

The Golden Rule of Complementary Feedback

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Abstract

This work demonstrates the occurrence of the Fibonacci sequence in the qualitative analysis of Lotka–Volterra dynamical systems. Herein we show the golden ratio to govern reciprocal effects between neighboring variables in simple food web models. Impacts to the entire community resulting from perturbation of a population variable can be predicted from the adjoint of the community (Jacobian) matrix, which we render in qualitative terms of complementary feedback cycles. Sequences of complementary feedback cycles follow the Fibonacci sequence, and are also configured as multiples and overlapping harmonics thereof. We derive an absolute-feedback matrix that clarifies the sequence. Patterns of complementary feedback cycles are determined by community structure, which can be portrayed and understood in terms of signed digraph structure.

1. Introduction

In the thirteenth century, Fibonacci (Leonardo Pisano) pondered the rate of reproduction in rabbits. This seemingly benign question brought forth a most enduring mathematical discipline, namely, number sequences. Fibonacci’s solution to the rate of reproduction in rabbits also gave birth, so to speak, to the discipline of population dynamics. Fibonacci’s rabbits, history tells us, were immortal. Benefiting from the protection of an enclosing wall, they reproduced unchecked by the forces of predation, disease, and starvation. While modern analyses otherwise make more realistic assumptions, Fibonacci’s basic principle of exponential population growth nevertheless endured, to be taken up much later, and more apocalyptically, by Thomas Malthus.

Fibonacci’s recurrence relation $n_{t+2} = n_t + n_{t+1}$, where t is generation class, produces a number sequence for an exponentially expanding population—1, 1, 2, 3, 5, 8, 13, ...—the dynamics of which can be expressed in Leslie matrix form as

$$\begin{bmatrix} 0 & 1 & 1 & \cdot & 1 & 1 \\ 1 & 0 & 0 & \cdot & 0 & 0 \\ 0 & 1 & 0 & \cdot & 0 & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & 0 & 0 & \cdot & 0 & 0 \\ 0 & 0 & 0 & \cdot & 1 & 1 \end{bmatrix}$$

which projects, through time, mating pairs of rabbits and offspring over t monthly generations. First row elements represent births of two offspring to each mating pair in generation t , and subdiagonal elements represent survival of each year class (here 100%). The final diagonal element confers immortality to the population. Over time, the ratio between successive generations of Fibonacci’s rabbits (n_t/n_{t-1}) converges to the golden ratio Φ (1.618...). The largest eigenvalue of this matrix equals Φ exactly, and is the exponentiated growth rate (r) of the

population—i.e. $\lambda_1 = e^r$. The next largest eigenvalue equals ϕ (0.618...), where $\phi = 1/\Phi$. Left to themselves in the 800 years since their discovery, Fibonacci's rabbits would today have a 'global' population of nearly 1.7×10^{2006} . Given that the number of electrons in the visible universe has been estimated at 10^{79} , some biological control is clearly in order! We are concerned therefore with limits to growth for an entire ecological community.

2. Community Dynamics

The dynamics of n interacting species can be described by Lotka–Volterra equations in the general form

$$\frac{dN_i}{dt} = \frac{r_i}{K_i} N_i \left(K_i - \sum_{j=1}^n \alpha'_{ij} N_j \right) \quad (1)$$

where N is the column vector of population size or density of species i , K is the column vector of carrying capacities, and α'_{ij} is the interaction coefficient for the per capita effect of species j on i . At equilibrium, with growth rates equal to zero, the carrying capacity for each population in the community becomes

$$K_i = \sum_{j=1}^n \alpha'_{ij} N_j^* \quad (2)$$

where N^* represents the equilibrium abundance of a population. Substituting this equilibrium into (1) gives, for each species, the nonlinear function

$$\frac{dN_i}{dt} = \frac{r_i}{K_i} N_i \sum_{j=1}^n \alpha'_{ij} (N_j^* - N_j) \quad (3)$$

which can be linearized through a Taylor series expansion around the equilibrium values of N_i^* , to give

$$\frac{dN_i^*}{dt} = f_i(N_1, N_2, N_3, \dots, N_n; c_1, c_2, c_3, \dots, c_m, t) \quad (4)$$

where f_i is the function for the growth rate of N_i , and $c_i = r_i/K_i$. The c 's represents general parameters related to carrying capacity and density independent rates of birth and death. Other forms of Lotka–Volterra equations can subsume additional parameters within c , such as prey capture efficiency for example. Linearization of (4) gives

$$\frac{dN_i^*}{dt} = \sum_{j=1}^n \frac{\partial f_i}{\partial N_j} (N_j - N_j^*) \quad (5)$$

The Jacobian matrix J is composed of the first partials of each ij -term in (5)

$$J = \begin{bmatrix} \frac{\partial f_1}{\partial N_1} & \frac{\partial f_1}{\partial N_2} & \dots & \frac{\partial f_1}{\partial N_n} \\ \frac{\partial f_2}{\partial N_1} & \frac{\partial f_2}{\partial N_2} & \dots & \frac{\partial f_2}{\partial N_n} \\ \vdots & \vdots & \ddots & \vdots \\ \frac{\partial f_n}{\partial N_1} & \frac{\partial f_n}{\partial N_2} & \dots & \frac{\partial f_n}{\partial N_n} \end{bmatrix} \quad (6)$$

Jacobian matrix elements are equivalent to the α_{ij} interaction coefficients comprising the community matrix A

$$A = \begin{bmatrix} \alpha_{1,1} & \alpha_{1,2} & \cdots & \alpha_{1,n} \\ \alpha_{2,1} & \alpha_{2,2} & \cdots & \alpha_{2,n} \\ \vdots & \vdots & \ddots & \vdots \\ \alpha_{n,1} & \alpha_{n,2} & \cdots & \alpha_{nn} \end{bmatrix} \quad (7)$$

which details all direct interactions between community members.

Sustained perturbations to the equilibrium of a community, through alterations in rates of population birth or death, can be assessed as a change in the parameter $\partial f_i / \partial c_h$ in (4) at or near equilibrium. Perturbations can arise from various biotic and abiotic causes, including natural selection acting upon the species, environmental change, and human intervention. Employing the rules of partial derivatives, with c_h as an independent variable

$$\frac{\partial}{\partial c_h} \left(\frac{dN_i}{dt} \right) = \frac{\partial}{\partial c_h} f_i(N_1, N_2, N_3, \dots, N_n; c_1, c_2, c_3, \dots, c_m, t) = 0 \quad (8)$$

and

$$\frac{\partial f_i}{\partial c_h} + \frac{\partial f_i}{\partial N_j} \frac{\partial N_j^*}{\partial c_h} = 0. \quad (9)$$

Knowing $\partial f_i / \partial c_h$, the parameters through which a perturbation is acting upon the system, a solution for $\partial N_j^* / \partial c_h$ is obtained through Cramer's Rule, which, by cofactor expansion, calculates the response of species i to a permanent change in growth parameter c_h associated with any j th species. We obtain this solution by replacing the j th column of the system determinant, denoted as $|A|$, with the column vector $-\partial f_i / \partial c_h$

$$\frac{\partial N_j^*}{\partial c_h} = \frac{\begin{vmatrix} \alpha_{1,1} & \alpha_{1,2} & \cdots & \alpha_{1,j-1} & -\frac{\partial f_1}{\partial c_h} & \alpha_{1,j+1} & \cdots & \alpha_{1,n} \\ \alpha_{2,1} & \alpha_{2,2} & \cdots & \alpha_{2,j-1} & -\frac{\partial f_2}{\partial c_h} & \alpha_{2,j+1} & \cdots & \alpha_{2,n} \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ \alpha_{n,1} & \alpha_{n,2} & \cdots & \alpha_{n,j-1} & -\frac{\partial f_n}{\partial c_h} & \alpha_{n,j+1} & \cdots & \alpha_{nn} \end{vmatrix}}{|A|}. \quad (10)$$

The denominator of the right side of (10) is the determinant of the community matrix A , and the numerator is the cofactor C_{ji} . Elements of the classical adjoint, or adjoint (adj) matrix are equivalent to transposed cofactors—i.e. $\text{adj}(A_{ij}) = C_{ji}$. The adjoint matrix divided by the system determinant yields a solution for the entire system, which by definition is equivalent to the inverse matrix

$$\frac{\partial N_i^*}{\partial c_h} = \frac{\text{adj}(-A_{ij})}{|A|} = -A_{ij}^{-1}. \quad (11)$$

Thus, in (11) we can anticipate the fate of equilibrium levels for all populations due to a sustained input or perturbation to a system variable. The full numerical response of each population is mediated or scaled by a system's determinant, which represents the overall feedback of the system and provides resistance to perturbation. Since the system determinant is constant in this equation, it is useful to distinguish the adjoint from the inverse of the community matrix, as the adjoint contains all variation of response strength or magnitude within a system. In derivation of the effects of input [3], we employ in (11) the negative community matrix, which maintains a sign convention in both even- and odd-sized systems, such that input to a system is interpreted as positive, through either an increase in birth rates or a decrease in death rates. Input to inverse and adjoint matrices is read down columns and responses along rows. Where input is negative, the signs of the inverse and adjoint matrix elements are simply reversed.

3. Signed Digraphs and Qualitative Analysis

Signed digraphs portray relationships detailed in the community matrix by connecting system variables (or vertices) with links (or edges) ending in arrows (\rightarrow), where there is a positive direct effect of one variable upon another, and filled circles ($\bullet\rightarrow$), where the direct effect is negative. Thus, all possible (nonneutral) pair-wise relationships can be described as predator prey or parasitism ($\bullet\rightarrow$), mutualism (\leftrightarrow), commensalism (\rightarrow), interference competition ($\bullet\bullet$), and amensalism ($\rightarrow\bullet$). Self-effects are shown by links originating and ending in the same variable and are typically negative ($\bullet\circ$), as in self-regulated variables or those with density dependence, but can also be positive (\circ) where variables are self-enhancing.

In (10), insertion of $-\partial f_i / \partial c_h$ into the j th column vector of the community matrix determinant has the effect of breaking all closed loops or cycles in the system, thus each cofactor—or adjoint matrix element—is a sum of feedback cycles, $n-1$ in length, formed by the product of conjunct and disjunct links. Conjunct links are composed of direct links along the path from species j to i , and disjunct links are associated with subsystems of variables that are complementary to variables on the j -to- i path. Here we define the term 'complementary feedback cycle' to mean more than just the feedback of complementary subsystems, but to identify the entire feedback cycle involved in a perturbation response. Thus, adjoint matrix elements are a sum of all complementary feedback cycles in a response, and detail all direct and indirect effects that propagate through perturbed dynamical systems.

Since it is difficult, or more often impossible, to actually measure all elements of the community matrix, a qualitative specification of a system's linkages is typically the best that ecologists can do. Yet simply knowing the signs of the interactions can provide important insights into the dynamics of complex systems. Counterintuitive behavior of a system often results from complex interactions, which can be revealed and understood through qualitative analyses [4]. When community matrix elements are qualitatively specified with $+1$, -1 , or 0 , denoted as \mathcal{A} , then $\text{adj}(-\mathcal{A}_{ij})$ yields the net number of complementary feedback cycles involved in a response. In qualitatively specified systems, adjoint matrix elements serve as a predictor of the direction, or sign, of change in a population resulting from a sustained input or perturbation to a system variable.

As an example, we present a model of the dynamics of snowshoe hare (H) (boreal forest relative of Fibonacci's rabbits) interactions with vegetation (V), and a guild of predators (P) including lynx and great horned owls [1], specified in both symbolic and qualitative form

$$A = \begin{bmatrix} -a_{1,1} & -a_{1,2} & 0 \\ a_{2,1} & 0 & -a_{2,3} \\ a_{3,1} & a_{3,2} & -a_{3,3} \end{bmatrix} \quad \begin{array}{c} \text{V} \\ \text{H} \\ \text{P} \\ \text{1} \\ \text{2} \\ \text{3} \end{array} \quad \circ A = \begin{bmatrix} -1 & -1 & 0 \\ 1 & 0 & -1 \\ 1 & 1 & -1 \end{bmatrix} \quad (12)$$

with associated adjoint matrices

$$\text{adj}(-A) = \begin{bmatrix} a_{2,3}a_{3,2} & -a_{1,2}a_{3,3} & a_{1,2}a_{2,3} \\ a_{2,1}a_{3,3} - a_{2,3}a_{3,1} & a_{1,1}a_{3,3} & -a_{1,1}a_{2,3} \\ a_{2,1}a_{3,2} & a_{1,1}a_{3,2} - a_{1,2}a_{3,1} & a_{2,1}a_{1,2} \end{bmatrix} \quad \text{adj}(-{}^\circ A) = \begin{bmatrix} 1 & -1 & 1 \\ 0 & 1 & -1 \\ 1 & 0 & 1 \end{bmatrix}. \quad (13)$$

In this system sustained fertilization of vegetation (read as a positive input down the first column of the adjoint matrix) can result in an increase of plant biomass, and hence forage, but can counterintuitively lead to a neutral response in hares—i.e. $\text{adj}(-{}^\circ A_{2,1}) = 0$. One might expect that more forage would equal more hares through an increase in their birth rate, but a neutral response can occur due to countervailing complementary feedback cycles—i.e. $\text{adj}(-A_{2,1}) = a_{2,1}a_{3,3} - a_{2,3}a_{3,1}$. This results from the positive effect that vegetative cover ($a_{3,1}$) confers upon predators, some of which are known to use hunting beds from which to ambush their prey.

Where complementary feedback cycles in a response are opposite in sign, as in $\text{adj}(-A_{2,1})$ in (13), then qualitative predictions are ambiguous and their sign determination depends upon knowledge of the relative strength of a_{ij} interaction terms. With increasing system size and connectance the number of complementary feedback cycles involved in response predictions grows not just exponentially, but factorially, and symbolic arguments can involve too many terms, perhaps hundreds, to reasonably interpret. In these instances, we ignore the symbolic content of the adjoint matrix and rely instead upon the countervailing balance of complementary feedback cycles. This indicates, in qualitative terms, the degree to which response predictions are ambiguous. While the adjoint matrix reveals the net number of complementary feedback cycles in a response, we are also interested in the absolute number of cycles to gauge the relative potential for sign determinacy of ambiguous response predictions. We account for the absolute number of terms in the adjoint matrix through use of the matrix permanent, denoted as $|\cdot|^{++}$, in minors (min) of a community matrix specified only by the absolute value of its links (i.e. by 1's or 0's only, essentially an adjacency matrix that includes self-loops; denoted here as \dot{A}), which, when transposed, gives the 'absolute-feedback matrix' T , where

$$T_{ij} = |\text{min } \dot{A}_{ij}|^{++\text{T}}. \quad (14)$$


Completing our snowshoe hare example, the absolute-feedback matrix then becomes

$$T = \begin{bmatrix} 1 & 1 & 1 \\ 2 & 1 & 1 \\ 1 & 2 & 1 \end{bmatrix}. \quad (15)$$

Taking the ratio of each element of the adjoint to the absolute-feedback matrix, we obtain a 'weighted-predictions matrix' W that scales the potential for sign determinacy in qualitative predictions of perturbation response. Adjoint matrix predictions with W_{ij} values near one are highly reliable, while those near zero have a low potential for sign determinacy. The weighted predictions metric is essentially a signal-to-noise ratio with practical ecological applications; though not discussed further here, we refer the interested reader to [2].

4. The Fibonacci Sequence

Having defined the terms of our argument, we now examine special properties of the adjoint and absolute-feedback matrices and find complementary feedback cycles following the Fibonacci sequence. To clearly reveal its occurrence in matrix form, we consider a system much larger than our snowshoe hare example. From a 10-variable straight-chain system, we obtain the following adjoint matrix



$$\text{adj}(-A) = \begin{bmatrix} 55 & 34 & 21 & 13 & 8 & 5 & 3 & 2 & 1 & 1 \\ -34 & 34 & 21 & 13 & 8 & 5 & 3 & 2 & 1 & 1 \\ 21 & -21 & 42 & 26 & 16 & 10 & 6 & 4 & 2 & 2 \\ -13 & 13 & -26 & 39 & 24 & 15 & 9 & 6 & 3 & 3 \\ 8 & -8 & 16 & -24 & 40 & 25 & 15 & 10 & 5 & 5 \\ -5 & 5 & -10 & 15 & -25 & 40 & 24 & 16 & 8 & 8 \\ 3 & -3 & 6 & -9 & 15 & -24 & 39 & 26 & 13 & 13 \\ -2 & 2 & -4 & 6 & -10 & 16 & -26 & 42 & 21 & 21 \\ 1 & -1 & 2 & -3 & 5 & -8 & 13 & -21 & 34 & 34 \\ -1 & 1 & -2 & 3 & -5 & 8 & -13 & 21 & -34 & 55 \end{bmatrix}. \quad (16)$$

In this matrix, ignoring the signs, one observes the Fibonacci sequence along the first and last columns and rows. The left and right off-diagonal elements of the other columns are multiples of the first or last column, respectively, and the multipliers themselves are of the Fibonacci sequence. Considering the signs, where positive input propagates down the trophic chain (read down the columns), impacts alternate between positive and negative values, corresponding to a reversed Fibonacci sequence (i.e. $n_{t-2} = n_t - n_{t-1}$, giving: ..., 34, -21, 13, -8, 5, -3, 2, -1, 1, 0, 1, 1). One also observes negative starting values for the reversed sequence (i.e. ..., 55, -34, 21, -13, 8, -5, 3, -2, 1, -1, 0, -1, -1). As positive input propagates up the trophic chain, impacts are uniformly positive. The matrix is trans-diagonally symmetrical. Since there is no countervailing feedback in this system, elements of the absolute-feedback matrix are equivalent to the absolute value of the adjoint matrix elements.

While a straight-chain system is a simple portrayal of interactions between trophic levels in an ecosystem, a 10-tiered system is highly improbable due to limitations in transfer efficiencies between trophic levels. In Figure 1 we portray a more complex and plausible 10-variable system, where there is direct (interference) competition between variables 6 and 7, and indirect (scramble or resource) competition for shared food resources between variables 1, 3, and 5. While the signs of the adjoint matrix elements in this system do not always correspond to a Fibonacci sequence, the values do. Here we find a break in the regular Fibonacci sequence in variables adjacent to 6 or 7. Comparison of the adjoint and absolute-feedback matrices reveals this break to be from separate harmonic sequences that underlie an absolute number of cycles following a regular Fibonacci sequence (or multiple thereof). The absolute-feedback matrix for this model is identical to that for the 10-variable straight-chain system in (16). In this respect, the model in Figure 1 behaves as a straight-chain system. Although countervailing cycles generate overlying harmonics, and thus different net responses in the adjoint matrix, the regular Fibonacci sequence becomes clear in the system's absolute-feedback matrix.

We consider next, in Figure 2, the behavior of an asymmetrical model with a branched structure incorporating interference competition and mutualism between basal species. Here competitive and mutualistic interactions impart positive feedback to subsystems in the model, ultimately leading to counterintuitive responses. For instance, increasing the birth rate of variables 5 and 10 can decrease their equilibrium population level. In this system, the Fibonacci sequence splits at the nodal fourth variable into separate sequences of unequal magnitude (or into Fibonacci sequences with different starting values). Harmonic sequences are isolated within branch segments containing the variable of input, and do not pass through the nodal fourth variable. As in Figure 1, these countervailing cycles sum to a greater Fibonacci sequence in the absolute-feedback matrix, however, the absolute-feedback matrix of this system differs from those of straight-chain systems.

Systems with long interaction loops, as in the snowshoe hare example in (12), have signed digraphs with Euler numbers greater than 1—i.e. Euler number = no. vertices - no. edges + no. faces. Adjoint matrices of such systems have aperiodic sequences of complementary feedback cycles that fold back upon themselves, causing the Fibonacci sequence to become less apparent. With increased structural connectivity the pattern becomes altogether lost, and the sequences appear as so much noise, although predictions from the adjoint matrix remain biologically interpretable.

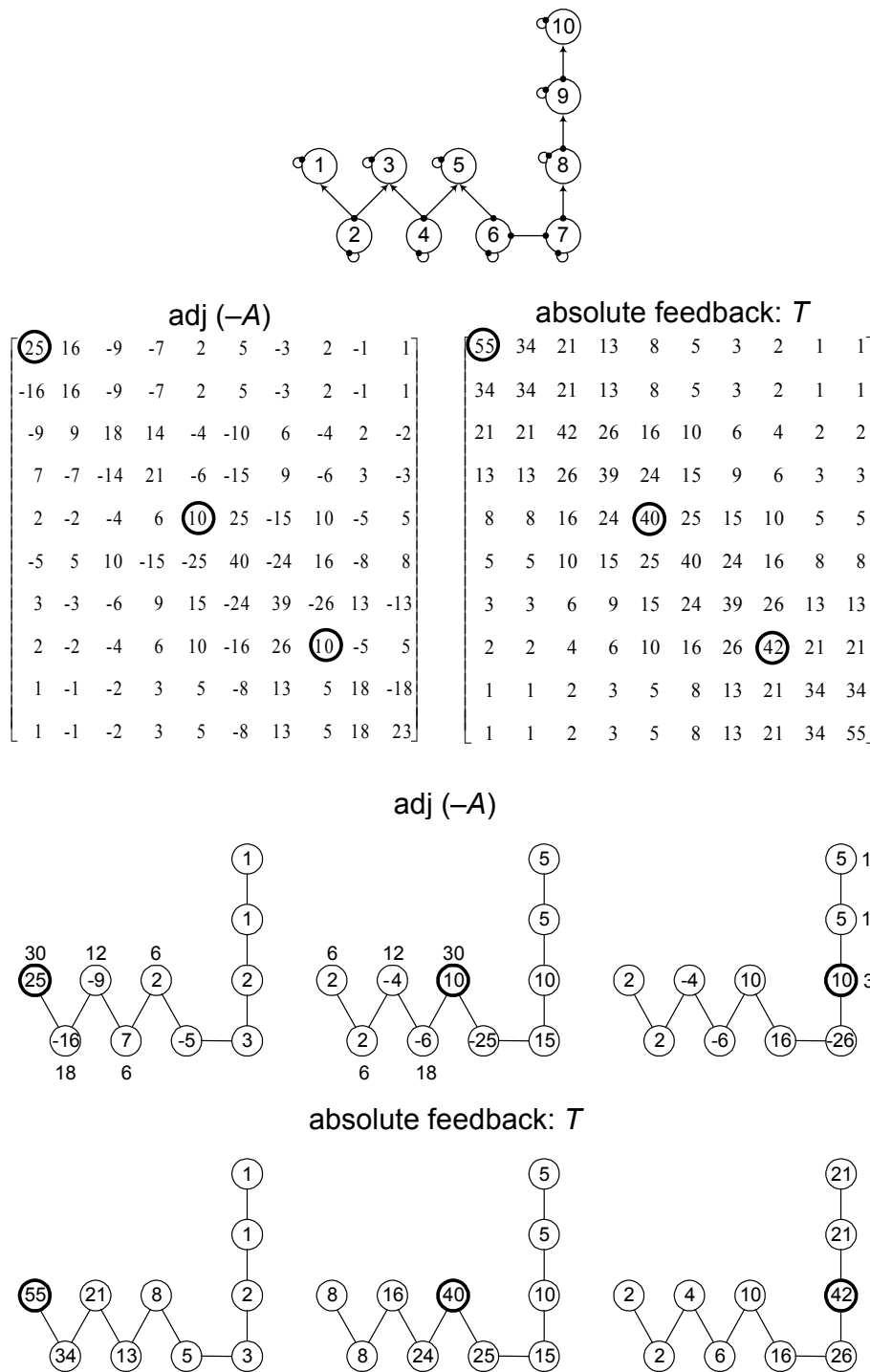


Figure 1. Ten-variable model system with direct and indirect competition. Selected columns of the adjoint (adj) and absolute-feedback matrices are portrayed in system response graphs, which detail the number of complementary feedback cycles generated from a given input. Variables receiving input are denoted by thick-lined circles. Numbers next to adjoint response graphs are total number of countervailing feedback cycles canceled in calculation of net response. These canceled cycles constitute overlaying harmonics that sum with adjoint matrix elements to equal the absolute amount of feedback in each response, all following a Fibonacci sequence or multiple thereof.

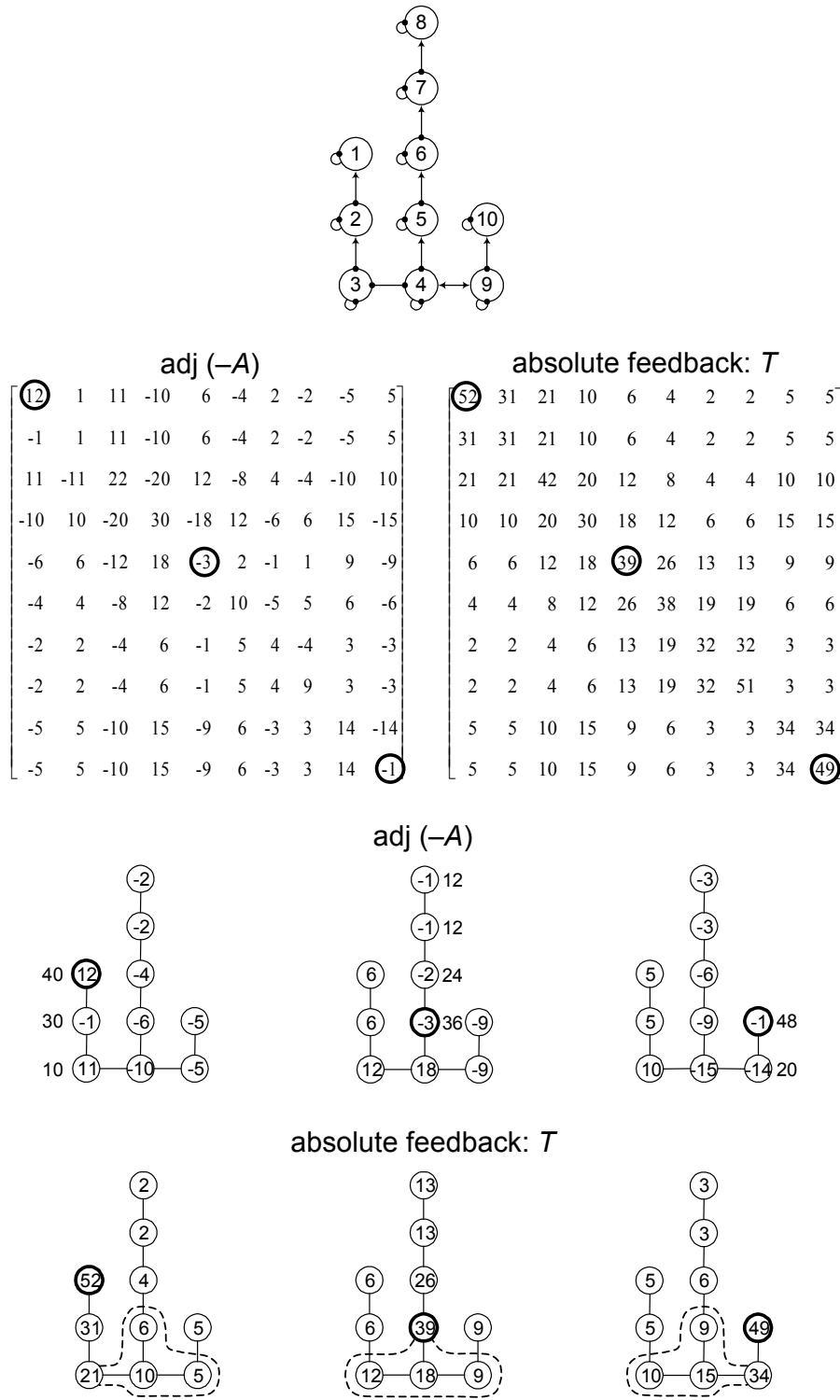


Figure 2. Asymmetrical and branched model system with mutualism and interference competition links specifically associated with nodal variable 4 (format follows Figure 1). Complementary feedback cycles passing through variable 4 split into separate sequences, but maintain an overall Fibonacci sequence in terms of absolute feedback. Consequently, variables immediately posterior to both variable 4 and the input variable (encompassed by dashed-line) have complementary feedback cycles summing to the absolute number in the variable that is either medial to the nodal and input variables, or the input variable itself (denoted by terminus of dashed-line).

5. Discussion

In biological terms, impacts from perturbations propagate through ecosystems via complementary feedback cycles that diminish in number away from the source of input according to the Fibonacci sequence. While Fibonacci's celebrated description of reproduction leads to a convergent value of Φ for a population's growth rate, so too does a convergent value of Φ (or ϕ) govern the proportion of complementary feedback cycles passed between adjacent members of an ecological community, as in the golden rule—*doing unto others...*—and accordingly determines the reciprocal effect of neighbor upon neighbor.

We report the discovery of the Fibonacci sequence in the adjoint of community (Jacobian) matrices arising from simple food web models. The presence of this sequence seems to have been unnoticed, or unreported, in matrix or graph theory literature. Given that complementary feedback cycles can be positive or negative under different conditions and thereby cancel each other, we derive the absolute-feedback matrix, the elements of which represent the absolute number of cycles in a response. This derivation makes use of the permanent rather than the determinant of matrix minors. Both the determinant and permanent are recursively defined functions, and consequently give rise to the observed Fibonacci sequence in our qualitatively specified systems. Our aim at this point has been to describe a previously unobserved pattern and its underlying cause. It is our hope that the general observations presented in the above examples may lead to a more formal analysis by matrix and graph theoreticians.

References

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