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Graph decompositions for demographic loop analysis

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Abstract A new approach to loop analysis is presented in which decompositions of the total elasticity of a population projection matrix over a set of life history pathways are obtained as solutions of a constrained system of linear equations. In loop analysis, life history pathways are represented by loops in the life cycle graph, and the elasticity of the loop is interpreted as a measure of the contribution of the life history pathway to the population growth rate. Associated with the life cycle graph is a vector space—the cycle space of the graph—which is spanned by the loops. The elasticities of the transitions in the life cycle graph can be represented by a vector in the cycle space, and a loop decomposition of the life cycle graph is then defined to be any nonnegative linear combination of the loops which sum to the vector of elasticities. In contrast to previously published algorithms for carrying out loop analysis, we show that a given life cycle graph admits of either a unique loop decomposition or an infinite set of loop decompositions which can be characterized as a bounded convex set of nonnegative vectors. Using this approach, loop decompositions which minimize or maximize a linear objective function can be obtained as solutions of a linear programming problem, allowing us to place lower and upper bounds on the contributions of life history pathways to the population growth rate. Another consequence of our approach to loop analysis is that it allows us to identify the exact tradeoffs in contributions to the population growth rate that must exist between life history pathways.

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1 Introduction

Demographic loop analysis was introduced by van Groenendael et al. in 1994 [11]
as a tool for decomposing the total elasticity in a population projection matrix over a
collection of life history pathways. This decomposition allows one to determine the
relative contributions of distinct life history pathways to the finite rate of population
growth λ. A review of methods of elasticity and loop analysis can be found in [5].
Loop analysis entails choosing a set of loops (directed cycles which correspond to life
history pathways) in the life cycle graph and assigning characteristic elasticities to the
loops so that they partition the elasticities of the edges they pass through. Wardle [12]
provides an algorithm for decomposing the life cycle graph into a set of independent
cycles using a spanning tree for the graph. A difficulty with this algorithm is that
for a given spanning tree, the cycles obtained may include biologically meaningless
"negative loops", that is, cycles in which not all edges are consistently oriented with
respect to an orientation of the cycle. The presence of negative loops complicates the
process of partitioning the elasticities. This difficulty is avoided with an algorithm
described by Sun and Wang [9] for decomposing weighted digraphs into a collection
of weighted subgraphs: when applied to a life cycle graph weighted by its transition
elasticities, their algorithm yields an independent set of weighted directed cycles. A
similar approach is described in [6]. In both [9,12], the authors point out that for suffi-
ciently complex life cycle graphs the decomposition into a set of weighted loops is not
necessarily unique since different choices in the course of executing either algorithm
may give rise to distinct sets of loops over which the elasticities are to be partitioned.
The existence of multiple decompositions introduces an unavoidable complication to
loop analysis since researchers must also determine which decompositions are most
suitable for demographic analysis of a population.

Both of the aforementioned algorithms share two weaknesses. First, in order to
produce a set of loops over which the elasticities can be partitioned, a maximal
linearly independent set of loops is generated. There are only finitely many such
sets and for each one there is a unique decomposition of the elasticities as required
in [11]. However, there are life cycle graphs for which the set of all loops forms a
linearly dependent set, and it is precisely those graphs which admit of more than one
possible loop decomposition. It is our view that if a set of life histories is observed in
a population, then the loop analysis should take the corresponding loops into account
whether or not they form a linearly independent set. We address this issue by relaxing
the requirement that the set of loops be linearly independent and proposing a mathe-
matical formalization of loop decompositions that allows for the use of dependent sets of
loops. With this approach, we show that finding a loop decomposition of the life cycle
graph is equivalent to finding a solution of a system of linear equations constrained

by a set of linear inequalities. This system will admit of either a unique solution or infinitely many solutions.

The second weakness is that these algorithms do not produce information that would allow one to evaluate the relative contributions of different life histories to the population growth rate. When the total elasticity is partitioned over a set of loops, each loop is assigned an elasticity which represents its proportional contribution to λ relative to the other loops in the set. When the life cycle graph admits of distinct decompositions, the assigned elasticity of any given loop may vary from one decomposition to another, making it difficult to compare in any absolute terms the contribution of that particular loop to all other loops independent of the choice of decomposition. Both of these weaknesses are resolved in our approach to loop analysis.

Geometrically, the set of loop decompositions can be represented as the feasible set of a linear programming problem and, as such, particular decompositions can be found which minimize or maximize a linear objective function of the loop elasticities. This approach allows us to place lower and upper bounds on the contributions to λ of individual life history pathways. The nullspace of the linear system we describe has an interesting combinatorial structure which allows us to identify the exact tradeoffs in contributions to λ that must exist between life history pathways. These results are illustrated by applying them to a previously published life cycle graph for teasel (*Dipsacus sylvestris*).

2 Loop decompositions

We begin by providing the definitions, notation, and results used in our discussion of loop decompositions. We refer the reader to Caswell [3] for a more detailed discussion of population projection matrices and life cycle graphs, and Bollobás [2] for an introduction to graph theory.

Let A be a population projection matrix of order n. To avoid having to deal with trivial or degenerate cases assume that $n \geq 2$. The matrix is nonnegative and we will also assume that it is irreducible, although not necessarily primitive. The finite rate of population growth λ is the dominant real eigenvalue of A. Associated with A is a directed graph D of order n, the *life cycle graph*, whose nodes correspond to the age or stage classes of the population and whose edges correspond to the transitions from one class to another. Letting $1, 2, \ldots, n$ denote the nodes of D, there is an edge (i, j) directed from node i to node j if and only if $a_{j,i} > 0$. (Note that $a_{i,j}$ goes with the transition from node j to node i.) Let $E(D)$ denote the edge set with $m = |E(D)|$. Since A is irreducible, D is strongly connected (see, for example, [7]).

A *loop* in D of length k is a nonempty sequence $(i_1, i_2), (i_2, i_3), \ldots, (i_k, i_1)$ of edges where the nodes $i_1, i_2, \ldots, i_k$ are distinct. (In the graph theory literature, this would be called a *directed k-cycle*, "loop" being the term usually reserved for cycles of length 1. However, we will adopt the term as it is used in the ecological research literature.) Since the edges must all share the same orientation with respect to the loop we can unambiguously identify a loop by its node sequence $i_1, i_2, \ldots, i_k, i_1$. Let $L(D) = \{L_1, \ldots, L_l\}$ denote the set of all loops in D with $l = |L(D)|$ and let l_i denote the length of loop L_i, $i = 1, \ldots, l$. In Sect. 3 we describe a systematic process for identifying all of the loops in D.

For each nonzero element $a_{i,j}$ of A, the *elasticity* of λ with respect to $a_{i,j}$ is defined to be

$$e_{i,j} = \frac{a_{i,j}}{\lambda} \frac{\partial \lambda}{\partial a_{i,j}}$$

representing the proportional change in λ with respect to proportional change in $a_{i,j}$. The elasticities can be easily computed using left and right eigenvectors for the eigenvalue λ [4]. Elasticities are always nonnegative and satisfy

$$\sum_{i,j} e_{i,j} = 1, \tag{1}$$

$$\sum_{j} e_{i,j} = \sum_{j} e_{j,i} \quad \text{for all } i. \tag{2}$$

We define a *loop decomposition* of D to be a function $g : L(D) \to \mathbb{R}$ which assigns to each loop L_k a nonnegative number $g(L_k)$ satisfying $e_{j,i} = \sum_{L_k \ni (i,j)} g(L_k)$ for each $(i, j) \in E(D)$. The number $g(L_k)$ is the *characteristic elasticity* of L_k and the *loop elasticity of L_k is $l_k g(L_k)$*. Notice that we allow characteristic elasticities to be 0. The *support* of g is the set of loops for which $g \neq 0$. Each loop in the support of g corresponds to one possible life history pathway in the life cycle graph. The loop elasticity is then interpreted as the relative contribution of that life history pathway to λ [11].

Each loop L_k is represented by an $m \times 1$ characteristic vector v_{L_k} whose components are indexed by the edges of D where

$$v_{L_k}(i, j) = \begin{cases} 1, & \text{when } (i, j) \in L_k, \\ 0, & \text{otherwise.} \end{cases}$$

The elasticities are represented by the vector e where $e(i, j) = e_{j,i}$. Let Λ be the $m \times l$ matrix whose rows are indexed by the edges of D and whose kth column is the vector v_{L_k}. We now show that nonnegative solutions of the matrix equation

$$\Lambda x = e \tag{3}$$

can be interpreted as loop decompositions. To do so we must work in a vector space associated with the life cycle graph.

The *edge space* of D is the vector space of real-valued functions $f : E(D) \to \mathbb{R}$, denoted $C_1(D)$. This space is isomorphic to $\mathbb{R}^m$. To see this, index the components of $\mathbb{R}^m$ with the edges of D and identify the function $f \in C_1(D)$ with the vector v_f where $v_f(i, j) = f(i, j)$ for each edge (i, j). A *circulation* in D is a function $f \in C_1(D)$ with the property that $\sum_k f(i, k) = \sum_k f(k, i)$ for all nodes i. The *flow* of f on the edge (i, j) is $f(i, j)$. A circulation f is similarly represented by an $m \times 1$ vector v_f where $v_f(i, j) = f(i, j)$. The set of all circulations in D forms an $(m - n + 1)$-dimensional subspace of $C_1(D)$ called the *cycle space* of D, denoted $Z(D)$ [2]. The

dimension of $Z(D)$ is also known as the *nullity* of D. In general, a circulation can have both negative and positive components.

Since the columns of Λ are the characteristic vectors of the loops, the following result of Thomasson [10] (expressed using our terminology and notation) suffices to show that the column space of Λ is $Z(D)$.

Proposition *If D is a strongly connected directed graph, then the loops generate $Z(D)$.*

By property (2) of elasticities, the vector e is a circulation, and therefore can be expressed as a linear combination of the columns of Λ. It follows that Eq. (3) is consistent. Now we show that there is at least one nonnegative solution.

The following algorithm will produce a nonnegative solution of Eq. (3). This algorithm is equivalent to the algorithm described by Sun and Wang [9] when applied to strongly connected graphs whose edges are weighted by the elasticities.

Input: Λ and a nonnegative circulation $f \in Z(D)$.
Output: A nonnegative solution x to $\Lambda x = f$.

1. Let U be the set of loops in the support of x, initialized to the empty set. The components $x(1), \ldots, x(l)$ of x are initialized to 0.
2. If f is identically 0, the algorithm terminates.
3. Identify an edge (a, b) in D with minimum nonzero flow $f(a, b)$ and identify a loop L_k, $L_k \notin U$, which includes (a, b). (Such a loop L_k will always be available since f is a nonzero circulation.)
4. Set $x(k) = f(a, b)$ and set $f' = f - f(a, b)v_{L_k}$. (Note that f' is a nonnegative circulation with $f'(a, b) = 0$.)
5. Add L_k to the set U, set $f = f'$, and go to Step 2.

The algorithm will terminate in a finite number of steps since the initial circulation f is nonnegative and D is finite. With input $f = e$, the output x is a nonnegative solution of Eq. (3). Moreover, since at each step the flow is reduced to 0 on some edge, the support of x is independent in the sense that the characteristic vectors $\{v_L : L \in U\}$ form a linearly independent set in $Z(D)$.

This algorithm can be used to produce a strictly positive solution. Let $l_{i,j}$ denote the number of loops containing the edge (i, j) and compute $\rho = \min\{e_{i,j}/l_{i,j} : (i, j) \in E(D)\}$. Let J be the all-1's vector of length l and note that ΛJ is a circulation. This, together with the definition of ρ, guarantees that $e - \rho \Lambda J$ is a nonnegative circulation. Now implement the algorithm with initial circulation $f = e - \rho \Lambda J$. Replace the nonnegative solution x produced when the algorithm terminates with $x + \rho \Lambda J$ to obtain a strictly positive solution of Eq. (3). This strictly positive solution exists for any life cycle graph, even if the set $L(D)$ is linearly dependent.

Let x be any nonnegative solution of Eq. (3). Since for each edge $(i, j) \in E(D)$, the components of x which correspond to the loops containing (i, j) must sum to $e_{j,i}$, the kth component of x can be interpreted as the characteristic elasticity of the loop L_k which is represented by the kth column of Λ. Conversely, given a loop decomposition g of D, the vector x whose kth component is $x(k) = g(L_k)$, the characteristic elasticity of loop L_k, is a nonnegative solution of Eq. (3). Thus we have established the main result of this paper.

Theorem *There is a one-to-one correspondence between the set of loop decompositions of D and the set $S = \{x \in \mathbb{R}^l : \Lambda x = e \text{ and } x \geq 0\}$.*

Let $N(\Lambda)$ denote the nullspace of Λ. Recalling that Λ has l columns and the dimension of its column space is $m - n + 1$, we set $\nu = l - (m - n + 1)$ which is the dimension of $N(\Lambda)$. If $\nu = 0$, then Eq. (3) has a unique solution and S contains a single positive vector which corresponds to the only possible loop decomposition of the life cycle graph. This will occur, for example, in the case of an age structured population modeled by a Leslie matrix (because the number of loops is equal to the number of reproductive age classes), or the simple stage structured populations described in [11]. If $\nu > 0$, then S is the intersection of $p + N(\Lambda)$ with the set $\{x \in \mathbb{R}^l : x(i) \geq 0, i = 1, \ldots, l\}$ where p is any particular solution of Eq. (3). We now give two useful characterizations of S when $\nu > 0$.

First, S is the feasible set of the following linear programming problem: minimize the linear objective function $F(x) = \sum_{k=1}^{l} c_k l_k x(k)$ subject to the constraints $\Lambda x = e$ and $x \geq 0$. Because we wish to treat F as a linear function of the loop elasticities, $l_k x(k)$, we write the constant coefficients of the $x(k)$'s as $c_k l_k$, $k = 1, 2, \ldots, l$. Note that S is a ν-dimensional convex polytope in $\mathbb{R}^l$. (For a discussion of the geometry of linear programming, see [8].) Moreover, S is bounded because every column of Λ consists of 0's and 1's, every column has at least one 1, and every component of e is positive. The extreme points of this set (i.e., the vertices of the polytope) correspond to those loop decompositions whose support is an independent set of loops [8, p. 116] and are precisely the solutions which can be obtained using the algorithms described in [9,12]. If we let $\{v_1, \ldots, v_s\}$ denote the set of extreme points of S, then

$$S = \left\{ \sum_{i=1}^{s} a_i v_i : a_i \geq 0 \text{ for all } i \text{ and } a_1 + \cdots + a_s = 1 \right\} \tag{4}$$

which expresses the fact that a bounded convex polytope is the convex hull of its extreme points. This provides a geometric characterization of the set of all possible loop decompositions of D as linear combinations of loop decompositions over linearly independent sets of loops.

In addition to the loop decompositions which correspond to the extreme points of S, the interior points of S also yield loop decompositions of the life cycle graph D. If x is an interior point of S, then the support of x is a linearly dependent set of loops, and there are infinitely many such decompositions whenever $\nu > 0$. These loop decompositions cannot be obtained using the algorithms in [6,9,12] since implementation of those algorithms will only yield loop decompositions over linearly independent sets of loops.

A single loop decomposition can be obtained by specifying the values of c_k, $k = 1, 2, \ldots, l$, and then using linear programming to minimize $F(x) = \sum_{k=1}^{l} c_k l_k x(k)$ subject to the constraints $\Lambda x = e$ and $x \geq 0$. Similarly, the maximum value of F can be found by minimizing the function $H(x) = -F(x)$ subject to the same constraints. (It is possible to choose the constants c_k so that the resulting function F is constant on S. This would occur, for example, if F were chosen to minimize the loop elasticity of a loop of length 1: since that loop would be the unique loop containing its transition in the life cycle graph, its elasticity would have to equal the elasticity of the transition

in any loop decomposition.) Since S is convex, given distinct loop decompositions x and y the vector $tx + (1 - t)y$ corresponds to a loop decomposition for any t in the interval $0 < t < 1$. The biological significance of these solutions will be discussed in Sect. 3.

Our second characterization of S comes from considering the combinatorial structure of $N(\Lambda)$. Let $\{b_1, b_2, \ldots, b_v\}$ be a basis of $N(\Lambda)$. Given a particular solution p of Eq. (3), every element of S can be written in the form

$$p + \sum_{i=1}^{v} c_i b_i \tag{5}$$

where $c_i \in \mathbb{R}$, $i = 1, 2, \cdots, v$ are chosen so that (5) is nonnegative. The vectors in $N(\Lambda)$ have an interesting interpretation in terms of the contributions of life history pathways to λ. Since the entries of Λ are 0's and 1's, and every column must have at least one 1, every nonzero vector in $N(\Lambda)$ must have both positive and negative components. Given distinct vectors $x, y \in S$, $b = y - x \in N(\Lambda)$. Let $b^+ = \{i : b(i) > 0\}$ and $b^- = \{i : b(i) < 0\}$. Replacing the loop decomposition x with the loop decomposition y corresponds to increasing the elasticity of each loop L_i by the amount $l_i b(i)$ where $i \in b^+$ and decreasing the elasticity of each loop L_j by the amount $l_j b(j)$ where $j \in b^-$. These changes depend only on b and therefore provide information about the tradeoffs in their contributions to λ between the sets of loops indexed by b^+ and b^-, independent of the initial loop decomposition x. In particular, if $x \in S$ is positive, then for any $b \in N(\Lambda)$, $x + \epsilon b \in S$ for sufficiently small positive values of ϵ.

3 Example

The question of determining which loop decompositions are most suitable for demographic analysis of a population is complicated by the existence of multiple solutions of Eq. (3). If $v = 0$, then there is only one possible loop decomposition of the life cycle graph and the elasticity of each loop is interpreted as the contribution of the corresponding life history pathway to λ. If $v > 0$, then there are infinitely many loop decompositions of the life cycle graph, all of which are consistent with the vital rates appearing in the population projection matrix.

Ideally, the elasticity of a loop L in a loop decomposition tells us the proportional contribution to the growth rate of the entire population made by the class of individuals whose life history pathways are represented by L [11]. While it may not be possible to measure the actual contributions, our ability to characterize the set S allows us to place lower and upper bounds on those contributions. In the simplest case, the minimum and maximum values attained by $F(x) = l_k x(k)$ on the set S give us the lower and upper bounds on the loop elasticity of L_k. In general, the minimum and maximum values attained by $F(x) = \sum_{i=1}^{t} l_{k_i} x(k_i)$ on the set S will give us bounds on the total contributions to λ of the loops $L_{k_1}, \ldots, L_{k_t}$. A loop decomposition in which the elasticity of a loop L is 0 tells us that the total elasticity has been partitioned over a set of loops that does not include L, i.e., the life history pathway represented by L need not occur in the population in order to account for the observed transitions

between stages. Conversely, if one observes individuals in a population whose life history pathways are represented by L, then a loop decomposition which describes the population should have a nonzero elasticity assigned to L. If all possible life history pathways are observed in a population, then the loop decomposition which best models that population might correspond to an interior point of S.

To illustrate our methods we will identify and discuss three possible loop decompositions for teasel (*Dipsacus sylvestris*) using the example which appears in Caswell [3, p. 60]. Unless noted otherwise, all computations were carried out using *Mathematica* Version 5.2.

Step 1. Determine the life cycle graph D and elasticities from the population projection matrix A.

In our example, the population projection matrix A is

$$
A = \begin{bmatrix}
0 & 0 & 0 & 0 & 0 & 322.38 \\
0.966 & 0 & 0 & 0 & 0 & 0 \\
0.013 & 0.01 & 0.125 & 0 & 0 & 3.448 \\
0.007 & 0 & 0.125 & 0.238 & 0 & 30.17 \\
0.008 & 0 & 0.038 & 0.245 & 0.167 & 0.862 \\
0 & 0 & 0 & 0.023 & 0.75 & 0
\end{bmatrix}.
$$

The stages, numbered to correspond to the row and column indices of A, are (1) first-year dormant seeds, (2) second-year dormant seeds, (3) small rosettes, (4) medium rosettes, (5) rosettes, and (6) flowering plants. The life cycle graph D is given in Fig. 1. For a discussion of how the life cycle graph and population projection matrix are related, see [3]. This life cycle graph has 6 nodes and 17 edges, hence the dimension of the cycle space $Z(D)$ is 12. The finite rate of population growth is approximately $\lambda = 2.334$.
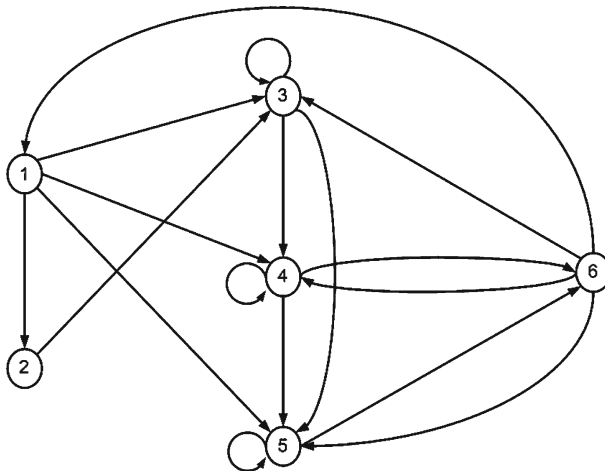

Fig. 1 Life cycle graph for teasel

Table 1 Elasticities of λ expressed as percentages of the total elasticity (rounded)

	1	2	3	4	5	6
1	–	–	–	–	–	6.67384
2	0.0746375	–	–	–	–	–
3	0.234424	0.0746375	0.0429623	–	–	0.450128
4	0.732362	–	0.249263	2.70639	–	22.8514
5	5.63241	–	0.509927	18.7481	2.2569	4.39362
6	–	–	–	5.08501	29.284	–

The row i, column j entry is the elasticity of the transition from node j to node i

Table 2 Loops of D

Loop	Node sequence	Length	Loop	Node sequence	Length
L_1	1, 2, 3, 4, 5, 6, 1	6	L_{10}	3, 3	1
L_2	1, 2, 3, 4, 6, 1	5	L_{11}	3, 4, 5, 6, 3	4
L_3	1, 2, 3, 5, 6, 1	5	L_{12}	3, 4, 6, 3	3
L_4	1, 3, 4, 5, 6, 1	5	L_{13}	3, 5, 6, 3	3
L_5	1, 3, 4, 6, 1	4	L_{14}	4, 4	1
L_6	1, 3, 5, 6, 1	4	L_{15}	4, 5, 6, 4	3
L_7	1, 4, 5, 6, 1	4	L_{16}	4, 6, 4	2
L_8	1, 4, 6, 1	3	L_{17}	5, 5	1
L_9	1, 5, 6, 1	3	L_{18}	5, 6, 5	2

The node sequences were produced and listed in dictionary order

The elasticities of λ are given in Table 1. Formulas for computing the elasticities can also be found in [3].

Step 2. Identify the loops of D and construct the matrix Λ.

The loops in this example were systematically identified by checking in dictionary order all possible node sequences for a loop in D where loops are listed with their node of smallest index as the initial (and terminal) node. Since the loops span the cycle space, the dimension of the cycle space is a lower bound on the number of loops: that is, $l \geq m - n + 1$. There are 18 loops in this graph, listed in Table 2.

The edge-loop matrix Λ is given in Table 3. It is a 17×18 matrix with rank 12, so dimension $N(\Lambda) = 6$. Basis vectors for the nullspace of Λ with components indexed by the loops are given in Table 4.

Inspection of Table 4 reveals that the characteristic elasticities of loops L_9, L_{10}, L_{14}, L_{17}, and L_{18} are fixed for all loop decompositions since any vector in $N(\Lambda)$ must have 0's in the components indexed by these loops. Each of these loops contain an edge which is unique to that particular loop and which can be identified by inspection of Λ: they are, respectively, (1,5), (3,3), (4,4), (5,5), and (6,5).

Using a *Mathematica* implementation of the Avis-Fukuda algorithm for enumerating the vertices of a convex polytope [1], we determined that the 6-dimensional set

Table 3 Edge-loop incidence matrix Λ

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
(1,2)	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
(1,3)	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
(1,4)	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
(1,5)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
(2,3)	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
(3,3)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
(3,4)	1	1	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0
(3,5)	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
(4,4)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
(4,5)	1	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0
(4,6)	0	1	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0
(5,5)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
(5,6)	1	0	1	1	0	1	1	0	1	0	1	0	1	0	1	0	0	1
(6,1)	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
(6,3)	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
(6,4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
(6,5)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Rows are indexed by the edges of D. The kth column is the characteristic vector v_{L_k} of loop L_k

Table 4 Basis vectors for $N(\Lambda)$

Loop	b_1	b_2	b_3	b_4	b_5	b_6
L_1	1	1	1	1	1	1
L_2	−1	0	−1	−1	0	−1
L_3	0	−1	0	0	−1	0
L_4	0	0	0	0	−1	−1
L_5	0	0	0	0	0	1
L_6	0	0	0	0	1	0
L_7	0	0	0	−1	0	0
L_8	0	0	0	1	0	0
L_9	0	0	0	0	0	0
L_{10}	0	0	0	0	0	0
L_{11}	0	−1	−1	0	0	0
L_{12}	0	0	1	0	0	0
L_{13}	0	1	0	0	0	0
L_{14}	0	0	0	0	0	0
L_{15}	−1	0	0	0	0	0
L_{16}	1	0	0	0	0	0
L_{17}	0	0	0	0	0	0
L_{18}	0	0	0	0	0	0

Table 5 Loop decompositions for teasel

Loop	v_1	Loop elasticity	v_2	Loop elasticity	Midpoint
L_1	0.0	0.0	0.0148389	0.0890336	0.0445168
L_2	0.0746375	0.373187	0.0	0.0	0.186594
L_3	0.0	0.0	0.0597985	0.298993	0.149496
L_4	0.0	0.0	0.234424	1.17212	0.586059
L_5	0.174625	0.698501	0.0	0.0	0.34925
L_6	0.0597985	0.239194	0.0	0.0	0.119597
L_7	0.0	0.0	0.0	0.0	0.0
L_8	0.732362	2.19709	0.732362	2.19709	2.19709
L_9	5.63241	16.8972	5.63241	16.8972	16.8972
L_{10}	0.0429623	0.0429623	0.0429623	0.0429623	0.0429623
L_{11}	0.0	0.0	0.0	0.0	0.0
L_{12}	0.0	0.0	0.0	0.0	0.0
L_{13}	0.450128	1.35038	0.450128	1.35038	1.35038
L_{14}	2.70639	2.70639	2.70639	2.70639	2.70639
L_{15}	18.7481	56.2442	18.4988	55.4964	55.8703
L_{16}	4.10338	8.20677	4.35265	8.70529	8.45603
L_{17}	2.2569	2.2569	2.2569	2.2569	2.2569
L_{18}	4.39362	8.78723	4.39362	8.78723	8.78723

The loop elasticity is the characteristic elasticity times the length of the loop. The loop elasticities for $(v_1 + v_2)/2$ are given in column 6

S of loop decompositions contains 36 extreme points. Thus, there are 36 distinct loop decompositions of D over linearly independent sets of loops.

Step 3. Identify loop decompositions of ecological interest.

The contributions of short and long reproductive cycles to the finite rate of population growth are of particular ecological interest [5]. The four longest individual life histories in our example correspond to the loops L_1, of length six, and loops L_2, L_3, and L_4, all of length five. We find a loop decomposition v_1 for which the total contribution of these four loops to the total elasticity is as small as possible by minimizing the objective function $F(x) = 6x(1) + 5x(2) + 5x(3) + 5x(4)$ subject to the constraints $\Lambda x = e$, $x \geq 0$. Similarly we find a loop decomposition v_2 for which the total contribution of these four loops to the total elasticity is as large as possible by minimizing the objective function $H(x) = -F(x)$. These solutions are given in Table 5. By adding the loop elasticities for loops L_1, L_2, L_3, and L_4 obtained from v_1 and v_2 respectively, we see that $F(v_1) = 0.373187$ and $F(v_2) = 1.5601466$. These values can be interpreted, respectively, as lower and upper bounds on the total contributions to λ of the long reproductive cycles given the vital rates appearing in A. From Eq. (4) we see that the vectors $tv_1 + (1 - t)v_2$, $0 \leq t \leq 1$, correspond to loop decompositions of D. For example, the vector determined by setting $t = 0.5$ is also a loop decomposition in which all four long cycles appear. Moreover, it is a loop decomposition over a linearly dependent set of loops, hence not obtainable using the

Table 6 Lower and upper bounds on the loop elasticities in the life cycle graph of teasel

Loop	Lower bound	Upper bound
L_1	0.0	0.447825
L_2	0.0	0.373187
L_3	0.0	0.373187
L_4	0.0	1.17212
L_5	0.0	0.937695
L_6	0.0	0.937695
L_7	0.0	2.92945
L_8	0.0	2.19709
L_9	16.8972	16.8972
L_{10}	0.0429623	0.0429623
L_{11}	0.0	0.997051
L_{12}	0.0	0.747788
L_{13}	0.602596	1.35038
L_{14}	2.70639	2.70639
L_{15}	53.2993	56.2442
L_{16}	8.20677	10.17
L_{17}	2.2569	2.2569
L_{18}	8.78723	8.78723

approaches in [6,9,12]. The loop elasticities of this decomposition are also included in Table 5.

In Table 6 we give the lower and upper bounds for the loop elasticities. As noted earlier, the loop elasticities of L_9, L_{10}, L_{14}, L_{17}, and L_{18} are the same for all loop decompositions since each of these loops contains a transition in the life cycle graph that is unique to that loop. The loop elasticities of L_1 through L_8, L_{11}, and L_{12} are all bounded below by 0. It is not possible to find a single loop decomposition in which all of these loops have characteristic elasticity 0. For example, the only loops which include the edge (1, 2) are L_1, L_2, and L_3, so a loop decomposition must include at least one of those three loops with nonzero elasticity and the characteristic elasticities of these three loops must total 0.0746375, the elasticity of the transition from stage 1 to stage 2. The loop elasticities of L_{13}, L_{15}, and L_{16} have positive lower bounds, implying that those life history pathways (along with those loops mentioned above whose characteristic elasticities are fixed) must be present in the population in order to account for the vital rates appearing in the population projection matrix.

4 Conclusions

By dropping the requirement that loop decompositions be restricted to linearly independent sets of loops, the mathematical treatment of loop analysis changes significantly. Our geometric characterization of the set of loop decompositions allows us to

place bounds on the contributions of sets of loops, representing life history pathways, to the finite rate of population growth. Linear programming techniques can now be applied to loop analysis and provide a method for selecting a particular loop decomposition from a continuum of solutions. We believe that these techniques will provide ecologists with an analytic tool for investigating the roles of various life history options on the population dynamics.

Elements of the nullspace of the edge-loop incidence matrix Λ can be interpreted as tradeoffs in characteristic elasticities that differentiate distinct loop decompositions. These tradeoffs are mathematically necessary if we are considering distinct loop decompositions for a fixed set of vital rates. It would be interesting to further investigate their biological significance.

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