as it is. This is because the computation requires too much memory and time. Therefore, we have transformed the above formula into the equivalent formulas in reduced form as follows.

Via factorization, we have derived the formulas:

$$\begin{aligned}
\exists p_{1,3} \exists p_{1,2} \left(0 < p_{1,2} \wedge 0 < p_{1,3} \wedge \right. \\
\left. -h(2p_{1,3} + g(p_{1,2} + p_{1,3})) == p_{1,2}(p_{1,3} + g(-1 + p_{1,2} + p_{1,3})) \wedge \right. \\
\left. e_1 < 0 \wedge e_2 < 0 \wedge e_3 < 0 \wedge e_4 < 0 \wedge e_5 < 0 \wedge e_6 < 0 \right)
\end{aligned}$$

with:

$$\begin{aligned}
e_1 &:= p_{1,3} + g(-1 + p_{1,2} + p_{1,3}), \\
e_2 &:= (g^2(p_{1,2}^2 + p_{1,2}(-2 + p_{1,3}) - p_{1,3}) + p_{1,2}p_{1,3} + g(-1 + p_{1,2})(p_{1,2} + 2p_{1,3})) \\
&\quad (p_{1,3}(p_{1,2}^2 + 2p_{1,3}) + g(p_{1,2}^3 + p_{1,2}^2(-1 + p_{1,3}) + p_{1,2}p_{1,3} + p_{1,3}^2)), \\
e_3 &:= (g^2(p_{1,2}^2 + p_{1,2}(-2 + p_{1,3}) - p_{1,3}) + p_{1,3}^2 + gp_{1,3}(-3 + 2p_{1,2} + p_{1,3})), \\
e_4 &:= (4p_{1,3} + g(-2 + 3p_{1,2} + 3p_{1,3})), \\
e_5 &:= g^2(p_{1,2}^2 + p_{1,2}(-2 + p_{1,3}) - p_{1,3}) + p_{1,2}p_{1,3} + g(-1 + p_{1,2})(p_{1,2} + 2p_{1,3}), \\
e_6 &:= g^2(p_{1,2}^2 + p_{1,2}(-2 + p_{1,3}) - p_{1,3}) + p_{1,3}^2 + gp_{1,3}(-3 + 2p_{1,2} + p_{1,3}),
\end{aligned}$$

under the physiological condition: $0 < h < 1, g > 0$. Mathematica 6.0.1 outputs: $0 < h < (\sqrt{8g + 5g^2} - g)/(2(2 + g))$. This shows that the equation between g and

the maximum value f of $N(AB)/N(AA)(= h)$ is $(g + 2)f^2 + gf - g = 0$.

Likewise, for the *linear* cell-lineage diagram without and with the cell-type order conservation rule, we have also used the QE method to derive the algebraic equations between f (the maximum of $N(AB)/N(AA)$) and g . The procedure for deriving these equations follows.

The eigenvalues of the growth matrix in the middle row of Table 1 are:

$$1 - p_{1,2}, 1 + 2p_{1,1} - p_{1,2}, (1 - p_{1,2})^2, 1 - p_{2,3}, 1 + 2p_{2,2} - p_{2,3}, \\ (1 - p_{1,2})(1 - p_{2,3}), (1 - p_{2,3})^2, 1 + 2p_{3,3}.$$

Therefore, the coexistence condition for the linear cell-lineage diagram without the rule is:

$$2p_{1,1} > p_{1,2} \wedge 2p_{1,1} - p_{1,2} > 2p_{2,2} - p_{2,3} \wedge 2p_{1,1} - p_{1,2} > 2p_{3,3}.$$

Under the constraint and the coexistence condition, we obtain the following relations:

$$N(AB)/N(AA) = \frac{(1 - p_{1,2})p_{1,2}}{2p_{1,1} + (1 - p_{1,2})p_{2,3}}, \\ p_{2,2} = (p_{1,1}(2p_{1,1} - p_{1,2} + p_{2,3})(p_{1,2}^2(-2p_{1,1} - (-1 + p_{1,2})(-2 + p_{2,3}))g \\ (4p_{1,1}^2 + -2p_{1,1}((-3 + p_{2,3})p_{2,3} + p_{1,2}(1 + p_{2,3})) + p_{2,3}(p_{1,2}^2 - (- \\ 2 + p_{2,3})p_{2,3} + p_{1,2}(-1 - 2p_{2,3} + p_{2,3}^2)))))/((-1 + p_{1,2})p_{1,2}(-4 \\ p_{1,1}^2 + (-1 + p_{1,2})p_{1,2}p_{2,3} - 2p_{1,1}(p_{1,2}(-1 + p_{2,3}) + p_{2,3}))2gp_{1,1}(\\ 4p_{1,1}^2 - 2p_{1,1}((-3 + p_{2,3})p_{2,3} + p_{1,2}(1 + p_{2,3})) + p_{2,3}(p_{1,2}^2 - (-2 + \\ p_{2,3})p_{2,3} + p_{1,2}(-1 - 2p_{2,3} + p_{2,3}^2))))), \\ p_{3,3} = ((1 + 2p_{1,1} - p_{1,2})(-1 + p_{1,2})p_{1,2}^2p_{2,3}^2 + gp_{1,1}(8p_{1,1}^3 - 4p_{1,1}^2((-2 + \\ p_{2,3})p_{2,3} + p_{1,2}(2 + p_{2,3})) + 2p_{1,1}(-p_{2,3}^2 + p_{1,2}^2(1 + 2p_{2,3}) + p_{1,2}p_{2,3} \\ (-3 + p_{2,3}^2)) + p_{2,3}(-p_{1,2}^3 + (-2 + p_{2,3})p_{2,3}^2 + p_{1,2}^2(1 + p_{2,3} - p_{2,3}^2) - \\ p_{1,2}p_{2,3}(1 - 3p_{2,3} + p_{2,3}^2)))))/((2p_{1,1} + p_{2,3} - p_{1,2}p_{2,3})(-(-1 + p_{1,2} \\)p_{1,2}p_{2,3} + 2gp_{1,1}(2p_{1,1} - p_{1,2} + 2p_{2,3} - p_{2,3}^2))).$$

To obtain the maximum value of $N(AB)/N(AA)$, we provided QE with the following input:

$$\exists p_{1,1} \exists p_{1,2} \exists p_{2,3} (\psi'(p_{1,1}, p_{1,2}, p_{2,3}, g) \wedge h == N(AB)/N(AA) \wedge 0 < p_{1,2} < 1 \wedge \\ 0 < p_{2,3} < 1 \wedge 0 < p_{1,1} \wedge 0 < p_{2,2} \wedge 0 < p_{3,3} < 1 \wedge p_{1,1} + p_{1,2} < 1 \wedge p_{2,2} + p_{2,3} < 1),$$

where $\psi'(p_{1,1}, p_{1,2}, p_{2,3}, g)$ is a formula derived by combining conjunctively all equations and inequalities appearing in the coexistence condition and the constraint. Again, the above formula was too complicated to analyze by the QE program (QEPCAD-B or Mathematica).

Therefore, we transform the formula in the following manner.

- From $h = N(AB)/N(AA)$,

$$p_{1,1} = \frac{(1 - p_{1,2})(p_{1,2} - hp_{2,3})}{2h} \quad (8)$$

holds. Using (8), we eliminate one variable, $p_{1,1}$.

- Next, via factorization, the inequalities with $p_{1,1}$ eliminated, can be transformed into the following formulas:

$$e'_1 < 0 \wedge e'_2 < 0 \wedge e'_3 > 0 \wedge e'_4 < 0 \wedge e'_5 < 0 \wedge e'_6 < 0 \wedge e'_7 < 0 \quad (9)$$

with:

$$\begin{aligned} e'_1 &:= -p_{1,2} + hp_{2,3}, \\ e'_2 &:= (1 - h - p_{1,2} + hp_{2,3})(-2h^2p_{1,2} + gp_{1,2} - hgp_{1,2} - hp_{1,2}^2 - gp_{1,2}^2 + hgp_{2,3} + 2h^2 \\ &\quad p_{1,2}p_{2,3} + hgp_{1,2}p_{2,3} - hgp_{2,3}^2)(-hp_{1,2}^2 + h^2p_{1,2}^2 - gp_{1,2}^2 + hgp_{1,2}^2 + hp_{1,2}^3 + gp_{1,2}^3 \\ &\quad + h^2p_{1,2}p_{2,3} - 2h^3p_{1,2}p_{2,3} - h^2gp_{1,2}p_{2,3} - 3h^2p_{1,2}^2p_{2,3} - 2hgp_{1,2}^2p_{2,3} + h^2gp_{2,3}^2 \\ &\quad + 2h^3p_{1,2}p_{2,3}^2 + hgp_{1,2}p_{2,3}^2 + h^2gp_{1,2}p_{2,3}^2 - h^2gp_{2,3}^3), \\ e'_3 &:= gp_{1,2}^3 - 2hgp_{1,2}^3 + h^2gp_{1,2}^3 - 2gp_{1,2}^4 + 2hgp_{1,2}^4 + gp_{1,2}^5 - 2hgp_{1,2}^2p_{2,3} + 3h^2gp_{1,2}^2 \\ &\quad p_{2,3} - h^3gp_{1,2}^2p_{2,3} + 5hgp_{1,2}^3p_{2,3} - 4h^2gp_{1,2}^3p_{2,3} - 3hgp_{1,2}^4p_{2,3} - 2h^4p_{1,2}p_{2,3}^2 \\ &\quad - h^2gp_{1,2}p_{2,3}^2 - h^3gp_{1,2}p_{2,3}^2 - 2h^3p_{1,2}^2p_{2,3}^2 - hgp_{1,2}^2p_{2,3}^2 - 3h^2gp_{1,2}^2p_{2,3}^2 + 2h^3 \\ &\quad gp_{1,2}^2p_{2,3}^2 + hgp_{1,2}^3p_{2,3}^2 + 3h^2gp_{1,2}^3p_{2,3}^2 + 2h^3gp_{2,3}^3 + 2h^4p_{1,2}p_{2,3}^3 + 3h^2gp_{1,2}p_{2,3}^3 \\ &\quad - 2h^2gp_{1,2}^2p_{2,3}^3 - h^3gp_{1,2}^2p_{2,3}^3 - 2h^3gp_{2,3}^4 + h^3gp_{1,2}p_{2,3}^4, \\ e'_4 &:= -2h^2p_{1,2}^2 + 2h^3p_{1,2}^2 - 2hgp_{1,2}^2 + 2h^2gp_{1,2}^2 + 2h^3p_{1,2}^3 + gp_{1,2}^3 + h^2gp_{1,2}^3 - hp_{1,2}^4 \\ &\quad + 3h^2p_{1,2}^4 - 2gp_{1,2}^4 + 2hgp_{1,2}^4 + hp_{1,2}^5 + gp_{1,2}^5 + 2h^3p_{1,2}p_{2,3} - 4h^4p_{1,2}p_{2,3} - 2h^3 \\ &\quad gp_{1,2}p_{2,3} + 2h^2p_{1,2}^2p_{2,3} - 6h^3p_{1,2}^2p_{2,3} - 2h^4p_{1,2}^2p_{2,3} + 2hgp_{1,2}^2p_{2,3} - 5h^2gp_{1,2}^2 \\ &\quad p_{2,3} - h^3gp_{1,2}^2p_{2,3} + h^2p_{1,2}^3p_{2,3} - 7h^3p_{1,2}^3p_{2,3} + hgp_{1,2}^3p_{2,3} - 4h^2gp_{1,2}^3p_{2,3} - 4 \\ &\quad h^2p_{1,2}^4p_{2,3} - 3hgp_{1,2}^4p_{2,3} + 2h^3gp_{2,3}^2 - 2h^3p_{1,2}p_{2,3}^2 + 8h^4p_{1,2}p_{2,3}^2 + h^2gp_{1,2}p_{2,3}^2 \\ &\quad + 5h^3gp_{1,2}p_{2,3}^2 + 4h^3p_{1,2}^2p_{2,3}^2 + 4h^4p_{1,2}^2p_{2,3}^2 - hgp_{1,2}^2p_{2,3}^2 + 5h^2gp_{1,2}^2p_{2,3}^2 + 2h^3 \\ &\quad gp_{1,2}^2p_{2,3}^2 + 5h^3p_{1,2}^3p_{2,3}^2 + hgp_{1,2}^3p_{2,3}^2 + 3h^2gp_{1,2}^3p_{2,3}^2 - 4h^3gp_{2,3}^3 - 4h^4p_{1,2}p_{2,3}^3 \\ &\quad - h^2gp_{1,2}p_{2,3}^3 - 4h^3gp_{1,2}p_{2,3}^3 - 2h^4p_{1,2}^2p_{2,3}^3 - 2h^2gp_{1,2}^2p_{2,3}^3 - h^3gp_{1,2}^2p_{2,3}^3 + 2 \\ &\quad h^3gp_{2,3}^4 + h^3gp_{1,2}p_{2,3}^4, \end{aligned}$$

$$\begin{aligned}
e'_5 &:= -1 + h + p_{1,2} - hp_{2,3}, \\
e'_6 &:= -hp_{1,2}^2 + h^2p_{1,2}^2 - gp_{1,2}^2 + hgp_{1,2}^2 + hp_{1,2}^3 + gp_{1,2}^3 + h^2p_{1,2}p_{2,3} - 2h^3p_{1,2}p_{2,3} - h^2 \\
&\quad gp_{1,2}p_{2,3} - 3h^2p_{1,2}^2p_{2,3} - 2hgp_{1,2}^2p_{2,3} + h^2gp_{2,3}^2 + 2h^3p_{1,2}p_{2,3}^2 + hgp_{1,2}p_{2,3}^2 + \\
&\quad h^2gp_{1,2}p_{2,3}^2 - h^2gp_{2,3}^3, \\
e'_7 &:= -gp_{1,2}^2 + hgp_{1,2}^2 + gp_{1,2}^3 - h^2p_{1,2}p_{2,3} - h^2gp_{1,2}p_{2,3} - 2hgp_{1,2}^2p_{2,3} + h^2gp_{2,3}^2 + \\
&\quad hgp_{1,2}p_{2,3}^2 + h^2gp_{1,2}p_{2,3}^2 - h^2gp_{2,3}^3.
\end{aligned}$$

Notice that in the above formulas, we show only those inequalities that maximize $N(AB)/N(AA)$; it is relatively easy to find these via polynomial factorization and confirmation by QE input for fixed values of g .

- Furthermore, the equality $gN(AB) = N(BC)$ in the constraint condition yields:

$$\begin{aligned}
0 = & -4gp_{1,1}^2p_{1,2} + 2gp_{1,1}p_{1,2}^2 + 4gp_{1,1}^2p_{1,2}^2 - 2gp_{1,1}p_{1,2}^3 + 4gp_{1,1}^2p_{2,3} - 2gp_{1,1}p_{1,2} \\
& p_{2,3} + p_{1,2}^2p_{2,3} + 2p_{1,1}p_{1,2}^2p_{2,3} + 2gp_{1,1}p_{1,2}^2p_{2,3} - 2p_{1,2}^3p_{2,3} - 2p_{1,1}p_{1,2}^3p_{2,3} + p_{1,2}^4 \\
& p_{2,3} + 2gp_{1,1}p_{2,3}^2 - 4gp_{1,1}^2p_{2,3}^2 - 2gp_{1,1}p_{1,2}p_{2,3}^2 - 2gp_{1,1}p_{2,3}^3 + 2gp_{1,1}p_{1,2}p_{2,3}^3.
\end{aligned}$$

Substituting (8) into the above equality yields:

$$g = \frac{hp_{1,2}p_{2,3}(-h - p_{1,2} + hp_{2,3})}{(-p_{1,2} + hp_{2,3})(p_{1,2} - hp_{1,2} - p_{1,2}^2 - p_{2,3} + hp_{1,2}p_{2,3} + p_{2,3}^2)}. \quad (10)$$

We therefore eliminate one more variable, g .

- By eliminating g from the equalities and inequalities and factorizing, we obtain the following reduced formulas suitable for QEPCAD-B:

$$\exists p_{2,3} \exists p_{1,2} (0 < h < 1 \wedge g > 0 \wedge 0 < p_{1,2} < 1 \wedge 0 < p_{2,3} < 1 \wedge e_{p0} == 0 \wedge e_{p1} < 0 \wedge e_{p2} < 0)$$

with:

$$\begin{aligned}
e_{p0} &:= hp_{1,2}p_{2,3}(-h - p_{1,2} + hp_{2,3}) - g(-p_{1,2} + hp_{2,3})(p_{1,2} - hp_{1,2} - p_{1,2}^2 \\
&\quad - p_{2,3} + hp_{1,2}p_{2,3} + p_{2,3}^2) \\
e_{p1} &:= 2hp_{1,2}^2 - 2h^2p_{1,2}^2 + p_{1,2}^3 - 3hp_{1,2}^3 - p_{1,2}^4 - 3hp_{1,2}p_{2,3} - h^2p_{1,2}p_{2,3} + \\
&\quad 2h^3p_{1,2}p_{2,3} - 2p_{1,2}^2p_{2,3} - hp_{1,2}^2p_{2,3} + 7h^2p_{1,2}^2p_{2,3} + p_{1,2}^3p_{2,3} + 4hp_{1,2}^3 \\
&\quad p_{2,3} + h^2p_{2,3}^2 + 5hp_{1,2}p_{2,3}^2 - 4h^3p_{1,2}p_{2,3}^2 + p_{1,2}^2p_{2,3}^2 - 2hp_{1,2}^2p_{2,3}^2 - 5h^2 \\
&\quad p_{1,2}^2p_{2,3}^2 - 2h^2p_{2,3}^3 - 2hp_{1,2}p_{2,3}^3 + h^2p_{1,2}p_{2,3}^3 + 2h^3p_{1,2}p_{2,3}^3 + h^2p_{2,3}^4, \\
e_{p2} &:= -p_{1,2} + hp_{1,2} + p_{1,2}^2 + hp_{2,3} + 2h^2p_{2,3} - hp_{1,2}p_{2,3} + hp_{2,3}^2.
\end{aligned}$$

- Last, because of the RAM limitation (up to 4 GB) of 32-bit software, we provided the above formulas for the QE program (we used QEPCAD-B Ver. 1.48 with measure-zero-error and +N670000000 option. It took from 4.5 to 12 hours

and 3.7 GB RAM with an Intel Xeon CPU 2.33 GHz processor), with g -space divided into $(0, 1/7]$, $(1/7, 1/4]$, $(1/4, 1)$, $[1, 2]$, $(2, \infty)$.

After all, with respect to the *linear* cell-lineage diagram without the rule, we obtained the following equivalent quantifier-free formulas as QE outputs:

$$\left\{ \begin{array}{ll} g \geq \text{root}_{-1} h^3 g^2 - 2h^2 g^2 - hg^2 + 2g^2 + 2h^4 g + h^3 g - 5h^2 g + 2h^4 & \text{For } (0, 1/7], \\ & (1/7, 1/4], (1/4, 1), \\ \left(\begin{array}{l} h^3 g^2 - 2h^2 g^2 - hg^2 + 2g^2 + 2h^4 g + h^3 g - 5h^2 g + 2h^4 \geq 0 \\ \wedge 6h^2 g + 3hg - 3g - 2h^2 - h \leq 0 \end{array} \right) & \text{For } [1, 2], \\ 6h^2 g + 3hg - 3g - 2h^2 - h \leq 0 & \text{For } (2, \infty), \end{array} \right. \quad (11)$$

where root_{-1} denotes the largest real root of the equation $h^3 g^2 - 2h^2 g^2 - hg^2 + 2g^2 + 2h^4 g + h^3 g - 5h^2 g + 2h^4 = 0$ in g . The equations for the linear diagram with the rule is the same as in [23]. The equations obtained between f and g are summarized in Table 2.

5 Discussion

So far, we have derived the algebraic equations between the cell-type diversity measure f and the parameter g under the constraint (5). We summarize in Table 2 and illustrate in Fig. 2 the equations between g and f in the three diagrams: the branching and linear cell lineage diagrams with and without the cell-type order conservation rule (3).

Let us look closely at the values of the natural number g that make f a rational number. The rational numbers of the maximum value of $N(AB)/N(AA)$ show that the pattern becomes periodic with respect to the two contiguous cell types as the cell chain becomes sufficiently long. We have searched for $g \in \mathbb{N}$ with corresponding rational f on the three curves (Table 2 and Fig. 2). Only on the curve of the branching diagram without the rule $(g+2)f^2 + gf - g = 0$ does there exist a pair that satisfies $\{(g, f) \mid g \in \mathbb{N}, f \in \mathbb{Q}\}$. The proof is given in Appendix A. On this curve, f is rational when g is in the following set: $\{2, 18, 128, 882, 6050, 41472, \dots\} = \{g_n \mid g_{n+2} = 7g_{n+1} - g_n + 4, g_0 = 0, g_1 = 2, n \geq 1\}$. The pair (g_n, f_n) can be described as $(2F_{2n}^2, F_{2n}/F_{2n+1})$, where F_n are *Fibonacci* numbers defined as $\{F_n \mid F_{n+2} = F_{n+1} + F_n, F_0 = 0, F_1 = 1, n \geq 1\} = \{1, 1, 2, 3, 5, 8, 13, 21, 34, 55, 89, \dots\}$. The $g \in \mathbb{N}$ and their corresponding values of f are summarized as follows.

- (a) When $g = 1$, for the branching diagram without the rule, f is $(\sqrt{13} - 1)/6 \sim 0.434259$; for the linear without the rule, f is $-1/2 + \{(9 + \iota\sqrt{687})^{1/3} + (9 - \iota\sqrt{687})^{1/3}\}/12^{2/3} \sim 0.557454$; and for the linear with the rule, f is $(1 + \sqrt{17})/8 \sim 0.640388$.
- (b) When $g > 1$ and $g \in \mathbb{N}$, for the branching diagram without the rule, f is a rational number if g is in $\{2F_{2n}^2 \mid n \geq 1\}$, otherwise f is a quadratic irrational number. For the linear diagram without and with the rule, f is always a quadratic irrational number (see also Appendix A). A quadratic irrational number is a solution to the quadratic equation $ax^2 + bx + c = 0$, where a, b, c are integers, and $b^2 - 4ac$ is positive and not a perfect square. The cell chain associated with a quadratic irrational number is quasiperiodic [11, 16]. Further, based on [9], we can reconstruct the rewriting rules that produce the pattern associated with a given quadratic irrational or rational number f via its continued fraction. We have constructed the sequences in the case of $g = 1, f = (1 + \sqrt{17})/8 = [0; 1, 1, 1, 3, 1, 1, 3, 1, 1, 3, 1, 1, 3, \dots]$ in the linear diagram with the rule; and $g = 2, f = 1/2$ in the branching diagram, respectively, as shown in Fig. 3. In this figure, we laid the two-dimensional space with 40,000 colored spiral cells, where the red, green, and blue boxes denote $A-$, $B-$, and $C-$ cell types. Figures 3 (B) and (C) show the quasiperiodic and periodic patterns, respectively.

Further, let us consider the region of small $g < 1, 1/g \in \mathbb{N}$. The curve \ddagger in Table 2 is transformed into the minimal model $y^2 + xy = x^3 - 7x + 9$ by birational transformation:

$$\begin{cases} f = (x - 2)/(x + 2), \\ g = (2 - x)(3 + y)/(2x(2 + x)), \\ x = 2(1 + f)/(1 - f), \\ y = (-3f + 3f^2 - 4g - 4fg)/((1 - f)f). \end{cases}$$

Likewise, the curve \dagger is transformed into $y^2 + xy + y = x^3 - x^2 - 9x + 9$ by:

$$\begin{cases} f = (3x + y - 1)/(x + y - 3), \\ g = (3x + y - 1)^2(x^2 - 4x + 3 - 2y)/(2(x + y - 3)(x - y + 5)(2x + y - 2)), \\ x = (f^2(3f + 1) + 2(f + 1)(f - 2)g)/(f^2(f - 1)), \\ y = 2(f + 1)(2f^2 - (f - 2)(f - 3)g)/(f^2(f - 1)^2). \end{cases}$$

These curves are *elliptic curves* [18, Ch. 3]. These two curves have Mordell–Weil rank = 1 and no torsion points over \mathbb{Q} . Concerning points such that $1/g \in \mathbb{N}$ and $f \in \mathbb{Q}$ ($g > 0, 0 < f < 1$), we have proved that such a point does not exist in the branching diagram and that only $(g, f) = (1/7, 1/4)$ and $(1/4, 1/3)$ exist on the curve † (the linear diagram without the rule) and the curve ‡ (the linear diagram with the rule), respectively. The finiteness of these points follows from Siegel’s theorem on the finiteness of integral points [18, Ch. 9]. In the above curves † and ‡, we transformed the curves into quartic elliptic equations in which one can compute all integral points based on [19, 20].

We have summarized in Table 3 the relations between f and g , showing that there are Fibonacci-related periodic and quasiperiodic patterns in the $g > 1, g \in \mathbb{N}$ region and that there are only two elliptic curve-related periodic patterns in $g < 1, 1/g \in \mathbb{N}$.

6 Conclusion

In this paper, using symbolic computation, we have derived relations between the measure of cell-type diversity and the cell-type ratio constraint over the bio-inspired Lindenmayer-system model. We have obtained the five equations between the measure and the constraint. Analysis of points on these equations has revealed frequent quasiperiodicity; and Fibonacci- and elliptic curve-related periodicity.

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Appendix A: Proof of the existence or non-existence of rational numbers f

- For the branching cell-lineage diagram without the cell-type order conservation rule, we obtain the equation between f and g :

$$(g + 2)f^2 + gf - g = 0. \quad (12)$$

The discriminant of the above equation is $D = 5g^2 + 8g$. We survey (g_n, f_n) such that g_n and f_n are natural and positive rational numbers, respectively. If and only if $D = m^2, m \in \mathbb{N}$, f is rational. $D = m^2$ yields $(5g + 4)^2 - 5m^2 = 4^2$. Let X be $5g + 4$. Then the equation $X^2 - 5m^2 = 4^2$ is a Pell's equation. It follows that $X + \sqrt{5}m = \pm 4 \left((3 + \sqrt{5})/2 \right)^n, n = 0, 1, 2, \dots$ yields a pair $\{(X, m) | X \in \mathbb{Z}, m \in \mathbb{Z}\}$. Therefore, from $X = 5g + 4, g + \sqrt{5}m' = 4 \left\{ \left((3 + \sqrt{5})/2 \right)^{2n} - 1 \right\} / 5, n = 1, 2, 3, \dots$ yields a natural number sequence $\{g_n | g_n \in \mathbb{N}\}$. Moreover, g_n can more explicitly be described as $2 \left\{ \left((3 + \sqrt{5})/2 \right)^{2n} + \left((3 - \sqrt{5})/2 \right)^{2n} - 2 \right\} / 5$. It follows from the golden ratio $\varphi = (1 + \sqrt{5})/2$ that g_n is $2(\varphi^{4n} + \varphi^{-4n} - 2) / 5$. Because *Fibonacci* number F_n can be described as $(\varphi^n - (-\varphi)^{-n}) / \sqrt{5}, g_n = 2F_{2n}^2 \square$

The recurrence formula of g_n can be derived as follows:

$$\begin{aligned} g_{n+2} &= 2F_{2(n+2)}^2 = 2(F_{2n+3} + F_{2(n+1)})^2 \\ &= 2(2F_{2(n+1)} + F_{2n+1})^2 \\ &= 2(3F_{2(n+1)} - F_{2n})^2 \\ &= 2(9F_{2(n+1)}^2 + F_{2n}^2 - 6F_{2(n+1)}F_{2n}) \\ &\quad \text{From the formula } 3F_{2(n+1)}F_{2n} = F_{2(n+1)}^2 + F_{2n}^2 - 1, \\ &= 2(7F_{2(n+1)}^2 - F_{2n}^2 + 2) \\ &= 7g_{n+1} - g_n + 4. \quad \square \end{aligned}$$

The corresponding f_n with respect to g_n on the curve (12) is calculated as:

$$f_n = \frac{F_{2n} \left(\sqrt{4 + 5F_{2n}^2} - F_{2n} \right)}{2(1 + F_{2n}^2)}.$$

The formulas on *Fibonacci* and *Lucas* numbers F_n and L_n [12, Ch. 5]:

$$F_{n+1}F_{n-1} - F_n^2 = (-1)^n, 5F_n^2 - L_n^2 = 4(-1)^{n+1}, F_n + L_n = 2F_{n+1}$$

reveal that $f_n = F_{2n}/F_{2n+1} \square$

- With respect to the cell-lineage diagram without the rule, we obtain:

$$2(3g - 1)f^2 + (3g - 1)f - 3g = 0. \quad (13)$$

The discriminant of the above equation is $D = 81g^2 - 30g + 1$. We survey (g_n, f_n) such that g_n and f_n are natural and positive rational numbers, respectively. If and only if $D = m^2, m \in \mathbb{N}, f$ is rational. $D = m^2$ yields $(27g - 5)^2 - (3m)^2 = 4^2$, which can be factorized as $(27g + 3m - 5)(27g - 3m - 5) = 4^2$. From $g \geq 1$ and $m \geq 1, 27g + 3m - 5 \geq 5^2$. Therefore, there exists no rational f_n for natural number g_n \square

- For the linear diagram with the rule, we obtain:

$$2gf^2 + (g - 1)f - g = 0. \quad (14)$$

We survey (g_n, f_n) such that g_n and f_n are natural numbers ($g > 0$) and positive rational numbers ($0 < f < 1$), respectively.

We prove the non-existence of such pairs in $0 < g, 0 < f < 1$. Assume that $f = n/m, \gcd(m, n) = 1, m \in \mathbb{N}, n \in \mathbb{N}$ because it is a positive rational number. Then, the equation (14) can be transformed into:

$$g(2n - m)(m + n) = mn. \quad (15)$$

From $0 < g$ and $0 < f < 1$, it follows that $m/2 < n < m$. Furthermore, from (15), $2n^2g \equiv 0 \pmod{m}$ and $m^2g \equiv 0 \pmod{n}$. It follows from $\gcd(m, n) = 1$ that $2g \equiv 0 \pmod{m}$ and $g \equiv 0 \pmod{n}$, revealing $2g \equiv 0 \pmod{mn}$. This fact, together with $g = mn/((2n - m)(m + n)), m/2 < n < m$, implies that the only possible value of g is $mn/2$. $g = mn/2$ yields an equation $(2n - m)(m + n) = 2$, which has a single solution $m = n = 1$, contradicting the assumption $f = n/m < 1$ \square

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Figure captions

Fig. 1. Intercalary regeneration in cockroach legs [1]. When mismatched portions of the growing legs are grafted together, new tissue is intercalated to fill the gap so that the noncontiguous positional values disappear. In this figure, we exemplify the rule: $I_8I_4 \rightarrow I_8I_7I_6I_5I_4$.

Fig. 2. The equations between g and f . The gray line denotes the equation in the branching cell lineage diagram without the cell-type order conservation rule. The black and broken lines denote the equations in the linear diagram with and without the rule, respectively. The derivative discontinuities are nearly 1.14254 (g_0) and 1.29661 (g_1). The intersection of the broken and gray lines is nearly 3.28773 (g_2), and that of the black and gray lines is nearly 3.83118 (g_3). The f -value of the broken and black lines approaches $1/2$ as $g \rightarrow \infty$, whereas that of the gray line approaches the reciprocal of the golden ratio $1/\varphi \sim 0.61803$ ($\varphi = (1 + \sqrt{5})/2$) as $g \rightarrow \infty$.

Fig. 3. Spiral tiling of cells. (A) Schematic illustration of spiral tiling of one-dimensional cell chain. (B) $g = 1$, $f = (1 + \sqrt{17})/8$ in the linear diagram with the rule. (C) $g = 2$, $f = 1/2$ in the branching diagram.

Table 1

The three growth matrices. We have calculated the matrices to estimate the composition of two contiguous cell types at step n . The top and middle matrices are of 9×9 form ($AA, AB, BA, AC, CA, BB, BC, CB, CC$) because of the nonexistence of the cell-type conservation rule, whereas the bottom matrix is of 7×7 form ($AA, AB, BA, BB, BC, CB, CC$) with the rule.

Branching diagram without the cell-type order conservation rule

$$\begin{pmatrix} m_{1,1} & m_{1,2} & m_{1,3} & m_{1,2} & p_{1,2}^2 & p_{1,2}p_{1,3} & m_{1,3} & p_{1,2}p_{1,3} & p_{1,3}^2 \\ p_{1,1} & m_{2,2} & 0 & 0 & p_{1,2} + p_{2,2} & 0 & 0 & p_{1,3} & 0 \\ p_{1,1} & 0 & m_{2,2} & 0 & 0 & p_{1,2} & 0 & 0 & p_{1,3} + p_{3,3} \\ p_{1,1} & 0 & 0 & m_{2,2} & p_{1,2} + p_{2,2} & p_{1,3} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 + 2p_{2,2} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & p_{2,2} & 1 & 0 & 0 & p_{3,3} \\ p_{1,1} & 0 & 0 & 0 & 0 & 0 & m_{2,2} & p_{1,2} & p_{1,3} + p_{3,3} \\ 0 & 0 & 0 & 0 & p_{2,2} & 0 & 0 & 1 & p_{3,3} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 + 2p_{3,3} \end{pmatrix}$$

$$\text{with } m_{1,1} = 2p_{1,1} + (1 - p_{1,2} - p_{1,3})^2, m_{1,2} = p_{1,2}(1 - p_{1,2} - p_{1,3}),$$

$$m_{1,3} = p_{1,3}(1 - p_{1,2} - p_{1,3}), m_{2,2} = 1 - p_{1,2} - p_{1,3}.$$

Linear diagram without the rule

$$\begin{pmatrix} m'_{1,1} & m'_{1,2} & 0 & m'_{1,2} & p_{1,2}^2 & 0 & 0 & 0 & 0 \\ p_{1,1} & m'_{2,2} & p_{2,3} - p_{1,2}p_{2,3} & 0 & m'_{2,5} & p_{1,2}p_{2,3} & 0 & 0 & 0 \\ p_{1,1} & 0 & 1 - p_{1,2} & 0 & 0 & p_{1,2} & 0 & 0 & p_{3,3} \\ p_{1,1} & 0 & 0 & m'_{2,2} & m'_{2,5} & 0 & p_{2,3} - p_{1,2}p_{2,3} & p_{1,2}p_{2,3} & 0 \\ 0 & 0 & 0 & 0 & m'_{5,5} & m'_{5,6} & 0 & m'_{5,6} & p_{2,3}^2 \\ 0 & 0 & 0 & 0 & p_{2,2} & 1 - p_{2,3} & 0 & 0 & p_{2,3} + p_{3,3} \\ p_{1,1} & 0 & 0 & 0 & 0 & 0 & 1 - p_{1,2} & p_{1,2} & p_{3,3} \\ 0 & 0 & 0 & 0 & p_{2,2} & 0 & 0 & 1 - p_{2,3} & p_{2,3} + p_{3,3} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 + 2p_{3,3} \end{pmatrix}$$

$$\text{with } m'_{1,1} = p_{1,1} + (1 - p_{1,2})^2, m'_{1,2} = p_{1,2}(1 - p_{1,2}), m'_{2,2} = (1 - p_{1,2})(1 - p_{2,3}),$$

$$m'_{2,5} = p_{1,2} + p_{2,2} - p_{1,2}p_{2,3}, m'_{5,5} = 2p_{2,2} + (1 - p_{2,3})^2, m'_{5,6} = p_{2,3}(1 - p_{2,3}).$$

Linear diagram with the rule

$$\begin{pmatrix} m''_{1,1} & m''_{1,2} & m''_{1,2} & p_{1,2}^2 & 0 & 0 & 0 \\ p_{1,1} & 1 - p_{1,2} & 0 & m''_{2,4} & p_{2,3} & 0 & 0 \\ p_{1,1} & 0 & 1 - p_{1,2} & m''_{2,4} & 0 & p_{2,3} & 0 \\ 0 & 0 & 0 & m''_{3,4} & m''_{3,5} & m''_{3,5} & p_{2,3}^2 \\ 0 & 0 & 0 & p_{2,2} & 1 - p_{2,3} & 0 & p_{2,3} + p_{3,3} \\ 0 & 0 & 0 & p_{2,2} & 0 & 1 - p_{2,3} & p_{2,3} + p_{3,3} \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 + 2p_{3,3} \end{pmatrix}$$

$$\text{with } m''_{1,1} = 2p_{1,1} + (1 - p_{1,2})^2, m''_{1,2} = (1 - p_{1,2})p_{1,2}, m''_{2,4} = p_{1,2} + p_{2,2} - p_{1,2}p_{2,3},$$

$$m''_{3,4} = 2p_{2,2} + (1 - p_{2,3})^2, m''_{3,5} = (1 - p_{2,3})p_{2,3}.$$

Table 2

The algebraic equations between g and f ; g denotes the parameter in the constraint (5) and f the measure of cell-type diversity. $root_{-1}$ denotes the largest real root of the equation $2(g+1)f^4 + g(g+1)f^3 - g(2g+5)f^2 - g^2f + 2g^2 = 0$ in g . g_1 and is nearly 1.29661, which is exactly the intersection of the two curves within $0 < g, 0 < f < 1$, the largest real root of $1 - 67g + 1224g^2 - 4008g^3 + 4599g^4 - 1701g^5 = 0$. Likewise, g_0 is nearly 1.14254 and is exactly the real root of $1 - 3g + 11g^2 - 8g^3 = 0$.

Branching without the cell-type order conservation rule

$$(g+2)f^2 + gf - g = 0$$

Linear without the rule

$$\begin{cases} g = root_{-1}2(g+1)f^4 + g(g+1)f^3 - g(2g+5)f^2 - g^2f + 2g^2 \dagger, & (0 \leq g < g_1) \\ 2(3g-1)f^2 + (3g-1)f - 3g = 0 & (g \geq g_1) \end{cases}$$

Linear with the rule

$$\begin{cases} 2(g-1)f^3 - g(g+3)f^2 + gf + g^2 = 0 \ddagger, & (0 \leq g < g_0) \\ 2gf^2 + (g-1)f - g = 0 & (g \geq g_0) \end{cases}$$

Table 3

The sequences in $g < 1$ and $g > 1$ regions. $g < 1$ and $g > 1$ correspond to the early developmental and mature stages, respectively. F_n denotes Fibonacci numbers. [‡]We should note that because of the mathematical difficulty, we have not completed the survey of quadratic irrational numbers (quasiperiodic patterns) of f in $g < 1, 1/g \in \mathbb{N}$ in the linear diagram without the rule, but we guess that such a number does not exist in this region.

	$g < 1, 1/g \in \mathbb{N}$	$g > 1, g \in \mathbb{N}$
Branching without rule	Quasiperiodic	Periodic ($g \in \{2F_{2n}^2\}$), Quasiperiodic (others)
Linear without rule	Periodic ($g = 1/7$), Indefinite (others [‡])	Quasiperiodic
Linear with rule	Periodic ($g = 1/4$), Quasiperiodic ($g = 1/3$), Indefinite (others)	Quasiperiodic

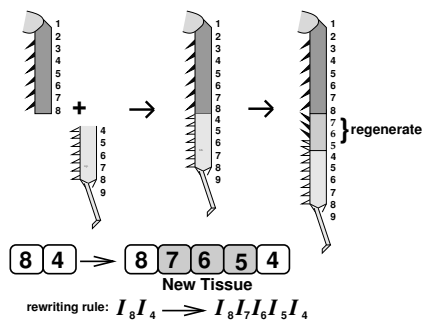


Fig. 1.

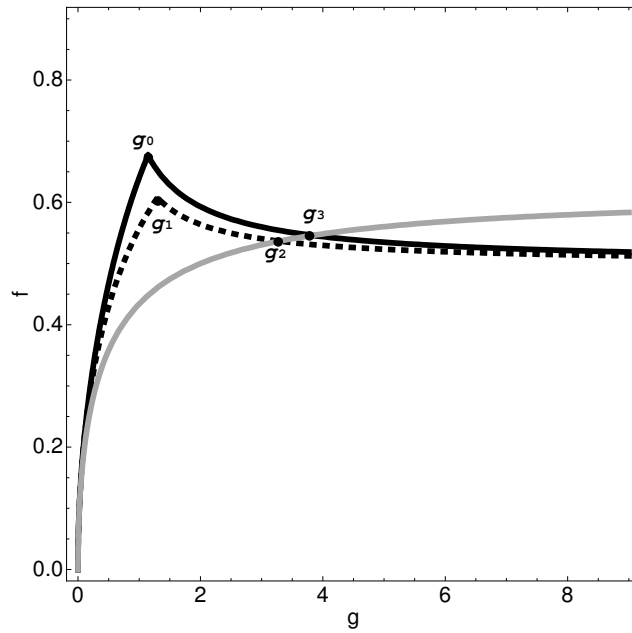
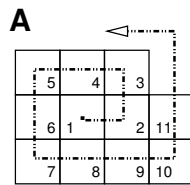
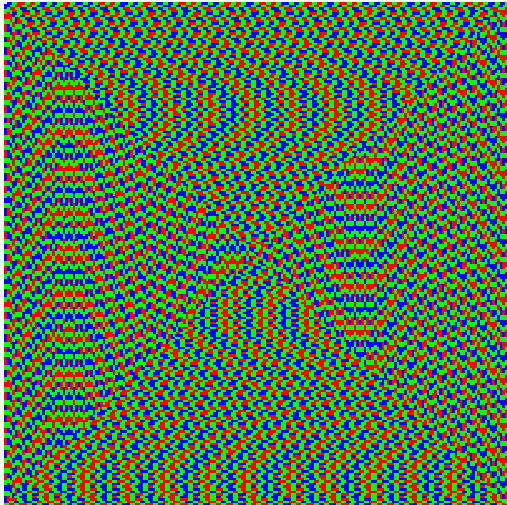


Fig. 2.



B g=1 (Linear with the rule)



C g=2 (Branching)

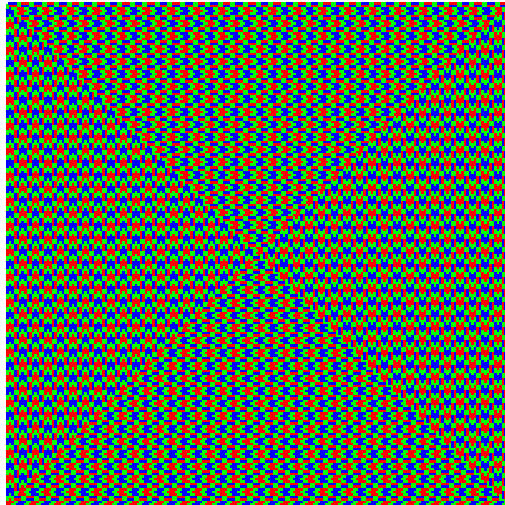


Fig. 3.

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