

1 Appendix 1. Life cycles competition

2 In the result of population dynamics described above, some life cycles become more abun-
3 dant, while others go extinct. The outcome of this life cycle competition is independent on
4 he resource limitation parameter (K) and is exactly the same as in the linear model without
5 resource limitation at all ($K \rightarrow \infty$).

6 To show this, consider the whole population describe by values $x_i^\kappa(t)$ - the number of
7 groups of size i in the lineage executing life cycle κ . We can decompose this value into a
8 form

$$9 \quad x_i^\kappa(t) = X(t)f^\kappa(t)\rho_i^\kappa(t), \quad (1)$$

10 where $X(t)$ is the total number of units in a population, $f^\kappa(t)$ is the fraction of units following
11 the life cycle κ , and $\rho_i^\kappa(t)$ is the fraction of them, which have a size i . Naturally,

$$12 \quad \sum_{\kappa} f^\kappa(t) = 1, \quad (2)$$

$$13 \quad \sum_i \rho_i^\kappa(t) = 1. \quad (3)$$

14
15 The quantity $f^\kappa(t)$ characterizes the evolutionary success of a life cycle, and we are generally
16 interested in its dynamics.

17 In Eqs. (3), the terms responsible for units growth, death, and fragmentation are linear
18 with respect to x_i , and therefore, these equations can be represented as

$$19 \quad \frac{d}{dt}x_i = \sum_j A_{ij}x_j - \frac{1}{K}Xx_i, \quad (4)$$

20
21 where A_{ij} is some constant matrix. In particular, this equation is valid independently for each
22 life cycle κ .

23 Combining Eqs. (4) and (1), we get

$$24 \quad \frac{d}{dt}(Xf^\kappa\rho_i^\kappa) = Xf^\kappa \sum_j A_{ij}\rho_j^\kappa - \frac{1}{K}X^2f^\kappa\rho_i^\kappa. \quad (5)$$

25
26 Summation over all units sizes i in Eq. (5) results with

$$27 \quad \frac{d}{dt}(Xf^\kappa) = Xf^\kappa \sum_{i,j} A_{ij}\rho_j^\kappa - \frac{1}{K}X^2f^\kappa. \quad (6)$$

29 And after rearranging the terms

$$\frac{d}{dt}f^\kappa = f^\kappa \sum_{i,j} A_{ij}\rho_j^\kappa - \frac{1}{K}Xf^\kappa - f^\kappa \frac{1}{X} \frac{d}{dt}X. \quad (7)$$

32 There, summation over all life cycles provides

$$\frac{1}{X} \frac{d}{dt}X = \sum_{i,j,\kappa} A_{ij}\rho_j^\kappa f^\kappa - \frac{1}{K}X. \quad (8)$$

35 Plugging Eq. (8) back into Eq. (7), we finally obtain

$$\frac{d}{dt}f^\kappa = f^\kappa \left(\sum_{i,j} A_{ij}\rho_j^\kappa - \sum_{i,j,\mu} A_{ij}\rho^\mu f^\mu \right). \quad (9)$$

38 The dynamics of life cycles competition explicitly given by Eq. (9) is independent on the
39 severity of the resources limitation K and the total number of units X . The competition of
40 life cycles has the same outcome in the model without resource competition at all ($K \rightarrow \infty$).

1 Appendix 2. Linear model of life cycles evolution

2 Without resource competition, the population dynamics is governed by a system of equations

3

$$4 \quad \frac{d}{dt}x_1 = -b_1x_1 - d_1x_1 + \pi_1(\kappa)mb'_m x_m \quad (1a)$$

$$5 \quad \frac{d}{dt}x_i = -ib_ix_i + (i-1)b_{i-1}x_{i-1} - d_ix_i + \pi_i(\kappa)mb'_m x_m \quad \text{for } 1 < i < m \quad (1b)$$

$$6 \quad \frac{d}{dt}x_m = -mb'_m x_m + (m-1)b_{m-1}x_{m-1} - d'_m x_m + \pi_m(\kappa)mb'_m x_m. \quad (1c)$$

8 The equation system Eq. (1) is linear with respect to x_i . Thus, it can be written as:

$$9 \quad \frac{d}{dt}\mathbf{x} = A\mathbf{x}, \quad (2)$$

10 where $\mathbf{x} = (x_1, x_2, \dots, x_m)^T$ and the matrix A is

$$11 \quad A = \begin{pmatrix} -b_1 - d_1 & 0 & 0 & \cdots & \pi_1(\kappa)mb'_m \\ b_1 & -2b_2 - d_2 & 0 & \cdots & \pi_2(\kappa)mb'_m \\ 0 & 2b_2 & -3b_3 - d_3 & \cdots & \pi_3(\kappa)mb'_m \\ 0 & 0 & 3b_3 & \cdots & \pi_4(\kappa)mb'_m \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \cdots & \pi_m(\kappa)mb'_m - mb'_m - d'_m \end{pmatrix} \quad (3)$$

12 In the long run, the solution of Eq. (2) converges to that of an exponentially growing popula-
13 tion with a stable distribution, i.e.,

$$14 \quad \lim_{t \rightarrow \infty} \mathbf{x}(t) = e^{\lambda t} \mathbf{w}. \quad (4)$$

15 The leading eigenvalue λ gives the total population growth rate, and its associated right eigen-
16 vector $\mathbf{w} = (w_1, \dots, w_m)$ gives the stable distribution of unit sizes.

17 The leading eigenvalue determines the evolutionary success of a population. In the com-
18 petition of populations utilizing different life cycles (and hence different λ), each of them will
19 grow independently of the others. Eventually, the population with the largest growth rate will
20 outcompete the others. Thus, natural selection would promote the life cycle that provides the
21 largest λ . We call this the evolutionarily optimal life cycle.

1 Appendix 3.

2 Characteristic equation for an arbitrary life cycle

3 Consider a life cycle in which the number of cells in a unit increases until the maturity size
 4 m is reached and once the next cell is born, a unit fragments according to a partition κ of
 5 $j' \leq m + 1$. The corresponding projection matrix is an $m \times m$ matrix of the form

$$6 \quad A = \begin{pmatrix} -b_1 - d_1 & 0 & 0 & 0 & \cdots & mb'_m \pi_1(\kappa) \\ b_1 & -2b_2 - d_2 & 0 & 0 & \cdots & mb'_m \pi_2(\kappa) \\ 7 \quad 0 & 2b_2 & -3b_3 - d_3 & 0 & \cdots & mb'_m \pi_3(\kappa) \\ 0 & 0 & \ddots & \ddots & \ddots & \vdots \\ 0 & 0 & 0 & \cdots & (m-1)b_{m-1} & mb'_m \pi_m(\kappa) - mb'_m - d'_m \end{pmatrix}. \quad (1)$$

8
 9 The population growth rate is given by the leading eigenvalue λ_1 of A , i.e., the largest solution
 10 of the characteristic equation

$$11 \quad \det(A - \lambda \mathbf{I}) = 0. \quad (2)$$

12 By using a Laplace expansion along the last column of $A - \lambda \mathbf{I}$, we can rewrite the left hand
 13 side of the above expression (i.e., the characteristic polynomial of A) as

$$14 \quad \det(A - \lambda \mathbf{I}) = \sum_{i=1}^{m-1} (-1)^{i+m} mb'_m \pi_i(\kappa) M_{i,m} + (-1)^{2m} (mb'_m \pi_m(\kappa) - mb'_m - d'_m - \lambda) M_{m,m} \\ 15 \quad = \sum_{i=1}^m (-1)^{i+m} mb'_m \pi_i(\kappa) M_{i,m} - (mb'_m + d'_m + \lambda) M_{m,m} \quad (3)$$

17 where $M_{i,m}$ is the (i, m) minor of $A - \lambda \mathbf{I}$. For all $i = 1, \dots, m$, the minor $M_{i,m}$ is the
 18 determinant of a block diagonal matrix, and hence equal to the product of the determinants of
 19 the diagonal blocks. Moreover, each diagonal block is either a lower triangular or an upper
 20 triangular matrix, whose determinant is given by the product of the elements in their main

21 diagonals. We can then write

$$22 \quad M_{i,m} = \prod_{j=1}^{i-1} (-jb_j - d_j - \lambda) \prod_{j=i}^{m-1} jb_j. \quad (4)$$

23 Substituting Eqs. (3) and (4) into Eq. (2), switching the order of the two terms and simplify-
24 ing, we obtain

$$25 \quad -(-1)^{m-1} (mb'_m + d'_m + \lambda) \prod_{j=1}^{m-1} (jb_j + d_j + \lambda) \\ 26 \quad + (-1)^{m-1} \sum_{i=1}^m mb'_m \pi_i(\kappa) \prod_{j=1}^{i-1} (jb_j + d_j + \lambda) \prod_{j=i}^{m-1} jb_j = 0.$$

28 Dividing both sides by

$$29 \quad (-1)^m \prod_{j=1}^m jb_j,$$

30 we get

$$31 \quad \frac{mb'_m + d'_m + \lambda}{mb_m} \prod_{j=1}^{m-1} \left(1 + \frac{d_j + \lambda}{jb_j}\right) \\ 32 \quad - \sum_{i=1}^m \frac{b'_m}{b_m} \pi_i(\kappa) \prod_{j=1}^{i-1} \left(1 + \frac{d_j + \lambda}{jb_j}\right) = 0.$$

34 We rewrite the factor in front of the product in the first line as

$$35 \quad \frac{mb'_m + d'_m + \lambda}{mb_m} = \left(1 + \frac{d_m + \lambda}{mb_m}\right) + \frac{m(b'_m - b_m) + d'_m - d_m}{mb_m}.$$

37 Thus,

$$38 \quad \prod_{j=1}^m \left(1 + \frac{d_j + \lambda}{jb_j}\right) + \frac{m(b'_m - b_m) + d'_m - d_m}{mb_m} \prod_{j=1}^{m-1} \left(1 + \frac{d_j + \lambda}{jb_j}\right) \\ 39 \quad - \frac{b'_m}{b_m} \sum_{i=1}^m \pi_i(\kappa) \prod_{j=1}^{i-1} \left(1 + \frac{d_j + \lambda}{jb_j}\right) = 0.$$

41 Simplifying this, we finally obtain that the characteristic equation (2) can be written as

$$42 \quad F_{m+1}(\lambda) + \Delta_m F_m(\lambda) - \frac{b'_m}{b_m} \sum_{i=1}^m \pi_i(\kappa) F_i(\lambda) = 0, \quad (5)$$

43 where

$$44 \quad F_i(\lambda) = \prod_{j=1}^{i-1} \left(1 + \frac{d_j + \lambda}{jb_j}\right). \quad (6)$$

45 and

$$46 \quad \Delta_i = \frac{i(b'_i - b_i) + d'_i - d_i}{ib_i}. \quad (7)$$

47 Note that two transformations preserve Eq. (5):

$$48 \quad d_i \rightarrow d_i - r, \quad d' \rightarrow d' - r, \quad \lambda_1 \rightarrow \lambda_1 + r, \quad r \leq \min(\mathbf{d}), \quad (8)$$

49

50 and

$$51 \quad \mathbf{d} \rightarrow s\mathbf{d}, \quad \mathbf{b} \rightarrow s\mathbf{b},$$
$$52 \quad b' \rightarrow sb', \quad d' \rightarrow sd', \quad \lambda_1 \rightarrow s\lambda_1, \quad s > 0.$$

53

54 These transformations allow us to set $b_1 = 1$ and $\min(\mathbf{d}) = 0$ without loss of generality.

55 **Forbidden fragmentation modes**

56 For any environment, for any combination of the fragmentation delay, risk and fixed loss,
57 the fragmentation mode having two different subsets of offspring with the same combined
58 size is dominated. To prove this, we use approach similar to one used in Appendix E in [1].

59 Consider positive integers m, j, k such that $m + 1 \geq 2j + k$, two partitions of j , τ_1 and
60 τ_2 , such that $\tau_1 \neq \tau_2$, and an arbitrary partition ϕ of k , and the following three deterministic
61 fragmentation modes:

- 62 1. $\kappa_1 = \tau_1 + \tau_2 + \phi$ – the partition of $2j + k \leq m + 1$, whereby a unit fragments upon the
63 increment of size from m to $m + 1$ into a number of offspring given by partitions τ_1 ,
64 τ_2 , and ϕ .
- 65 2. $\kappa_2 = \tau_1 + \tau_1 + \phi$ – the partition of $2j + k \leq m + 1$, whereby a unit fragments upon the
66 increment of size from m to $m + 1$ into a number of offspring given by two partitions
67 τ_1 and one partition ϕ .
- 68 3. $\kappa_3 = \tau_2 + \tau_2 + \phi$ – the partition of $2j + k \leq m + 1$, whereby a unit fragments upon the
69 increment of size from m to $m + 1$ into a number of offspring given by two partitions
70 τ_2 and one partition ϕ .

71 Denoting by $\lambda(\kappa_i)$ the leading eigenvalue of the projection matrix induced by fragmentation
72 mode κ_i , we can show that, for any environment, either $\lambda(\kappa_1) \leq \lambda(\kappa_2)$ or $\lambda(\kappa_1) \leq \lambda(\kappa_3)$
73 holds. Thus, a fragmentation mode with two different subsets of offspring with the same
74 combined size is dominated by a mode where one of these subsets repeats twice, while the
75 other one is not present.

76 To prove the statement above, let us define the polynomial $p_i(\lambda)$ as the left hand side of
77 Eq. (5) with $\kappa = \kappa_i$, so that $\lambda(\kappa_i)$ is the largest root of $p_i(\lambda)$. We obtain

$$78 \quad p_1(\lambda) = F_{m+1}(\lambda) + \Delta_m F_m(\lambda) - \frac{b'_m}{b_m} \left(\sum_{i=1}^m \pi_i(\tau_1) F_i(\lambda) + \sum_{i=1}^m \pi_i(\tau_2) F_i(\lambda) + \sum_{i=1}^m \pi_i(\phi) F_i(\lambda) \right) \quad (9a)$$

$$79 \quad p_2(\lambda) = F_{m+1}(\lambda) + \Delta_m F_m(\lambda) - \frac{b'_m}{b_m} \left(2 \sum_{i=1}^m \pi_i(\tau_1) F_i(\lambda) + \sum_{i=1}^m \pi_i(\phi) F_i(\lambda) \right) \quad (9b)$$

$$80 \quad p_3(\lambda) = F_{m+1}(\lambda) + \Delta_m F_m(\lambda) - \frac{b'_m}{b_m} \left(2 \sum_{i=1}^m \pi_i(\tau_2) F_i(\lambda) + \sum_{i=1}^m \pi_i(\phi) F_i(\lambda) \right) \quad (9c)$$

81
82 These polynomials satisfy the following two properties. First,

$$83 \quad \lim_{\lambda \rightarrow \infty} p_i(\lambda) = \infty, \quad (10)$$

84 as the leading coefficient of the left hand side of (5) is given by $(b_1 \cdot b_2 \cdot \dots \cdot b_m m!)^{-1}$, which
85 is always positive. Second,

$$86 \quad p_1(\lambda) = \frac{p_2(\lambda) + p_3(\lambda)}{2}. \quad (11)$$

87 Since $\lambda(\kappa_1)$ is a root of $p_1(\lambda)$, evaluating Eq. (11) at $\lambda(\kappa_1)$ leads to

$$88 \quad p_2(\lambda(\kappa_1)) = -p_3(\lambda(\kappa_1)).$$

89 Hence, one of the following three scenarios is satisfied:

$$90 \quad \text{(i) } p_2(\lambda(\kappa_1)) < 0 < p_3(\lambda(\kappa_1)),$$

$$91 \quad \text{(ii) } p_2(\lambda(\kappa_1)) > 0 > p_3(\lambda(\kappa_1)), \text{ or}$$

$$92 \quad \text{(iii) } p_2(\lambda(\kappa_1)) = p_3(\lambda(\kappa_1)) = 0.$$

93 If $p_2(\lambda(\kappa_1)) < 0 < p_3(\lambda(\kappa_1))$ due to Eq. (10) and Bolzano's theorem (if a continuous func-
94 tion has values of opposite sign inside an interval, then it has a root in that interval), $p_2(\lambda)$ has

95 a root between $\lambda(\kappa_1)$ and ∞ . Therefore, $\lambda(\kappa_1) \leq \lambda(\kappa_2)$ holds, i.e. the largest root of $p_2(\lambda)$ is
96 larger than the largest root of $p_1(\lambda)$. Next, let us focus on (ii): If $p_2(\lambda(\kappa_1)) > 0 > p_3(\lambda(\kappa_1))$,
97 then $\lambda(\kappa_1) \leq \lambda(\kappa_3)$ holds. Finally, if $p_2(\lambda(\kappa_1)) = p_3(\lambda(\kappa_1)) = 0$, then both $\lambda(\kappa_1) \leq \lambda(\kappa_2)$
98 and $\lambda(\kappa_1) \leq \lambda(\kappa_3)$ hold.

99 We conclude that either $\lambda(\kappa_1) \leq \lambda(\kappa_2)$ or $\lambda(\kappa_1) \leq \lambda(\kappa_3)$ must hold. Thus, the life cycle
100 corresponding to κ_1 can never lead to the highest growth rate.

101 **References**

- 102 [1] Y. Pichugin, J. Peña, P. Rainey, and A. Traulsen. Fragmentation modes and the evolution
103 of life cycles. *PLoS Computational Biology*, 13(11):e1005860, 2017.

1 **Appendix 4. Random environments**

2 **Uncorrelated random environments**

3 We numerically investigate the distribution of optimal life cycles on two sets of environments:
4 random environments and random detrimental environments, which strongly disfavour mul-
5 ticellular units. Both sets are explored by 10000 environments generated only once and then
6 used to assess all three scenarios: delay, risk, and loss.

7 In the set of random environments, each element of the division and death rates vector (**b**
8 and **d**) was sampled independently from the uniform distribution $U(0, 1)$.

9 **Random detrimental environments**

10 To construct an unbiased set of random detrimental environments we used a method adopted
11 from [1]. For each environment, we initially sampled two sequences of $n = 19$ random
12 numbers from the uniform distribution $U(0, 1)$. Then, the first sequence has been sorted
13 in descending order to form the vector of the division rates **b** and the second sequence has
14 been sorted in ascending order to form the vector of death rates **d**. Thus, in all detrimental
15 environments, the values of division rates monotonically decreased with the unit size, while
16 the values of death rates monotonically increased. Therefore, life cycles that fragment at
17 large sizes only are strongly disfavoured.

18 **Random beneficial environments**

19 The set of random beneficial environments was constructed in a similar way. There, for
20 each environment, we first sampled two sequences of $n = 19$ random numbers from the
21 uniform distribution $U(0, 1)$. Then, the first sequence has been sorted in ascending order to
22 form the vector of the increasing division rates **b** and the second sequence has been sorted
23 in descending order to form the vector of decreasing death rates **d**. In the result, the largest
24 possible size is the most productive and the most defended state of a multicellular unit.

25 **Random unimodal environments**

26 To construct the set of random unimodal environments, we again started with two sorted
27 sequences of random numbers from the uniform distribution $U(0, 1)$. Then, to construct the
28 division rates vector, the largest value of the first sequence was assigned to the optimal size of
29 10 cells. The second largest value was randomly assigned either to the position on the left (9
30 cells) or the right (11 cells). Then, the next largest value was randomly assigned to either of
31 two free slots closest to 10-th position. Hence, the vector of division rates has the maximum
32 at 10 cells and monotonically decreases in both directions away from it. The vector of death
33 rates was constructed in the similar way, with the minimum of death rate being at the optimal
34 size of 10 cells.

35 **References**

- 36 [1] J. Peña, B. Wu, and A. Traulsen. Ordering structured populations in multiplayer cooper-
37 ation games. *Journal of the Royal Society Interface*, 13:20150881, 2016.

1 **Appendix 5. Binary fragmentation and (nearly) equal split**
2 **are overrepresented in beneficial and unimodal environments.**

3 Besides environments with uncorrelated random values of birth and death rates (see Fig. 4
4 in the main text) and detrimental environments (see Fig. 5 in the main text), we investigated
5 beneficial and unimodal environments. Both demonstrated patterns qualitatively similar to
6 the environments with uncorrelated random values, see Figs. 1 and 2.

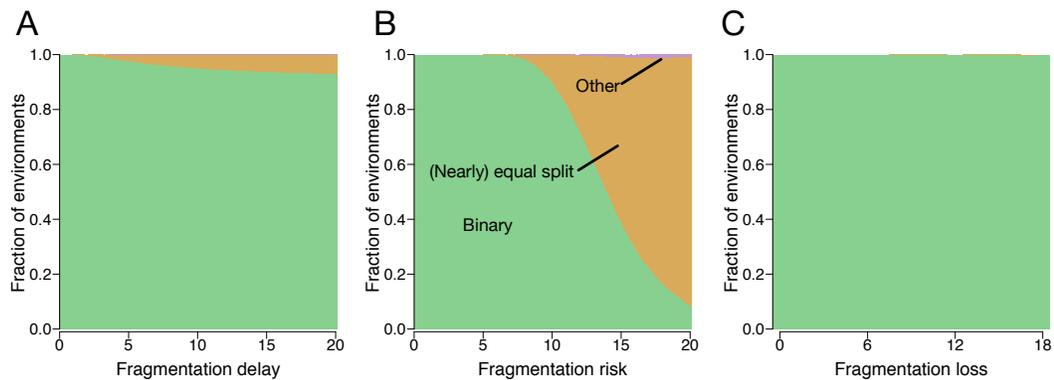


Figure 1: **Binary fragmentation and (nearly) equal split are overrepresented in beneficial environments.** In this case, fragmentation always occurs at the largest possible size. The fractions of each of four classes of life cycles under (A) delay, (B) risk, and (C) loss fragmentation costs.

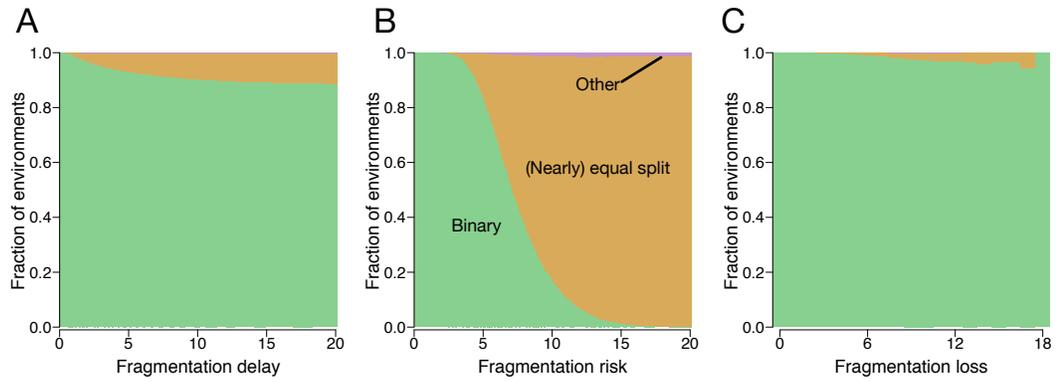


Figure 2: **Binary fragmentation and (nearly) equal split are overrepresented in unimodal environments.** The fractions of each of four classes of life cycles under (A) delay, (B) risk, and (C) loss fragmentation costs.

1 **Appendix 6. Only deterministic fragmentation modes can be** 2 **evolutionarily optimal under any environment**

3 Following [2], the state of the population can be described by the vector \mathbf{x} , where x_i denotes
4 the abundance of units of size i . All processes changing the state vector \mathbf{x} – birth, death and
5 fragmentation – occur with a constant rate. Thus, the dynamics of the population state can
6 be described by a set of linear differential equations or, equivalently, by a matrix differential
7 equation

$$8 \quad \dot{\mathbf{x}} = A\mathbf{x}, \quad (1)$$

9 where A is a projection matrix defined by demographics of the population [1]. An element
10 $a_{i,j}$ of the projection matrix describes the rate of change of the number of units of size i
11 caused by processes occurring with units of size j .

12 To construct the projection matrix elements, consider units of a certain size j . We denote
13 by $q_{j,\kappa}$ the probability that upon the increase in size from j to $j + 1$, the unit will fragment by
14 a partition κ of $j' \leq j + 1$ (where the “ \leq ” indicates that cells can be lost upon fragmentation).
15 Among these partitions we distinguish the trivial partition of $j + 1$ that corresponds to the
16 cell division without fragmentation; we denote this by $q_{j,(j+1)}$. The combined probability of
17 all outcomes is equal to one:

$$18 \quad \sum_{\kappa} q_{j,\kappa} = 1. \quad (2)$$

19 For deterministic life cycles, only one partition occurs in all cell clusters in a population.
20 Thus, for unit sizes j up to maturity size m , the trivial partition occurs with probability one
21 ($q_{j,(j+1)} = 1$), while all other partitions have zero probability. Once a cell divides in a cluster
22 that reached the maturity size, a certain non-trivial partition of $j' \leq m + 1$ occurs with
23 probability one. In a stochastic life cycle, more than one partition has non-zero probability at
24 least at one unit size.

25 To show that stochastic life cycles are dominated by deterministic ones, we construct the
26 projection matrix for an arbitrary stochastic life cycle. The number of cells in a unit increases
27 by one cell at a time, thus no process can increase the size of a cluster by more than one unit

28 at once, so $a_{i,j} = 0$ for all $i > j + 1$. Thus, the projection matrix may contain non-zero
 29 elements only in the upper right triangle (emergence of smaller units during fragmentation),
 30 on the main diagonal (fragmentation, cell division and death of units), and on the first lower
 31 subdiagonal (increment of a unit size due to a cell division).

32 The first lower subdiagonal describes the rate of emergence of new larger units due to cell
 33 division without fragmentation. These rates are equal to the product of the number of cells in
 34 a unit, their division rate, and the probability the fragmentation does not occur:

$$35 \quad a_{j+1,j} = j b_j q_{j,(j+1)}. \quad (3)$$

36 The upper right triangle of the matrix describes the emergence of new units as a result of
 37 fragmentation of larger units. For a given partition κ and given size of the newborn unit i ,
 38 the rate of production of new units is equal to the product of the fragmentation rate ($j b'_j$),
 39 the probability to fragment according to the given partition ($q_{j,\kappa}$), and the number of units of
 40 given size produced in the act of fragmentation with this partition ($\pi_i(\kappa)$). The value of an
 41 element $a_{i,j}$ in the upper left triangle is equal to the sum of rates provided by all partitions
 42 available to clusters of size j ,

$$43 \quad a_{i,j} = j b'_j \sum_{\kappa} q_{j,\kappa} \pi_i(\kappa). \quad (4)$$

44 The main diagonal $a_{j,j}$ describes the changes in units numbers due to cell division and
 45 fragmentation as well as the death of units. The first component of $a_{j,j}$ captures that once a
 46 unit of size j increase in size or fragments, the number of units of that size decreases. The
 47 rates of decrease are equal to $j b_j q_{j,(j+1)}$ due to cell division and $j b'_j \sum_{\kappa} q_{j,\kappa}$ due to fragmen-
 48 tation. The second component is provided by a fragmentation with partition $\kappa = j + 1$, which
 49 produce units of size equal to the size of parent. This leads to an increase in the number of
 50 units of size j at rate $j b'_j q_{j,j+1} \pi_j(j + 1)$, where $\pi_1(1 + 1) = 2$ and $\pi_j(j + 1) = 1$ if $j > 1$.
 51 The last component of $a_{i,i}$ comes from the death of units, which leads to a decrease in their
 52 number at rate $d_j q_{j,(j+1)} + d'_j \sum_{\kappa} q_{j,\kappa}$, where the first term describes the death rate in the ab-
 53 sence of the fragmentation and the second term describes the death rate of fragmenting units.

54 Combined, the diagonal elements of projection matrix are

$$55 \quad a_{j,j} = -jb_j q_{j,(j+1)} - jb'_j \sum_{\kappa} q_{j,\kappa} + jb'_j q_{j,j+1} \pi_j (j+1) - d_j q_{j,(j+1)} - d'_j \sum_{\kappa} q_{j,\kappa}. \quad (5)$$

56 All elements of the projection matrix given by Eq. (3)-(5) are linear with respect to any
57 probability $q_{j,\kappa}$. As shown in [2], in this case the optimal life cycle is always deterministic,
58 independent of the parameter values, such as the division and death rates and the scenario of
59 the fragmentation cost.

60 **References**

61 [1] H. Caswell. *Matrix population models*. Sinauer Associates, Sunderland MA, 2nd edition,
62 2001.

63 [2] Y. Pichugin, J. Peña, P. Rainey, and A. Traulsen. Fragmentation modes and the evolution
64 of life cycles. *PLoS Computational Biology*, 13(11):e1005860, 2017.