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Algebraic and Combinatorial Approaches for Counting Cycles Arising in Population Biology

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ALGEBRAIC AND COMBINATORIAL APPROACHES FOR COUNTING CYCLES
ARISING IN POPULATION BIOLOGY

by

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A thesis submitted in partial fulfillment of the requirements
for the Honors Undergraduate Thesis Program in Mathematics
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ABSTRACT

Within population biology, models are often analyzed for the net reproduction number or other generalized target reproduction numbers, which describe the growth or decline of the population based on specific mechanisms. This is useful in determining the strength and efficiency of control measures for inhibiting or enhancing population growth. The literature contains many algebraic and combinatorial approaches for deriving the net reproduction number and generalized target reproduction numbers from digraphs and associated matrices. Finding, categorizing, and counting the permutations of disjoint cycles, or cycle unions is a requirement of the Cycle Union approach by Lewis et al. (2019). These cycles and subsequent cycle unions can be found via the digraphs and associated matrices. We developed cycle counting patterns for targeting fertilities within Leslie Matrices, Lefkovitch Matrices, Sub-Diagonal Lower Triangle Transition Matrices, and Lower Triangle Transition Matrices to serve as a foundation for future work. Presented are the counting patterns and closed form summations of the cycle unions.

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INTRODUCTION

Population Projection Models

We consider each population to be divided into several ages/stages, such that the population can be described as a column vector in terms of individuals in each age/stage, each represented by a row in the matrix. We model each population's life cycle with a matrix A , and a corresponding digraph (Caswell, 2001). The matrix A is a *non-negative population matrix*, that when left multiplied with the column vector representing a population at time t , returns the population at time $t + 1$. The matrix A can be considered the sum of two matrices, the *state-transition matrix* T , and the *fertility matrix* F . The state-transition matrix contains the terms $t_{i,j}$ which describe the probabilities that individuals transition from into state j at time t to state i at time $t + 1$. Each column sums to at total of one or less. The fertility matrix contains the fertility rates of offspring in state i at time $t + 1$ produced by an individual in state j at time t . Each term is non-negative. By controlling for the fertility of a population for equilibrium, we derive the *next-generation matrix*. The effort needed to control the population is given as the spectral radius of the next-generation matrix, or the *basic reproduction number* R_0 .

- $n_{t+1} = An_t$ a population projection model where n_t gives the population at time t , and A is a non-negative population projection matrix.
- $A = T + F$ where T is the state-transition matrix, and F is the fertility matrix.
- $T = [t_{i,j}]$ (with $t_{i,j} \in [0,1]$ and $\sum_j t_{i,j} \leq 1$) contains probabilities that individuals transition from state j to state i .
- $F = [f_{i,j}]$ (with $f_{i,j} \geq 0$) contains fertility rates of offspring in state i produced by an individual in state j .
- $R_0 = \rho[F(I - T)^{-1}]$ is the spectral radius of the next-generation matrix.

Walks, Paths, Loops, Cycles

The population model can be graphically represented by an analogous digraph in which each age/stage in the life cycle is represented by a *node*. Directed *arcs* connect nodes, and are weighted by corresponding entries in the state-transition matrix and fertility matrix, such that an arc $a_{i,j}$ shows that node i is reached by node j with a weight describing either the probability that an individual in node j enters node i , or the fertility rate of individuals produced in node i by an individual in node j . Arcs that correspond to an entry in the state-transition matrix T are *transition arcs* and arcs that correspond to an entry in the fertility matrix F are *fertility arcs* (deCamino-Beck & Lewis, A New Method for Calculating Net Reproductive Rate from Graph Reduction with Applications to the Control of Invasive Species, 2007). A *path* is a series of connected arcs, with each arc starting from the node that the preceding arc ended (e.g. $t_{4,3}t_{3,2}t_{2,1}$). A *cycle* is a path that starts and ends at the same node (e.g. $t_{2,1}t_{1,4}t_{4,3}t_{3,1}t_{1,2}$). A cycle is an *elementary cycle* if it reaches each non-starting/ending node in the cycle only once, such that the starting/ending node is reached exactly twice, when the cycle starts and ends (e.g. $t_{1,4}t_{4,3}t_{3,1}$). All cycles referenced in this paper will be elementary cycles. A *loop* contains exactly one arc from the main diagonal (e.g. $t_{4,4}$). A *fertility cycle* contains exactly one fertility arc and any number of transition arcs (e.g. $t_{3,2}t_{2,1}f_{1,3}$). We will refer to a *survivor cycle* as one without any fertility arcs (e.g. $t_{1,2}t_{2,1}$). Cycles are considered *disjoint* if the cycles have no nodes in common, a set of such disjoint cycles forms a *cycle union* (e.g. $t_{3,2}t_{2,1}f_{1,3}t_{5,5}$).

- A *node* represents an age/stage in the life cycle.
- An *arc* denoted $a_{i,j}$ directionally connects two nodes, node i is reached by node j .
- A *path* is a series of connected arcs.

- A *cycle* is a path that starts and ends at the same node.
- A *loop* is a cycle of length one from a node to itself.
- A *fertility cycle* contains exactly one fertility arc and any number of transition arcs.
- A *survivor cycle* contains any number of and only transition arcs.
- An *elementary cycle* reaches each non-starting/ending node in the cycle only once.
- A *cycle union* is a set of cycles that have no nodes in common, these cycles are considered *disjoint*.

Basic, Type, and Target Reproduction Numbers

Basic Reproduction Number

The basic reproduction number, or basic reproductive rate describes the mean number of offspring per individual that survive to become adults. It is useful in that it indicates the survival or extinction of a population and can be used to determine the effort needed to control a population. When organized into a sum of terms based on fertility, R_0 can be helpful in explaining the relative biological importance of population mechanisms behind population control (Caswell, 2001).

Different values of R_0 can be found when using different definitions of reproduction, or when targeting different portions of the population for the effect of control strategies, this makes it difficult to standardize R_0 . Other issues result in R_0 being unsuitable for being used as a persistence threshold such as backward bifurcations and stochastic effects (Li, Blakeley, & Smith, 2011). In this paper, we discuss methods to improve the calculation of R_0 , but leave the interpretation and analysis of reproduction numbers separate.

It is often the case that the selection of terms and the decomposition of the population projection matrix into state-transitions and fertilities can alter the resulting R_0 and biological

interpretation, this paper will deal with generic placeholders within common population modeling matrices (Cushing & Diekmann, 2016).

- R_0 is the *basic reproductive number* and gives the mean surviving offspring per individual. It is useful in determining major contributions to equilibrium for population control strategies. When it is greater than 1, the population grows, when it is less than 1, the population declines, and eventually becomes extinct.

Type Reproduction Number

Another special type of target reproduction number is the *type reproduction number*, which targets all mechanisms entering or leaving a certain age/stage (Roberts & Heesterbeek, 2003) (Heesterbeek & Roberts, 2007). It is useful when a specific category of the population is easier to identify or control. Some populations have young that are hard to distinguish from the young of other populations, some control measures may only apply to individuals greater than or less than a certain body size or weight.

Target Reproduction Number

A *target reproduction number* describes the effort needed to control a population when a control measure affects specific mechanism (Shuai, Heesterbeek, & van den Driessche, 2012). We consider the basic reproductive number R_0 , a special type of target reproduction number that targets the fertility rates, furthermore we consider the type reproduction number a special type of target reproduction number that targets all rates in a single row or column of the population matrix.

Approaches for Reproduction Number Calculation

We follow the evolution of the Cycle Union Approach to calculating the target reproduction number through its predecessors the Graph Reduction Approach and the Residual Sub-Matrix Approach.

Graph Reduction Approach

In de-Camino-Beck and Lewis (2007), a graph reduction method of calculating R_0 was developed from existing procedures for calculating λ via graph reduction found in Caswell (2001). It was further developed in de-Camino-Beck and Lewis (2008), to allow for the calculation of the timing of reproductive output, used to calculate the mean and variance of the generation time.

This approach is based on a digraph analogous to the next generation matrix. It is well suited to simple graphs as complex graphs result in convoluted reduction techniques. This method can take up a significant amount of space to use. The resulting summation form of the reproduction number is often well suited to biological interpretation, with the advantage of visual tracing of the source of the terms being available.

First, is the identification of survivorship (loops) and fecundity (fertility) transitions. Second, all fecundity transitions $f_{i,j}$ in the graph are multiplied by R_0^{-1} . Next, using rule A (loop elimination), loops are eliminated. The graph is then reduced to a single node with a single loop by rule A (loop elimination), B (parallel path elimination), and C (node elimination). Finally, the value of the final loop is set equal to one and solved for R_0 .

Residual Sub-Matrix Approach

In Rueffler and Metz (2012) a fully algebraic counterpart of the graph-reduction approach was developed. The algebraic counterpart makes use of the determinants of residual sub-matrices formed when the rows and columns associated to an arc in a cycle are removed.

It is well suited to smaller graphs, as larger graphs with more cycles require the calculation of more determinants, a computationally heavy task. It also requires that all paths from birth to reproduction pass through a common state (node). If there are more than one non-zero eigenvalues for the next-generation matrix, then the equation will be difficult to interpret.

First each fertility cycle is found, and a corresponding sub-matrix is formed by the removal of all rows and columns corresponding to nodes used in the fertility cycle from the full state-transition matrix S . Second the determinants of $I - S$ and all sub-matrices of $I - S$ are calculated. Finally, R_0 is a sum of each fertility cycle multiplied by the determinant of the identity matrix minus the corresponding sub-matrix and divided by the determinant of the identity matrix minus the full state-transition matrix.

Cycle Union Approach

In Moon et al. (2014), using determinant and cofactor expansions, the reproduction numbers are described in terms of cycle unions, which can be described as sets of disjoint cycles. This was done to remove the need to calculate determinants, which are computationally heavy. The theory is generalized and further developed in Lewis et al. (2019), where relations between the target reproduction number and basic reproduction number are proven, and the target reproduction number is applied in several practical cases.

This approach relies on numerous simple calculations; however, the resulting fractional form of the reproduction number is more difficult to interpret biologically without rearrangement.

Every cycle union is found and sorted into four categories based on two criteria: whether any fertility arcs are within the cycle, and if the number of cycles within the union is even or odd. A single large fraction is formed with all fertility containing cycle unions in the numerator and non-fertility containing cycle unions in the denominator. In the numerator, odd count cycle unions are added, while even count cycle unions are subtracted. In the denominator, even count cycle unions are added, while odd count cycle unions are subtracted. Each cycle union is multiplied by the inverse of the corresponding control efforts for each time the control effort is applied to the cycle union, and the fraction, set equal to one, can be solved.

In the case of calculating R_0 , each cycle union is multiplied by R_0^{-1} for each fertility arc contained. If the rule of all paths from birth to reproduction passing through a common state(node) discussed in the residual sub-matrix approach is true, then it can be noted that the numerator of the fraction found in the cycle union approach is multiplied by R_0^{-1} , so the original fraction derived is equivalent to R_0 .

COMMON POPULATION MATRICES

Single Node Matrices

A *Single Node Matrix*, which is rarely considered, has a single node and a single entry comprised of a summation of loops. Each of these loops represent a different type of arc. This matrix is often not used in population analysis, however it will be useful when considering composite matrices, as a representative of a disjoint matrix.

$$A = [a_{1,1}]$$

Diagonal Matrices

A *Diagonal Matrix*, defined on pg 7 of Caswell (2001), has entries in only the main diagonal or $A = [a_{i,i}]$. Each term in the main diagonal matrix can be considered a loop corresponding to a particular node. This matrix is often not used in population analysis, however it will be useful when considering composite matrices, as a composite of disjoint matrices.

$$A = \begin{bmatrix} a_{1,1} & 0 & 0 & \cdots & 0 & 0 \\ 0 & a_{2,2} & 0 & \cdots & 0 & 0 \\ 0 & 0 & a_{3,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & a_{n-1,n-1} & 0 \\ 0 & 0 & 0 & \cdots & 0 & a_{n,n} \end{bmatrix}$$

Leslie Matrices

A *Leslie Matrix*, defined on pg 10 of Caswell (2001), has only fertilities in the top row and state-transitions in the sub-diagonal. Such a matrix usually corresponds to an age-based model, with each node corresponding to an age range. In this paper we will consider state-transition full Leslie Matrices, in which all individuals may die or proceed to the next stage

without skipping ages, with no individuals able to live past the maximum age. The cycle unions corresponding to each fertility term will be analyzed.

$$A = \begin{bmatrix} f_{1,1} & f_{1,2} & f_{1,3} & \cdots & f_{1,n-1} & f_{1,n} \\ t_{2,1} & 0 & 0 & \cdots & 0 & 0 \\ 0 & t_{3,2} & 0 & \cdots & 0 & 0 \\ 0 & 0 & t_{4,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & t_{n,n-1} & 0 \end{bmatrix}$$

Lefkovitch Matrices

A *Lefkovitch Matrix*, defined in Lewis et al. (2019), has only fertilities in the top row and state-transitions in the main diagonal and sub-diagonal. Such a matrix usually corresponds to a stage-based model, with each node corresponding to a physically or socially distinct life stage. In this paper we will consider state-transition full Lefkovitch Matrices, in which all individuals may die, remain in their current stage, or proceed to the next stage without skipping stages, with individuals being able to remain in the final stage until they die. The cycle unions corresponding to each fertility term will be analyzed.

$$A = \begin{bmatrix} t_{1,1} + f_{1,1} & f_{1,2} & f_{1,3} & \cdots & f_{1,n-1} & f_{1,n} \\ t_{2,1} & t_{2,2} & 0 & \cdots & 0 & 0 \\ 0 & t_{2,2} & t_{3,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \ddots & t_{n-1,n-1} & 0 \\ 0 & 0 & 0 & \cdots & t_{n,n-1} & t_{n,n} \end{bmatrix}$$

Sub-Diagonal Triangle Transition Matrices

A *Sub-Diagonal Transition Triangle Matrix*, defined here, has only transitions below the diagonal. Such a matrix would correspond to a size-based model, with each node corresponding to a size range. Though we refer to an individual proceeding through the model, this may be

more representative of a highly group-dependent bacterial colony, with each node corresponding to a colony population size range. In this paper we will consider state-transition full Sub-Diagonal Triangle Transition Matrices, in which all individuals may die or proceed to a future size possibly skipping stages, with no individuals able to sustain themselves past the maximum size. The cycle unions corresponding to each fertility term will be analyzed. Note that the 2×2 sub-diagonal transition triangle matrix is identical to the 2×2 Leslie matrix.

$$A = \begin{bmatrix} f_{1,1} & f_{1,2} & f_{1,3} & \cdots & f_{1,n-1} & f_{1,n} \\ t_{2,1} & 0 & 0 & \cdots & 0 & 0 \\ t_{3,1} & t_{2,2} & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ t_{n-1,1} & t_{n-1,2} & t_{n-1,3} & \cdots & 0 & 0 \\ t_{n,1} & t_{n,2} & t_{n-1,3} & \cdots & t_{n,n-1} & 0 \end{bmatrix}$$

Lower Triangle Transition Matrices

A *Lower Triangle Transition Matrix*, defined here, has only state-transitions in and below the diagonal. Such a matrix would correspond to a size-based model, with each node corresponding to a size range. Though we refer to an individual proceeding through the mode, this may be more representative of a bacterial or fungal colony, with each node corresponding to a colony population size range. In this paper we will consider state-transition full Lower Triangle Transition Matrices, in which all individuals may die, remain at their current size, or proceed to a future size possibly skipping sizes, with individuals being able to remain at the maximum size until they die. The cycle unions corresponding to each fertility term will be analyzed. Note that the 2×2 lower triangle transition triangle matrix is identical to the 2×2 Lefkovitch matrix.

$$A = \begin{bmatrix} t_{1,1} + f_{1,1} & f_{1,2} & f_{1,3} & \cdots & f_{1,n-1} & f_{1,n} \\ t_{2,1} & t_{2,2} & 0 & \cdots & 0 & 0 \\ t_{3,1} & t_{2,2} & t_{3,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ t_{n-1,1} & t_{n-1,2} & t_{n-1,3} & \cdots & t_{n-1,n-1} & 0 \\ t_{n,1} & t_{n,2} & t_{n-1,3} & \cdots & t_{n,n-1} & t_{n,n} \end{bmatrix}$$

TECHNICAL APPROACH

First, we inspect a single node to make note that the possible cycle union permutations must be one plus the number of cycles supported by the node. Second, we inspect a diagonal node to make note that the possible cycle union permutations must be the product of the cycle unions supported by each node, since the nodes are entirely disjoint.

We then inspect the Leslie, Lefkovitch, sub-diagonal triangle transition, and lower triangle transition matrices in the following manner. We count the number of cycle unions that do not contain fertility arcs, or the *survivor cycle unions*. We then count the number of cycle unions associated with the top right most fertility term, or the *late fertility cycle unions*. We then count the number of cycle unions associated with any other given fertility term, or *early fertility cycle unions*.

We will consider the *null cycle union*, which is the cycle union containing no cycles as a survivor cycle union, in which no cohorts are able to successfully shift to a node, and the entire population dies out. The cycle unions can be biologically interpreted as an expression that indicates a change in the population if every individual was sorted into a cohort based on the nodes in the population model and every cohort shifted through a full cycle as indicated by the specific disjoint cycles in the cycle union.

- The *late fertility cycle unions* are the cycle unions consisting of exactly one fertility cycle using the late fertility arc and any number of survivor cycles.
- The *early fertility cycle unions* are the cycle unions consisting of exactly one fertility cycle not using the late fertility arc and any number of survivor cycles.
- The *survivor cycle unions* are the cycle unions consisting of any number of and only survivor cycles.
- The *null cycle union* is the survivor cycle union consisting of only null cycles.

The results, or Lemmas of the survivor, late fertility, and early fertility cycle union counts are combined to form a Theorem detailing the total number of cycle unions for a transition full matrix, with fertility arcs ranging from f_k to f_n . For the sub-diagonal and lower triangle transition matrices, we require $n \geq k \geq 2$ as our counting method applies to fertility cycles that do not include f_1 . Such incomplete matrices represent populations in which an organism only has fertility if it has reached or surpassed a certain checkpoint in its life. As a Corollary, we note the total number of cycle unions for a complete matrix, where all possible transitions and fertility arcs are fully represented. Such complete matrices represent populations in which all organisms are fecundity ready and can immediately contribute to the next generation.

In order to better describe our process in choosing arcs and marking nodes as already considered, and non-applicable for future arc choices within a cycle union, we will use the terms forward moving, backward moving, and stationary to describe arcs that are below the diagonal, above the diagonal, and on the diagonal respectively. In this way, we describe an individual following a potential cycle (which is a closed path), through the population digraph. Note that in this paper, we will not consider population matrices that have backward moving state-transitions. The only backward moving arcs considered will be the fertility terms.

Single Node Matrices

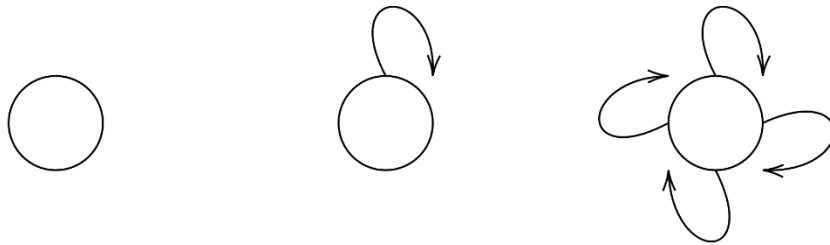


Figure 1: Single Node Matrix Cycle Counting

For a single node matrix, the only entry is comprised of a sum of arcs, which must be loops. While any number of arcs could be defined, in this paper we are only concerned with transition arcs and fertility arcs. Since any given loop makes use of the single node, there are no possible cycle unions consisting of multiple cycles. As we will be counting the empty cycle union, there is one cycle union per type of loop represented and the null cycle union. For a single node matrix, with k arcs, there must be $k + 1$ cycle unions.

Lemma 1. *For a single node matrix A in the form*

$$A = [a_{1,1}],$$

where $a_{1,1} = a_1 + a_2 + \dots + a_k$.

1. *The total number of cycle unions is: $k + 1$.*
2. *The number of cycle unions containing a_g is: 1.*

Diagonal Matrices

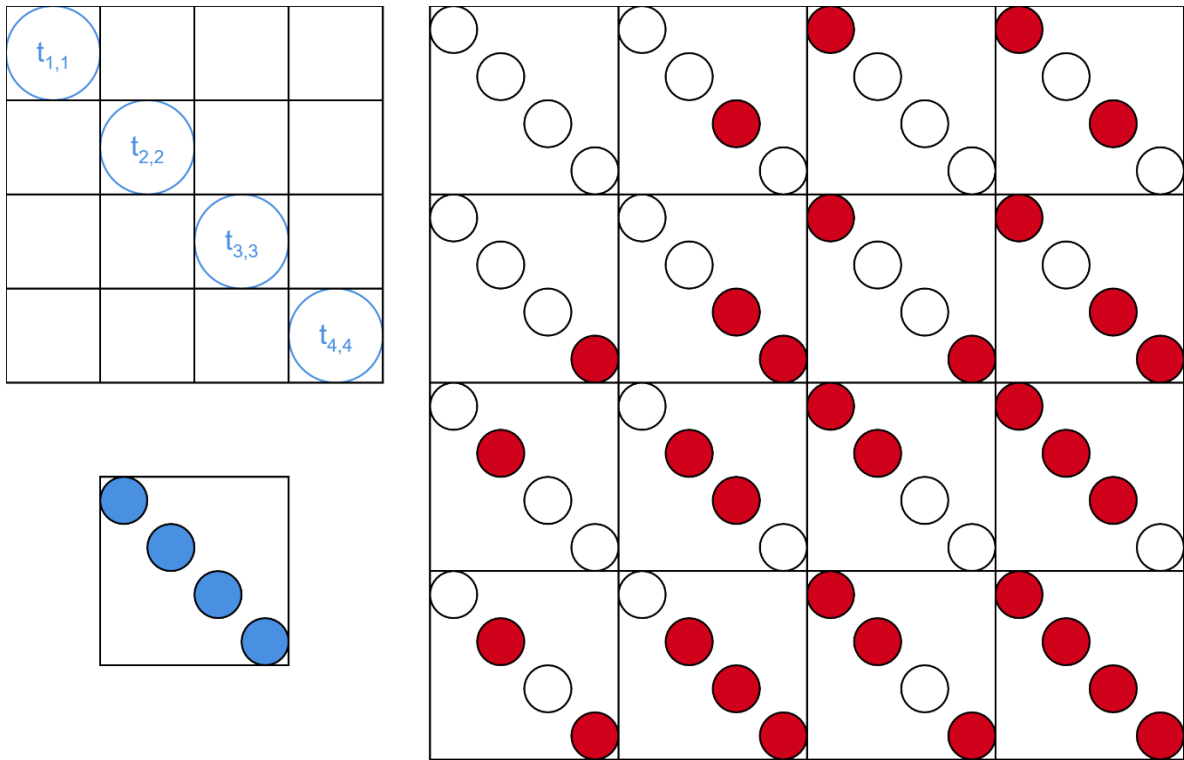


Figure 2: Diagonal Matrix Cycle Counting

For a diagonal matrix, it is clear since none of the nodes are connected, every loop within any given node is disjoint to any loop within any other node. We see that any combination of loops represented by their respective nodes can be considered. This makes up all possible cycle unions. When only one type of arc is represented in every diagonal, that there are two possible cycles per node: the null cycle and the loop. Therefore, the total number of cycle unions can be described simply as 2^n .

Lemma 2. *For a diagonal matrix A in the form*

$$A = \begin{bmatrix} t_{1,1} & 0 & 0 & \cdots & 0 & 0 \\ 0 & t_{2,2} & 0 & \cdots & 0 & 0 \\ 0 & 0 & t_{3,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & t_{n-1,n-1} & 0 \\ 0 & 0 & 0 & \cdots & 0 & t_{n,n} \end{bmatrix},$$

where $n \geq 1$.

1. The total number of cycle unions is: 2^n .
2. The number of cycle unions containing $t_{g,g}$ is: 2^{n-1} .

Using the same logic, multiplying the number of cycles per disjoint node (including the null cycle) gives the total number of possible cycle unions for the entire model. This is important because it allows us to conclude that the same would be true for compound matrices made up of sub-matrices that are entirely disjoint. This idea will be used when considering Lefkovitch and Lower Triangle Transition Matrices.

Theorem 3. For a diagonal matrix A in the form

$$A = \begin{bmatrix} a_{1,1} & 0 & 0 & \cdots & 0 & 0 \\ 0 & a_{2,2} & 0 & \cdots & 0 & 0 \\ 0 & 0 & a_{3,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & a_{n-1,n-1} & 0 \\ 0 & 0 & 0 & \cdots & 0 & a_{n,n} \end{bmatrix},$$

where

$$a_{1,1} = a_{1_1} + a_{1_2} + \cdots + a_{1_{k_1}},$$

$$a_{2,2} = a_{2_1} + a_{2_2} + \cdots + a_{2_{k_2}},$$

...

$$a_{n,n} = a_{n_1} + a_{n_2} + \cdots + a_{n_{k_n}}.$$

1. The total number of cycle unions is: $\prod_{i=1}^n [k_i + 1]$
2. The number of cycle unions containing $a_{g,g}$ is: $\prod_{i=1}^n [k_i + 1] / (k_g + 1)$

Leslie Matrices

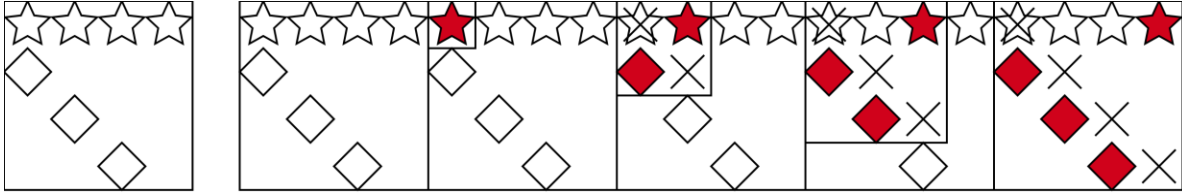


Figure 3: Leslie Matrix Cycle Counting

For the survivor cycle unions of the Leslie matrix, since there are only entries under the diagonal, and none on or above the diagonal, it is impossible to form any cycles that are not the null cycle. That is, there are forward moving transitions, but no stationary transitions, and no backward moving transitions; thus, there is no way for an individual to remain in their current node, or to return to their original node after moving forward.

Lemma 4. *For a reduced Leslie matrix A^s in the form*

$$A^s = \begin{bmatrix} 0 & 0 & 0 & \cdots & 0 & 0 \\ t_{2,1} & 0 & 0 & \cdots & 0 & 0 \\ 0 & t_{3,2} & 0 & \cdots & 0 & 0 \\ 0 & 0 & t_{4,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & t_{n,n-1} & 0 \end{bmatrix},$$

where $n \geq 1$.

1. *The number of survivor cycle is: 1.*

For the late fertility cycle unions of the Leslie matrix, it is clear that for an individual of the last age to contribute to the node through its offspring, the offspring must grow from the first age to last age, and there is only one way to do so, sequentially through each node.

Lemma 5. For a reduced Leslie matrix A^l with the late fertility $f_{1,n}$ in the form

$$A^l = \begin{bmatrix} 0 & 0 & 0 & \cdots & 0 & f_{1,n} \\ t_{2,1} & 0 & 0 & \cdots & 0 & 0 \\ 0 & t_{3,2} & 0 & \cdots & 0 & 0 \\ 0 & 0 & t_{4,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & t_{n,n-1} & 0 \end{bmatrix},$$

where $n \geq 1$.

1. The number of late fertility cycle unions is: 1.

For the early fertility cycle unions of the Leslie matrix, it is clear that for an individual of any given age to contribute to the node through its offspring, the offspring must grow from the first age to that age, and there is only one way to do so, sequentially through each prior node. As every node up to and including this node has been considered, we can approximate the 1-k nodes as a single node with one possible cycle (the null cycles have all been accounted for already). We can then turn our attention to the rest of the matrix as if this were a matrix of sub-matrices. The remaining entries are similar to that of the reduced matrix in **Lemma 4.**, that is, there are no possible cycles other than the null cycle to be made with the remaining nodes. As there are no other cycles to permute with, there is only one cycle and thus one cycle union associated with any given early fertility cycle.

Lemma 6. For a reduced Leslie matrix A^e with the early fertility $f_{1,k}$ in the form

$$A^e = \begin{bmatrix} 0 & 0 & \cdots & f_{1,k} & \cdots & 0 \\ t_{2,1} & 0 & 0 & \cdots & 0 & 0 \\ 0 & t_{3,2} & 0 & \cdots & 0 & 0 \\ 0 & 0 & t_{4,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & t_{n,n-1} & 0 \end{bmatrix},$$

where $n \geq k \geq 1$.

1. The number of early fertility cycle unions for $f_{1,k}$ is: 1.

With the previous results, the total number of cycle unions for an incomplete Leslie matrix is the sum of the number of cycle unions associated with no fertilities, and number of cycle unions associated with fertilities. We also note that since every cycle must connect every node between the first node that the last node in the cycle, every transition from one arc to the next arc is included in every cycle that proceeds to and past the next arc.

Theorem 7. For an incomplete Leslie matrix A in the form

$$A = \begin{bmatrix} 0 & \cdots & 0 & f_{1,k} & \cdots & f_{1,n} \\ t_{2,1} & 0 & 0 & \cdots & 0 & 0 \\ 0 & t_{3,2} & 0 & \cdots & 0 & 0 \\ 0 & 0 & t_{4,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & t_{n,n-1} & 0 \end{bmatrix},$$

where $n \geq k \geq 1$.

1. The total number of cycle unions is: $n - k + 2$.
2. The number of fertility cycle unions for $f_{1,g}$ is: 1.
3. The number of cycle unions containing $t_{g+1,g}$ is: $n - k + 1$ if $g < k$ or $n - g$ if $g \geq k$.
4. The number of survivor cycle is: 1.

Corollary 8. For a complete Leslie matrix A in the form

$$A = \begin{bmatrix} f_{1,1} & f_{1,2} & f_{1,3} & \cdots & f_{1,n-1} & f_{1,n} \\ t_{2,1} & 0 & 0 & \cdots & 0 & 0 \\ 0 & t_{3,2} & 0 & \cdots & 0 & 0 \\ 0 & 0 & t_{4,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & t_{n,n-1} & 0 \end{bmatrix},$$

where $n \geq 1$.

1. The total number of cycle unions is: $n + 1$.
2. The number of fertility cycle unions for $f_{1,g}$ is: 1.
3. The number of cycle unions containing $t_{g+1,g}$ is: $n - g$.
4. The number of survivor cycle is: 1.

Lefkovitch Matrices

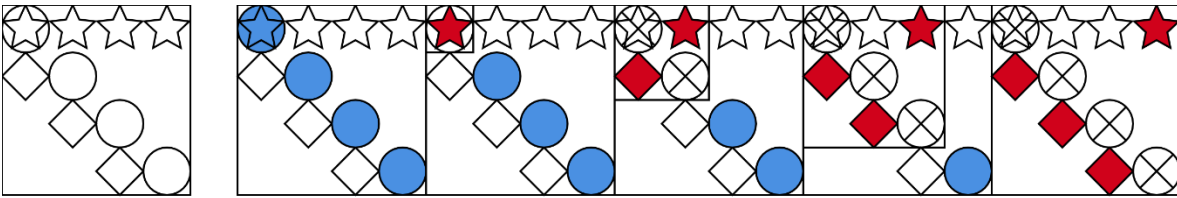


Figure 4: Lefkovitch Matrix Cycle Counting

For the survivor cycle unions of the Lefkovitch matrix, it is clear that since there are only entries under or on the diagonal, and none above the diagonal, it is impossible to form any cycles that are not the null cycle or stationary cycles. That is, there are forward moving transitions and stationary transitions, but no backward moving transitions; thus, there is no way for an individual to return to their original node after moving forward. As there are no backwards moving transitions, all forward moving transitions can be ignored. This leaves us with the stationary transitions, or the entries on the diagonal. As per **Lemma 2**, there are 2^n survivor cycle unions. Sub-Diagonal Triangle Transition Matrices

Lemma 9 For a reduced Lefkovitch matrix A^s with the form

$$A^s = \begin{bmatrix} t_{1,1} + 0 & 0 & 0 & \cdots & 0 & 0 \\ t_{2,1} & t_{2,2} & 0 & \cdots & 0 & 0 \\ 0 & t_{2,2} & t_{3,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \ddots & t_{n-1,n-1} & 0 \\ 0 & 0 & 0 & \cdots & t_{n,n-1} & t_{n,n} \end{bmatrix},$$

where $n \geq 1$.

1. The number of survivor cycle is: 2^n .

For the late fertility cycle unions of the Lefkovitch matrix, it is clear that for an individual of the last age to contribute to the node through its offspring, the offspring must grow from the first age to last age, and there is only one way to do so, sequentially through each node. We note that since we have already considered every node, that there are $n - n = 0$ nodes left to create cycles to permute the single cycle using the first 1 through n nodes with.

Lemma 10. For a reduced Lefkovitch matrix A^l with the late fertility $f_{1,n}$ in the form

$$A^l = \begin{bmatrix} t_{1,1} + 0 & 0 & 0 & \cdots & 0 & f_{1,n} \\ t_{2,1} & t_{2,2} & 0 & \cdots & 0 & 0 \\ 0 & t_{2,2} & t_{3,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \ddots & t_{n-1,n-1} & 0 \\ 0 & 0 & 0 & \cdots & t_{n,n-1} & t_{n,n} \end{bmatrix},$$

where $n \geq 1$.

1. The number of late fertility cycle union is: 1.

For the early fertility cycle unions of the Lefkovitch matrix, it is clear that for an individual of any given age to contribute to the node through its offspring, the offspring must grow from the

first age to that age, and there is only one way to do so, sequentially through each prior node. As every node up to and including this node has been considered, we can approximate the 1-k nodes as a single node with one possible cycle (the null cycles have all been accounted for already, and the loops can be ignored as their corresponding nodes have already been considered). We can then turn our attention to the rest of the matrix as if this were a matrix of sub-matrices. It is clear that the remaining entries are similar to that of the reduced matrix in **Lemma 9**, that is, there are no possible cycles other than the null cycle and stationary cycles left to make with the remaining nodes. We note that the single cycle can be permuted disjointly with all the stationary cycles, of which there are $n - k$ of.

Lemma 11. *For a reduced Lefkovich matrix A^e with the early fertility $f_{1,k}$ in the form*

$$A^e = \begin{bmatrix} t_{1,1} + 0 & 0 & \cdots & f_{1,k} & \cdots & 0 \\ t_{2,1} & t_{2,2} & 0 & \cdots & 0 & 0 \\ 0 & t_{2,2} & t_{3,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \ddots & t_{n-1,n-1} & 0 \\ 0 & 0 & 0 & \cdots & t_{n,n-1} & t_{n,n} \end{bmatrix},$$

where $n \geq k \geq 1$.

1. *The number of early fertility cycle unions for f_k is: 2^{n-k} .*

With the previous results, it is clear that the total number of cycle unions for an incomplete Lefkovich matrix is the sum of the number of cycle unions associated with no fertilities, and number of cycle unions associated with fertilities.

Theorem 12. *For an incomplete Lefkovich matrix A in the form*

$$A = \begin{bmatrix} t_{1,1} + 0 & \cdots & 0 & f_{1,k} & \cdots & f_{1,n} \\ t_{2,1} & t_{2,2} & 0 & \cdots & 0 & 0 \\ 0 & t_{2,2} & t_{3,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \ddots & t_{n-1,n-1} & 0 \\ 0 & 0 & 0 & \cdots & t_{n,n-1} & t_{n,n} \end{bmatrix},$$

where $n \geq k \geq 1$.

1. The total number of cycle unions is: $2^n + 2^{n-k+1} - 1$.
2. The number of fertility cycle unions for f_g is: 2^{n-g} .
3. The number of survivor cycle is: 2^n .

As a corollary, we note the results for a complete Lefkovitch matrix.

Corollary 13. For a complete Lefkovitch matrix A in the form

$$A = \begin{bmatrix} t_{1,1} + f_{1,1} & f_{1,2} & f_{1,3} & \cdots & f_{1,n-1} & f_{1,n} \\ t_{2,1} & t_{2,2} & 0 & \cdots & 0 & 0 \\ 0 & t_{2,2} & t_{3,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \ddots & t_{n-1,n-1} & 0 \\ 0 & 0 & 0 & \cdots & t_{n,n-1} & t_{n,n} \end{bmatrix},$$

where $n \geq 1$.

1. The total number of cycle unions is: $2^{n+1} - 1$.
2. The number of fertility cycle unions for f_g is: 2^{n-g} .
3. The number of survivor cycle is: 2^n .

Sub-Diagonal Triangle Transition Matrices

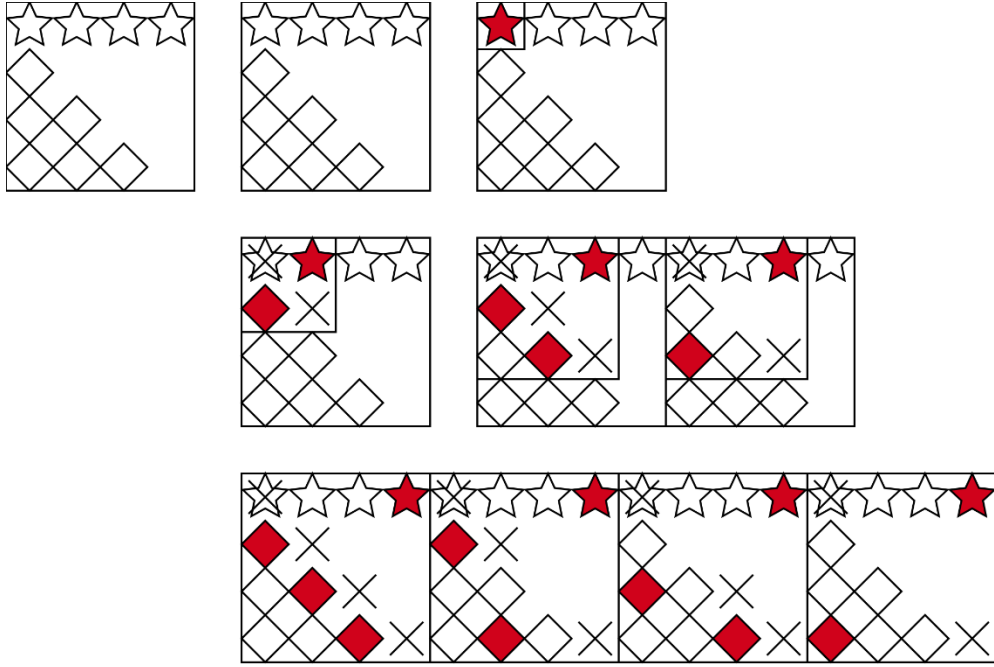


Figure 5: Sub-Diagonal Triangle Transition Matrix Cycle Counting

For the survivor cycle unions of the sub-diagonal triangle matrix, we note that similarly to the reduced Leslie matrix in **Lemma 4**, as there are only forward moving transitions corresponding to sub-diagonal entries, there is only the null cycle union.

Lemma 14. *For a reduced sub-diagonal triangle transition matrix A^s in the form*

$$A^s = \begin{bmatrix} 0 & 0 & 0 & \cdots & 0 & 0 \\ t_{2,1} & 0 & 0 & \cdots & 0 & 0 \\ t_{3,1} & t_{2,2} & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots & \vdots \\ t_{n-1,1} & t_{n-1,2} & t_{n-1,3} & \ddots & 0 & 0 \\ t_{n,1} & t_{n,2} & t_{n-1,3} & \cdots & t_{n,n-1} & 0 \end{bmatrix},$$

where $n \geq 1$.

1. The total number of cycle unions containing no fertility arcs is: 1.

For the late fertility cycle unions of the sub-diagonal triangle transition matrix, for an individual of the last age to contribute to the node through its offspring, the offspring must grow from the first age to last age. There are $n - 2$ nodes in between nodes 1 and n . As the sub-triangle diagonal is full, we can see that there are $\binom{n-2}{0}$ ways for an individual to pass through all these nodes. We note that there are $\binom{n-2}{1}$ ways for an individual to pass through all but one of these nodes. We see that this is true through $\binom{n-2}{n-2}$ ways to pass through none of these nodes. However, this formula only works if the matrix is of size $n = 2$ or greater.

Lemma 15. *For a reduced sub-diagonal triangle transition matrix A^l with the late fertility $f_{1,n}$ in the form*

$$A^l = \begin{bmatrix} 0 & 0 & 0 & \cdots & 0 & f_{1,n} \\ t_{2,1} & 0 & 0 & \cdots & 0 & 0 \\ t_{3,1} & t_{2,2} & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots & \vdots \\ t_{n-1,1} & t_{n-1,2} & t_{n-1,3} & \ddots & 0 & 0 \\ t_{n,1} & t_{n,2} & t_{n-1,3} & \cdots & t_{n,n-1} & 0 \end{bmatrix},$$

where $n \geq 2$.

1. *The number of late fertility cycle unions is: 2^{n-2} .*

For the early fertility cycle unions of the sub-diagonal triangle transition matrix, we make use of our previous observations in **Lemma 15** and **Lemma 14** to note that for the nodes 2 through k , there are $\sum_{i=0}^{k-2} \binom{k-2}{i}$ cycle unions to be permuted with no possible cycle unions but the null cycle union remaining in the rest of the matrix.

Lemma 16. *For a reduced sub-diagonal triangle transition matrix A^e with the early fertility $f_{1,k}$ in the form*

$$A^e = \begin{bmatrix} 0 & 0 & \cdots & f_{1,k} & \cdots & 0 \\ t_{2,1} & 0 & 0 & \cdots & 0 & 0 \\ t_{3,1} & t_{2,2} & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots & \vdots \\ t_{n-1,1} & t_{n-1,2} & t_{n-1,3} & \ddots & 0 & 0 \\ t_{n,1} & t_{n,2} & t_{n-1,3} & \cdots & t_{n,n-1} & 0 \end{bmatrix},$$

where $n \geq k \geq 2$.

1. The total number of cycle unions is: 2^{k-2} .

With the previous results, the total number of cycle unions for an incomplete sub-diagonal triangle transition matrix is the sum of the number of cycle unions associated with no fertilities, and number of cycle unions associated with fertilities.

Theorem 17. For an incomplete sub-diagonal triangle transition matrix A in the form

$$A = \begin{bmatrix} 0 & \cdots & 0 & f_{1,k} & \cdots & f_{1,n} \\ t_{2,1} & 0 & 0 & \cdots & 0 & 0 \\ t_{3,1} & t_{2,2} & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots & \vdots \\ t_{n-1,1} & t_{n-1,2} & t_{n-1,3} & \ddots & 0 & 0 \\ t_{n,1} & t_{n,2} & t_{n-1,3} & \cdots & t_{n,n-1} & 0 \end{bmatrix},$$

where $n \geq k \geq 2$.

1. The total number of cycle unions is: $1 + 2^{n-1} - 2^k$.
2. The number of cycle unions containing f_g is: 2^{g-2} where $g > 1$.
3. The number of cycle unions containing no fertility arcs is: 1.

As a corollary, we note the results for a complete sub-diagonal triangle transition matrix.

Corollary 18. For a complete sub-diagonal triangle transition matrix A in the form

$$A = \begin{bmatrix} f_{1,1} & f_{1,2} & f_{1,3} & \cdots & f_{1,n-1} & f_{1,n} \\ t_{2,1} & 0 & 0 & \cdots & 0 & 0 \\ t_{3,1} & t_{2,2} & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \ddots & \vdots & \vdots \\ t_{n-1,1} & t_{n-1,2} & t_{n-1,3} & \ddots & 0 & 0 \\ t_{n,1} & t_{n,2} & t_{n-1,3} & \cdots & t_{n,n-1} & 0 \end{bmatrix},$$

where $n \geq 1$.

1. The total number of cycle unions is: $1 + 2^{n-1}$.
2. The number of cycle unions containing f_g is: 2^{g-2} if $g > 1$ or 1 if $g = 1$.
3. The number of cycle unions containing no fertility arcs is: 1.

Lower Triangle Transition Matrices

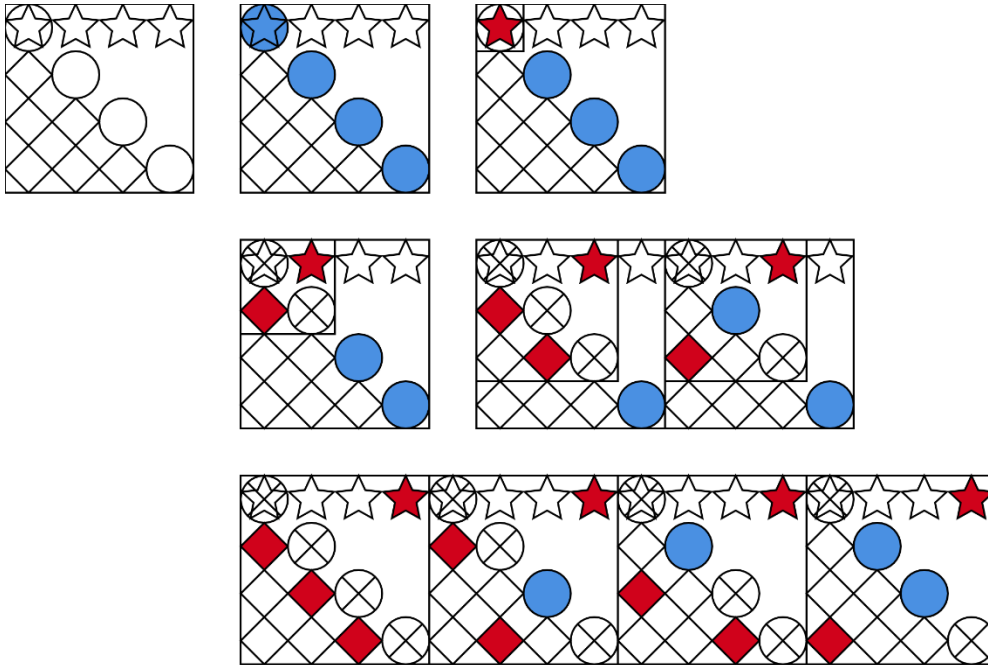


Figure 6: Lower Triangle Transition Matrix Cycle Counting

For the survivor cycle unions of the lower-diagonal triangle matrix, we note that similarly to the reduced Lefkovich matrix in **Lemma 9**, as there are only forward moving transitions corresponding to lower-diagonal entries, and the stationary transitions corresponding to diagonal entries, a diagonal matrix can be approximated for 2^n cycle unions as per **Lemma 2**.

Lemma 19. For a reduced lower triangle transition matrix A^s in the form

$$A = \begin{bmatrix} t_{1,1} + 0 & 0 & 0 & \cdots & 0 & 0 \\ t_{2,1} & t_{2,2} & 0 & \cdots & 0 & 0 \\ t_{3,1} & t_{2,2} & t_{3,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ t_{n-1,1} & t_{n-1,2} & t_{n-1,3} & \cdots & t_{n-1,n-1} & 0 \\ t_{n,1} & t_{n,2} & t_{n-1,3} & \cdots & t_{n,n-1} & t_{n,n} \end{bmatrix},$$

where $n \geq 1$.

1. The number of cycle unions containing no fertility arcs is: 2^n .

For the late fertility cycle unions of the lower triangle transition matrix, we must return to our observations on the reduced sub-diagonal triangle transition matrix in **Lemma 15**, where we noted that there were $\binom{n-2}{i}$ ways to form a cycle that ignored i of the nodes between node 1 and node n . While it may be difficult to see without some rearrangement, we can take the ignored i nodes as disjoint nodes with loops, that can be permuted with the cycles that ignore them. The product gives us $\sum_{i=0}^{n-2} [\binom{n-2}{i} 2^i]$ late fertility cycle unions.

Lemma 20. For a reduced lower triangle transition matrix A^l with the late fertility $f_{1,n}$ in the form

$$A^l = \begin{bmatrix} t_{1,1} + 0 & 0 & 0 & \cdots & 0 & f_{1,n} \\ t_{2,1} & t_{2,2} & 0 & \cdots & 0 & 0 \\ t_{3,1} & t_{2,2} & t_{3,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ t_{n-1,1} & t_{n-1,2} & t_{n-1,3} & \cdots & t_{n-1,n-1} & 0 \\ t_{n,1} & t_{n,2} & t_{n-1,3} & \cdots & t_{n,n-1} & t_{n,n} \end{bmatrix},$$

where $n \geq 2$.

1. The number of cycle unions containing the arc f_n is: 2^{n-2} .

For the early fertility cycle unions of the lower triangle transition matrix, we can apply our findings in **Lemma 20** and **Lemma 19** to see that the $n - k$ nodes past the first n nodes provide an additional 2^{n-k} cycles to permute with the $\sum_{i=0}^{k-2} \binom{k-2}{i} 2^i = 3^{k-2}$ cycles found in the first n nodes.

Lemma 211. *For a reduced lower triangle transition matrix A^e with the early fertility $f_{1,k}$ in the form*

$$A^e = \begin{bmatrix} t_{1,1} + 0 & \cdots & 0 & f_{1,k} & \cdots & 0 \\ t_{2,1} & t_{2,2} & 0 & \cdots & 0 & 0 \\ t_{3,1} & t_{2,2} & t_{3,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ t_{n-1,1} & t_{n-1,2} & t_{n-1,3} & \cdots & t_{n-1,n-1} & 0 \\ t_{n,1} & t_{n,2} & t_{n-1,3} & \cdots & t_{n,n-1} & t_{n,n} \end{bmatrix},$$

where $n \geq k \geq 2$.

1. The number of early fertility cycle unions for f_k is: $2^{n-k} 3^{k-2}$.

With the previous results, the total number of cycle unions for an incomplete lower triangle transition matrix is the sum of the number of cycle unions associated with no fertilities, and number of cycle unions associated with fertilities.

Theorem 22. *For an incomplete lower triangle transition matrix A in the form*

$$A = \begin{bmatrix} t_{1,1} + 0 & \cdots & 0 & f_{1,k} & \cdots & f_{1,n} \\ t_{2,1} & t_{2,2} & 0 & \cdots & 0 & 0 \\ t_{3,1} & t_{2,2} & t_{3,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ t_{n-1,1} & t_{n-1,2} & t_{n-1,3} & \cdots & t_{n-1,n-1} & 0 \\ t_{n,1} & t_{n,2} & t_{n-1,3} & \cdots & t_{n,n-1} & t_{n,n} \end{bmatrix}$$

where $n \geq k \geq 2$.

1. The total number of cycle unions is: $2^n + 3^{n-1} - 3^{k-2} 2^{n-k+1}$.

2. The number of fertility cycle unions for $f_{1,g}$ is: $2^{n-g}3^{g-2}$ where $g > 1$.
3. The number of survivor cycle is: 2^n .

As a corollary, we note the results for a complete lower triangle transition matrix.

Corollary 23. For a complete lower triangle transition matrix A in the form

$$A = \begin{bmatrix} t_{1,1} + f_{1,1} & f_{1,2} & f_{1,3} & \cdots & f_{1,n-1} & f_{1,n} \\ t_{2,1} & t_{2,2} & 0 & \cdots & 0 & 0 \\ t_{3,1} & t_{2,2} & t_{3,3} & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ t_{n-1,1} & t_{n-1,2} & t_{n-1,3} & \cdots & t_{n-1,n-1} & 0 \\ t_{n,1} & t_{n,2} & t_{n-1,3} & \cdots & t_{n,n-1} & t_{n,n} \end{bmatrix},$$

where $n \geq 1$.

1. The total number of cycle unions is: $2^n + 3^{n-1}$.
2. The number of fertility cycle unions for $f_{1,g}$ is: $2^{n-g}3^{g-2}$ if $g > 1$ or 2^{n-1} if $g = 1$.
3. The number of survivor cycle unions is: 2^n .

DISCUSSION AND FUTURE WORK

We have developed a procedure of cycle union counting that first evaluates the number of cycle union independent of fertility terms, then each of the fertility terms from the term spanning the greatest range of nodes to the least. Through the Lefkovitch matrix counting, we have shown that once a cycle has been completed, if it is disjoint from the rest of the matrix, it can be permuted with the cycle unions of the remaining matrix to find all associated cycle unions. Through the sub-diagonal triangle transition matrix, we have shown an orderly way to find and categorize cycle unions by the number of nodes used and bypassed by a primary cycle that has a single backward moving arc and several possible forward moving arcs to use. By combining the results, we can show in the lower triangle transition matrix, how to permute disjoint cycles both within and outside of a cycle that skips nodes.

In this paper we have shown the cycle union counts for matrices with only forward moving transitions and backwards moving fertilities along the top row, that is, we have only shown results for populations that can remain in their node or advance, and in which all offspring are born to the same node. Future work could expand on deriving the number of cycle unions associated to given transitions within these models. Future work could derive the cycle union count for models in which backwards moving transitions are present, that is, populations that can revert to an earlier life stage.

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