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## Linear Algebra and its Applications

www.elsevier.com/locate/laa

# Tipping cycles

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### ARTICLE INFO

Article history: Received 9 July 2021 Accepted 23 March 2022 Available online 25 March 2022 Submitted by R. Brualdi

MSC: 93D15

Keywords: Combinatorial matrix theory

### АВЅТ КАСТ

Instability in Jacobians is determined by the presence of an eigenvalue lying in the right half plane. The coefficients of the characteristic polynomial contain information related to the specific matrix elements that play a greater destabilising role. Yet the destabilising circuits, or cycles, constructed by multiplying these elements together, form only a subset of all the cycles comprising a given system. This paper looks at the destabilising cycles in three sign-restricted forms in terms of sets of the matrix elements to explore how sign structure affects how the elements contribute to instability. This leads to quite rich combinatorial structure among the destabilising cycle sets as set size grows within the coefficients of the characteristic polynomial.

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There are three standard matrix forms that emerge from the linearisation of Lotka-Volterra type dynamical equations ([3],[11]) within the field of ecology. Each of the forms is represented through differing sign conventions as can be seen in the following  $3 \times 3$ examples ( $\{a, b, c, ..., k\} > 0$ ), which shall be referred to by their ecological names:

https://doi.org/10.1016/j.laa.2022.03.019

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Table 1 The Routh table for Eq. (0.1). The number of sign changes as one moves down the first column indicate the number of roots in the right half plane. In this case, two.  $x^4 \mid 1 \quad 3 \quad 5$ 

$$\begin{array}{c|cccc} x^3 & 2 & 4 \\ x^2 & 1 & 5 \\ x^1 & -6 \\ x^0 & 5 \end{array}$$

Predator-Prey	Mutualistic	Competitive				
$\begin{bmatrix} -a & b & c \\ -d & -e & f \\ -g & -h & -k \end{bmatrix}$	$\begin{bmatrix} -a & b & c \\ d & -e & f \\ g & h & -k \end{bmatrix}$	$\begin{bmatrix} -a & -b & -c \\ -d & -e & -f \\ -g & -h & -k \end{bmatrix}$				

Stability of these systems is determined by whether all of the eigenvalues lie in the left half of the complex plane. The characteristic polynomial of an  $n \times n$  matrix is an  $n^{th}$ order monic polynomial (or made so by change of sign), whose roots are the eigenvalues of the system. A necessary condition for the roots of a polynomial to all lie in the left half plane, and therefore for the system to be stable, is for all of its coefficients to be positive. However, this condition is not sufficient. The Routh-Hurwitz stability criterion ([8],[1]) provides a further, and sufficient, condition. The following equation is an example of a polynomial satisfying the necessary condition of positive coefficients,

$$x^4 + 2x^3 + 3x^2 + 4x + 5 = 0, (0.1)$$

yet whose Routh table (Table 1) reflects the existence of two roots in the right half plane and is therefore not Routh-Hurwitz stable.

Polynomials of the example just described can only have roots in the right half plane that are complex conjugate pairs. This was proven by Obrechkoff [6], who showed that there are no solutions to polynomials with positive coefficients that lie on the positive real axis (the right half plane roots of Eq. (0.1) are  $0.29 \pm 1.42i$ ).

Therefore, any systems that have a real maximal (largest real part) eigenvalue (with imaginary part zero) have their tipping point between stability and instability just where the last coefficient of their characteristic polynomial becomes positive.

The coefficients of the characteristic polynomial are derived from the minors of the matrix. These minors may be exhaustively described by the terms consisting of sets of multiplied elements, or cycles, of the matrix. Such cycles may consist of directed graph cycles, as well as the union of disjoint, or composite, cycles of the given length.

Within each coefficient of a characteristic polynomial, one can distinguish the cycles that contribute to the coefficient becoming more positive, and therefore stabilising, or more negative and destabilising. For example, consider the general characteristic polynomial of the  $3 \times 3$  predator-prey system described above,

$$a_3x^3 + a_2x^2 + a_1x + a_0,$$

which expands, in terms of its matrix elements as,

$$x^3 + (a+e+k)x^2 + (bd+ae+cg+fh+ak+ek)x + (ceg+bfg+afh+bdk+aek-cdh).$$

Given that characteristic polynomials are monic, we know that the highest order coefficient,  $a_3$ , is 1 and therefore positive,  $a_2$  is the negative of the trace, and therefore positive, and as can be seen,  $a_1$ , the summed combination of 2-tuples, is also positive. This leaves only  $a_0$  able to switch between being positive or negative and therefore able to destabilise the system. For clarity of explanation, we have used the change of sign of the coefficient for consideration of stability, even though this is only a clear indication in systems with a maximal real-valued eigenvalue. But the effect of increasing the positive or negative value of a coefficient on its stability applies to all of the systems. Within  $a_0$ , the only destabilising circuit, or tipping cycle, is cdh,

$$\begin{bmatrix} -a & b & c \\ -d & -e & f \\ -g & -h & -k \end{bmatrix}.$$

This means that however large the other elements are, they cannot force the system to become unstable (if it is not already so), only the circuit of c, d and h can do that. Given that there are five other cycles of size three that make up the  $a_0$  coefficient, it is helpful to consider a ratio, the coefficient sensitivity,  $\tilde{a}_i$ , which in this case is

$$\tilde{a_0} = 1/6.$$

Table 2 shows the values of  $\tilde{a}_i$  for predator-prey, mutualistic and competitive systems up to size  $8 \times 8$ .

Consider the  $4 \times 4$  predator-prey system,

$$\begin{bmatrix} -a & b & c & d \\ -e & -f & g & h \\ -k & -l & -m & p \\ -q & -r & -s & -t \end{bmatrix},$$

then the coefficient  $a_1$ , consisting of 3-cycles (n-i) is,

$$cfk + bgk + agl + bem + afm + dfq + bhq + dmq + cpq + ahr + hmr + gpr + aps + fps + bet + aft + ckt + glt + amt + fmt - cel - der - dks - hls.$$

We define the tipping cycle set of  $a_1$  as  $\hat{a_1} = \{cel, der, dks, hls\}$ . These four negative cycles  $(\tilde{a_1} = 4/24, \text{ and } |\hat{a_1}| = 4)$ , that if strong enough, could tip the  $a_1$  coefficient from positive to negative, destabilising the system, consist of only eight distinct matrix

#### Table 2

For the three forms under discussion  $\tilde{a}_i$  is presented for systems up n = 8. By the inherent sign symmetries and proportions it would be reasonable to suggest that, for any size n,  $\tilde{a}_i < 1/2$  in predator-prey (P-P) systems (but as n increases,  $\tilde{a}_0$  asymptotically tends to 1/2),  $\tilde{a}_i \ge 1/2$  in mutualistic (M) systems (the case when  $\tilde{a}_i = 1/2$  only when the diagonal terms do not play a role in the cycles contributing to destabilisation), and  $\tilde{a}_i = 1/2$  in competitive (C) systems. Coefficients indicated by a + have no negative destabilising cycles and therefore  $\tilde{a}_i = 0$ . The total number of terms (denominator) for each  $a_i$  is n!/i!. The values of the numerators of the highest predator-prey  $\tilde{a}_i$  follow the tetrahedral numbers, while the mutualistic and competitive highest order numerators of the  $a_i$  are the triangular numbers. The sequence of tipping cycles of the competitive systems for a given n as i decreases follows the sequence of path polynomials of the complete graph  $K_n$  [10].

	n	$a_8 x^8$	$a_7 x^7$	$a_6 x^6$	$a_5 x^5$	$a_4x^4$	$a_3 x^3$	$a_2 x^2$	$a_1x$	$a_0$
P-P	2							+	+	+
	3						+	+	+	1/6
	4 5				+	+	+	+ 10/60	4/24 40/120	8/24 52/120
	6			+	+	+	$\frac{1}{20}/120$	120/360	$\frac{40}{120}$ 312/720	344/720
	7		+	÷	÷	35/210	280/840	1092/2520	2408/5040	2488/5040
	8	+	+	+	56/336	560/1680	2912/6720	9632/20160	19904/40320	20096/40320
С	2							+	+	1/2
	3					+	+	+ 6/12	3/0	3/0
	5				+	÷	10/20	30/60	60/120	60/120
	6			+	+	15/30	60/120	180/360	360/720	360/720
	7		+	+	21/42	105/210	420/840	1260/2520	2520/5040	2520/5040
14	8	+	+	28/56	168/336	840/1680	3360/6720	10080/20160	20160/40320	20160/40320
101	3						+	+	$\frac{1}{3}/6$	$\frac{1}{2}$
	4					+	÷	6/12	20/24	20/24
	5				+	+	10/20	50/60	100/120	84/120
	6			+	+	15/30	100/120	300/360	504/720	424/720
	8	1	+	+ 28/56	21/42 280/336	175/210	100/840	1/04/2520	2968/3040	2080/5040
	8	т	T	28/30	280/330	1400/1080	4704/0720	11872/20100	21440/40320	20344/40320

elements, c, d, e, h, k, l, r and s, with each element included in a differing number of cycles. That is, each element has a specific weight. If we construct a weighted matrix of the elements of this tipping cycle set ( $[\hat{a}_1]$ ) by counting the number of times each element is represented in the  $\hat{a}_1$  set and placing this number in the element's position in the matrix, one can clearly see the patterning of the key elements that play a role in destabilisation,

$$[\hat{a_1}] = \begin{bmatrix} 0 & 0 & 1 & 2\\ 2 & 0 & 0 & 1\\ 1 & 2 & 0 & 0\\ 0 & 1 & 2 & 0 \end{bmatrix}$$

Applied to all the different forms, we can see that the sign structure of the matrix has an effect on the different elements in their role in the destabilising cycles,

	Pre	dat	or-F	Prey	С	omp	etit	ive	Mutualistic					
$[\hat{a_0}] =$	$\begin{bmatrix} 1\\ 3\\ 3\\ 1 \end{bmatrix}$	$     \begin{array}{c}       1 \\       1 \\       3 \\       3     \end{array}   $	${ { 1 } \atop { 1 } \atop { 3 } }$	$\begin{bmatrix} 3\\ 3\\ 1\\ 1 \end{bmatrix}$	$\begin{bmatrix} 3\\ 3\\ 3\\ 3 \end{bmatrix}$	3 3 3 3	3 3 3 3	3 3 3 3	5 ; 5 ; 5 ; 5 ;	5 5 5 5	55555	5 5 5 5		
$[\hat{a_1}] =$	$\begin{bmatrix} 0\\2\\1\\0 \end{bmatrix}$	${0 \\ 0 \\ 2 \\ 1}$	$egin{array}{c} 1 \\ 0 \\ 0 \\ 2 \end{array}$	$\begin{bmatrix} 2\\1\\0\\0\end{bmatrix}$	$\begin{bmatrix} 3\\2\\2\\2 \end{bmatrix}$	$2 \\ 3 \\ 2 \\ 2$	$2 \\ 2 \\ 3 \\ 2$	$\begin{bmatrix} 2\\2\\2\\3 \end{bmatrix}$	$egin{array}{cccccccccccccccccccccccccccccccccccc$	$4 \\ 3 \\ 4 \\ 4$	$4 \\ 4 \\ 3 \\ 4$	$\begin{array}{c}4\\4\\4\\3\end{array}$		

In addition, the total weighting of the elements in their role in destabilisation across all the coefficients is a summation of the individual coefficient tipping cycle set weightings,

	Predator-Prey					Co	$^{\mathrm{mp}}$	etit	ive	Mutualistic					
$\frac{n}{2}$	Γ1	1	4	5		[6	6	6	6	[8]	10	10	10	Ĺ	
$\sum [\hat{a_i}] =$	5	1	1	4		6	6	6	6	10	8	10	10		
$\overline{i=0}$	4	5	1	1		6	6	6	6	10	10	8	10	Ľ	
	[1	4	5	1		6	6	6	6	10	10	10	8		

Extending the summed weightings to the  $5 \times 5$  systems,

Predator-Prey						Competitive						Mutualistic						
[12]	11	20	23	24]		[30]	25	25	25	25		$\lceil 46 \rceil$	38	38	38	38		
24	12	11	20	23		25	30	25	25	25		38	46	38	38	38		
23	24	12	11	20		25	25	30	25	25		38	38	46	38	38		
20	23	24	12	11		25	25	25	30	25		38	38	38	46	38		
11	20	23	24	12		25	25	25	25	30		38	38	38	38	46		

The symmetry seen in the competitive and mutualistic  $\sum_{i=0}^{n} [\hat{a}_i]$  is clearly a consequence of the symmetry in the sign structure of these two forms, while for the predator-prey systems it reflects its lack of sign symmetry. Such bias in the weighting of certain individual elements in the predator-prey case raises the question as to how much stability or instability is an artifact of the structure. For example, in larger systems, positioning of one species over another in the governing equations from which the Jacobians are constructed may prove crucial for the outcome. That is, it posits the question of whether the medium may well be the message.

If the elements comprising tipping cycles are considered in terms of set inclusion, in which for a given  $\hat{a}_i$ , set comparability is considered as an antichain, and the set inclusion properties of smaller to larger sized cycles is likewise determined by the collection of elements, then we can describe the inclusion properties of  $\hat{a}_i$  as *i* decreases for a given *n*. To see this, we again look at the 4 × 4 predator-prey system, where the 4-cycles are  $\hat{a}_0 = \{chlq, dgkr, demr, cepr, dfks, bhks, ahls, celt\}$ . In terms of the constituent elements, the set of 3-cycles of  $\hat{a}_1$  are subsets of some of the 4-cycles of  $\hat{a}_0$  (i.e. cel  $\in$  celt):

$$\hat{a_1} \subset \hat{a_0}$$

This property, in which the smaller tipping cycle sets are a subset of the larger sized sets holds across all the forms of matrices for a given n:

$$\hat{a}_i \subset \hat{a}_{j, \forall j < i}.$$

Yet the way the different forms (i.e. predator-prey, mutualistic and competitive) result in different element weightings is also reflected in the different ways their  $\hat{a}_i$  flow through their  $a_i$  as *i* decreases.

For example, with the  $4 \times 4$  predator-prey system, there are four tipping cycles in  $\hat{a}_1$  and eight tipping cycles in  $\hat{a}_0$ . While the smaller sets of  $\hat{a}_1$  are subsets of four of the sets in  $\hat{a}_0$ , the four remaining sets of  $\hat{a}_0$  do not have such an embedding from sets of  $\hat{a}_1$ , but are new configurations of elements from the  $4 \times 4$  system (i.e.  $\{cel, der, dks, hls\} \subset \{celt, derm, dksf, hlsa\} + \{bhks, cepr, chlq, dgkr\}$ ). The sets of 4cycles of  $\hat{a}_0$  that contain the 3-cycles from  $\tilde{a}_1$  are composite cycles in which the remaining disjoint diagonal term has been added ( $\{cel(t), der(m), dks(f), hls(a)\}$ ), while the noncomposite  $\tilde{a}_0$  configurations ( $\{bhks, cepr, chlq, dgkr\}$ ) are the addition of new directed graph cycles.

In the 4 × 4 competitive case, the six sets in  $\hat{a}_2$  are subsets in two sets each in  $\hat{a}_1$ (with each set in  $\hat{a}_2$  a part of two new composite cycles in  $\hat{a}_1$  through their construction with the remaining distinct disjoint diagonal terms), but in this case there are no new configurations of directed graph cycles. Six of the twelve sets of  $\hat{a}_0$  consist of two sets each from  $\hat{a}_1$  (constructed through merging two of the composite cycles in  $\tilde{a}_1$  which share the same directed graph cycle from  $\tilde{a}_2$ ), with the remaining six sets new directed graph cycle configurations:

$$\begin{pmatrix} \hat{a}_{2} & \hat{a}_{1} & \hat{a}_{0} \\ \\ k \\ k \\ dq \\ gl \\ hr \\ ps \end{pmatrix} \subset \begin{cases} bem \\ bet \\ ckf \\ dqf \\ dqm \\ gla \\ gla \\ gla \\ gla \\ hra \\ hra \\ hrm \\ psa \\ psf \end{cases} \subset \begin{cases} bemt \\ ckft \\ dqfm \\ glat \\ hram \\ psaf \end{cases} + \begin{cases} bgpq \\ bhks \\ cepr \\ chlq \\ dgkr \\ dels \end{cases}$$

or, explicitly showing the composite cycles,

$$\begin{array}{ccc} \hat{a_2} & \hat{a_1} & \hat{a_0} \\ \\ be \\ ck \\ dq \\ gl \\ hr \\ ps \end{array} \subset \quad \begin{cases} be(m) \\ be(t) \\ ck(f) \\ ck(f) \\ dq(f) \\ dq(f) \\ dq(m) \\ gl(a) \\ gl(a) \\ gl(a) \\ gl(t) \\ hr(a) \\ hr(a) \\ hr(a) \\ hr(m) \\ ps(a) \\ ps(f) \end{array} \subset \quad \begin{cases} be(m)(t) \\ ck(f)(t) \\ dq(f)(m) \\ gl(a)(t) \\ hr(a)(m) \\ ps(a)(f) \end{array} \} + \begin{cases} bgpq \\ bhks \\ cepr \\ chlq \\ dels \\ dgkr \end{cases}$$

With the 4 × 4 mutualistic system, there are six tipping cycles in  $\hat{a}_2$ , and as with the competitive case, each of these are in two composite cycles in  $\hat{a}_1$ . However, unlike in the competitive case, there are eight new tipping cycles that include none of the  $\hat{a}_2$  as subsets. In the next tipping cycle set,  $\hat{a}_0$ , it follows the competitive case in having six sets, each of which consists of two sets from  $\hat{a}_1$ , and six sets that are new configurations (the same new configurations as in the competitive case). In addition, there are eight composite cycles generated from the new directed cycles begun in  $\hat{a}_1$ , indicating a general pattern:

Thus, the differences in the specific sign structure of the matrices alter the flow of the inclusion properties of the tipping cycle sets as their cycle size increases. A full combinatorial characterisation of the flows in general yields the values reflected in the  $\tilde{a}_i$  of the different forms, yet in a more intricate way.

For example, in the competitive case, the way the size of each tipping cycle set  $(|\hat{a}_i|)$  unfolds as *i* decreases for a given *n* is as follows. For n = 8, the tipping cycle set size of  $a_6$  (the first  $a_i$  where  $\tilde{a}_i > 0$ ) is

$$|\hat{a}_6| = \frac{1}{2} \times \frac{8!}{6!}.$$

The sets from  $\hat{a}_6$  are then carried, through inclusion (i.e. as composite cycles), as subsets into  $\hat{a}_5$ ,

$$|\hat{a}_{5_{\hat{a}_6}}| = 6 \times \frac{|\hat{a}_6|}{1}$$

where the expression  $\hat{a}_{5_{\hat{a}_6}}$  indicates the sets first seen in  $\hat{a}_6$  now included in the  $\hat{a}_5$  sets, and where the value of  $|\hat{a}_6|$  is divided by 1 (the first step in which the set is included, and reflecting the number of additional disjoint elements that are included in the construction of each new composite cycle), and multiplied by 6 (i.e. i + 1, the coefficient index of the smaller (in set size), preceding set, and reflecting the number of remaining disjoint diagonal elements with which the preceding cycle size can draw on to form a composite cycle).

In the case of competitive systems, we know that the number of tipping cycle sets for each  $a_i$  is  $\frac{1}{2} \times \frac{n!}{i!}$ , which for i = 5 (n = 8) equals the value of  $|\hat{a}_{5_{\hat{a}_6}}|$ . Therefore there are no new additional sets arising in  $\hat{a}_5$  that are not supersets of  $\hat{a}_6$ ,

$$|\hat{a}_5| = |\hat{a}_{5_{\hat{a}_6}}|.$$

Moving to the supersets of the next coefficient,

$$|\hat{a}_{4_{\hat{a}_6}}| = 5 \times \frac{|\hat{a}_{5_{\hat{a}_6}}|}{2}.$$

Again, with  $|\hat{a}_{5_{\hat{a}_6}}|$  divided by 2 (the second step from  $|\hat{a}_6|$ ), and multiplied by 5 (i+1).

In addition to the supersets of  $\hat{a}_6$  (via  $\hat{a}_{5_{\hat{a}_6}}$ ), there are a number of newly formed sets  $(\hat{a}_{4_{\hat{a}_4}})$  easily calculated from the total number of sets,

$$|\hat{a}_{4_{\hat{a}_4}}| = \frac{1}{2} \times \frac{8!}{4!} - |\hat{a}_{4_{\hat{a}_6}}|$$

Therefore,

$$|\hat{a}_4| = |\hat{a}_{4_{\hat{a}_6}}| + |\hat{a}_{4_{\hat{a}_4}}|.$$

This process can continue as i decreases as follows,

$$|\hat{a}_{3_{\hat{a}_{6}}}| = 4 \times \frac{|\hat{a}_{4_{\hat{a}_{6}}}|}{3}, |\hat{a}_{3_{\hat{a}_{4}}}| = 4 \times \frac{|\hat{a}_{4_{\hat{a}_{4}}}|}{1}$$

where again the denominator indicates the number of steps away from the original set construction,

$$|\hat{a}_{3_{\hat{a}_3}}| = \frac{1}{2} \times \frac{8!}{3!} - |\hat{a}_{3_{\hat{a}_6}}| - |\hat{a}_{3_{\hat{a}_4}}|$$

and

$$|\hat{a}_3| = |\hat{a}_{3_{\hat{a}_6}}| + |\hat{a}_{3_{\hat{a}_4}}| + |\hat{a}_{3_{\hat{a}_3}}|$$

Continuing,

$$\begin{split} |\hat{a}_{2_{\hat{a}_{6}}}| &= 3 \times \frac{|\hat{a}_{3_{\hat{a}_{6}}}|}{4}, |\hat{a}_{2_{\hat{a}_{4}}}| = 3 \times \frac{|\hat{a}_{3_{\hat{a}_{4}}}|}{2}, |\hat{a}_{2_{\hat{a}_{3}}}| = 3 \times \frac{|\hat{a}_{3_{\hat{a}_{3}}}|}{1} \\ |\hat{a}_{2_{\hat{a}_{2}}}| &= \frac{1}{2} \times \frac{8!}{2!} - |\hat{a}_{2_{\hat{a}_{6}}}| - |\hat{a}_{2_{\hat{a}_{4}}}| - |\hat{a}_{2_{\hat{a}_{3}}}| \\ |\hat{a}_{2}| &= |\hat{a}_{2_{\hat{a}_{6}}}| + |\hat{a}_{2_{\hat{a}_{4}}}| + |\hat{a}_{2_{\hat{a}_{3}}}| + |\hat{a}_{2_{\hat{a}_{2}}}| \end{split}$$

and so on, down to  $a_0$ ,

$$\begin{split} |\hat{a}_{1_{\hat{a}_{6}}}| &= 2 \times \frac{|\hat{a}_{2_{\hat{a}_{6}}}|}{5}, |\hat{a}_{1_{\hat{a}_{4}}}| = 2 \times \frac{|\hat{a}_{2_{\hat{a}_{4}}}|}{3}, |\hat{a}_{1_{\hat{a}_{3}}}| = 2 \times \frac{|\hat{a}_{2_{\hat{a}_{3}}}|}{2}, |\hat{a}_{1_{\hat{a}_{2}}}| = 2 \times \frac{|\hat{a}_{2_{\hat{a}_{2}}}|}{1} \\ &|\hat{a}_{1_{\hat{a}_{1}}}| = \frac{1}{2} \times \frac{8!}{1!} - |\hat{a}_{1_{\hat{a}_{6}}}| - |\hat{a}_{1_{\hat{a}_{4}}}| - |\hat{a}_{1_{\hat{a}_{3}}}| - |\hat{a}_{1_{\hat{a}_{2}}}| \\ &|\hat{a}_{1}| = |\hat{a}_{1_{\hat{a}_{6}}}| + |\hat{a}_{1_{\hat{a}_{4}}}| + |\hat{a}_{1_{\hat{a}_{3}}}| + |\hat{a}_{1_{\hat{a}_{2}}}| + |\hat{a}_{1_{\hat{a}_{1}}}| \\ &|\hat{a}_{0_{\hat{a}_{6}}}| = \frac{|\hat{a}_{1_{\hat{a}_{6}}}|}{6}, |\hat{a}_{0_{\hat{a}_{4}}}| = \frac{|\hat{a}_{1_{\hat{a}_{4}}}|}{4}, |\hat{a}_{0_{\hat{a}_{3}}}| = \frac{|\hat{a}_{1_{\hat{a}_{3}}}|}{3}, |\hat{a}_{0_{\hat{a}_{2}}}| = \frac{|\hat{a}_{1_{\hat{a}_{2}}}|}{2}, |\hat{a}_{0_{\hat{a}_{1}}}| = \frac{|\hat{a}_{1_{\hat{a}_{1}}}|}{1} \\ &|\hat{a}_{0_{\hat{a}_{0}}}| = \frac{1}{2} \times \frac{8!}{0!} - |\hat{a}_{1_{\hat{a}_{6}}}| - |\hat{a}_{1_{\hat{a}_{4}}}| - |\hat{a}_{1_{\hat{a}_{3}}}| - |\hat{a}_{1_{\hat{a}_{2}}}| - |\hat{a}_{1_{\hat{a}_{1}}}| \\ &|\hat{a}_{0}| = |\hat{a}_{0_{\hat{a}_{6}}}| + |\hat{a}_{0_{\hat{a}_{4}}}| + |\hat{a}_{0_{\hat{a}_{3}}}| + |\hat{a}_{0_{\hat{a}_{2}}}| + |\hat{a}_{0_{\hat{a}_{1}}}| + |\hat{a}_{0_{\hat{a}_{0}}}| \end{split}$$

In general, for competitive systems, and a given n,

$$|\hat{a}_{n-2}| = \frac{1}{2} \frac{n!}{(n-2)!}$$

and for i < n-2, for individual supersets derived from smaller  $\hat{a}_j$  sets, each smaller set is divided by the number of steps (j - i) removed from their original construction (at index j) and the whole expression multiplied by i + 1,

$$|\hat{a}_{i_{\hat{a}_{j}}}| = (i+1) \times \frac{|\hat{a}_{(i+1)_{\hat{a}_{j}}}|}{j-i}.$$

Therefore, for a given index i the supersets are

#### Table 3

Values of  $\Gamma_i$  for each  $|\hat{a}_i|$  for competitive systems up to n = 12. There is rich structure among the  $\Gamma_i$ . For example, the  $a_0$  values ({6, 20, 135, 924, ...}) are the rencontres numbers with two fixed points; the first entries for each n ({ $\alpha_4, \alpha_5, \alpha_6, \alpha_7, ...$ } = {6, 30, 90, 210, ...}) are n(n-1)(n-2)(n-3)/4 (or  $\alpha_n = \alpha_{n-1} + (n-1)(n-2)(n-3)$ ); the second set of values ({ $\beta_5, \beta_6, \beta_7, \beta_8, ...$ } = {20, 120, 420, 1120, ...}) in each n can be described as  $\beta_n = \beta_{n-1} + (n-1)(2\binom{n-2}{3} + (n-2)\binom{n-3}{2})$ ; the third set of values ({ $\delta_6, \delta_7, \delta_8, \delta_9, ...$ } = {135, 945, 3780, 11340, ...}) is  $\delta_n = \delta_{n-1} + (n-1)(\binom{\binom{n-3}{2}}{n-6!} + (n-2)\binom{\binom{n-3}{2}}{(n-6)!}$ .

$(100, 07, 08, 09, \dots) = (100, 010, 010, 010, 010, \dots) = 0n - 1 + (n - 1)((-2) + (n - 2)(n-6)!).$											
n	$a_8$	$a_7$	$a_6$	$a_5$	$a_4$	$a_3$	$a_2$	$a_1$	$a_0$		
4									6		
5								30	20		
6							90	120	135		
7						210	420	945	924		
8					420	1120	3780	7392	7420		
9				756	2520	11340	33264	66780	66744		
10			1260	5040	28350	110880	333900	667440	667485		
11		1980	9240	62370	304920	1224300	3670920	7342335	7342280		
12	2970	15840	124740	731808	3672900	14683680	44054010	88107360	88107426		

$$\Omega_i = (i+1) \times \sum_{j=i+1,k=1}^{j=n-2,k=n-2-i} \frac{|\hat{a}_{(i+1)_{\hat{a}_j}}|}{k}$$

while the number of newly formed sets in each i that are not supersets are,

$$\Gamma_i = \frac{1}{2} \frac{n!}{i!} - \Omega_i.$$

The  $\Gamma_i$  values for competitive systems up to n = 12 are shown in Table 3. Each  $\hat{a}_i$ , consisting of the cumulative supersets and the newly formed sets, is then

$$|\hat{a}_i| = \Omega_i + \Gamma_i.$$

While the  $\Omega_i$  follows a similar patterning for mutualistic and predator-prey systems, a natural question arises as to what a full characterisation of the  $\Omega_i$  and  $\Gamma_i$  for any  $n \times n$  system with any sign structure might suggest. For example, the discussion so far has considered forms of matrices with diagonal entries whose elements are all negative which is an assurance of stability, given large enough diagonal values. A diagonal of all positive entries, on the other hand, would result in an unstable system through a positive trace, and therefore a negative coefficient for  $x^{n-1}$  (i.e.  $\tilde{a}_{n-1} = 1$ ). In the case in which the diagonal elements are all 0, then all the  $\Omega_i = 0$  in the competitive example above. That is, all the composite cycles, which are constructed with diagonal elements, would be removed. The significance of the diagonal, and its role in assuring stability, becomes even more apparent when generalising to other sign structures and sparser matrices.

There is a long history of studying sign-stable and potential sign-stable matrices ([9], [7], [4], [2], [5]), which explores the stability of systems solely based on the sign (and 0) of their elements. Consider a few examples

$$\mathbf{A} = \begin{bmatrix} 0 & + & 0 \\ - & - & 0 \\ 0 & 0 & - \end{bmatrix} \quad \mathbf{B} = \begin{bmatrix} 0 & + & 0 \\ 0 & - & + \\ - & 0 & - \end{bmatrix} \quad \mathbf{C} = \begin{bmatrix} + & 0 & + \\ 0 & 0 & + \\ - & + & - \end{bmatrix}$$

$$\mathbf{D} = \begin{bmatrix} 0 & + & -\\ - & 0 & 0\\ + & 0 & - \end{bmatrix} \quad \mathbf{E} = \begin{bmatrix} - & + & 0\\ 0 & 0 & +\\ - & - & 0 \end{bmatrix} \quad \mathbf{F} = \begin{bmatrix} + & + & +\\ + & - & +\\ + & + & + \end{bmatrix}.$$

Applying the coefficient sensitivities approach to these matrices needs care. Matrices A, B, D and E have all their  $\tilde{a}_i = 0$ ; C has  $\tilde{a}_0 = 0$ ,  $\tilde{a}_1 = 2/3$  and  $\tilde{a}_2 = 1/2$ ; F has  $\tilde{a}_0 = 3/6$ ,  $\tilde{a}_1 = 5/6$  and  $\tilde{a}_2 = 2/3$ . Matrices A, B, D and C are potentially stable, however matrices E and F are not. While systems that are potentially stable must have all their  $\tilde{a}_i < 1$ , it is not the case in general that if all  $\tilde{a}_i < 1$  the system is potentially stable. Questions remain as to the extent to which certain of the approaches that have been described for the specific sign-restricted forms may be extended to more general matrix structures.

## **Declaration of competing interest**

There is no competing interest.

## Acknowledgements

The author wishes to thank a referee for useful comments and suggestions that helped improve the paper. This study is part of the British Antarctic Survey Polar Science for Planet Earth Programme. It was funded by The Natural Environment Research Council, a part of UK Research and Innovation.

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