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BRIEF COMMUNICATION

Applying symmetries of elasticities in matrix population models

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Abstract

Elasticity analysis is a key tool in the analysis of matrix population models, which describe the dynamics of stage-structured populations in ecology and evolution. Elasticities of the dominant eigenvalue of a matrix model to matrix entries obey certain symmetries. Yet not all consequences of these symmetries are fully appreciated, as they are sometimes hidden in mathematical detail. Here, we propose a method to reason about these symmetries directly by visual inspection of the life cycle graph that corresponds to the matrix model. We present two applications of this method, one in ecology and one in evolution. First, we prove several conjectures about elasticities that were obtained from purely numerical results and that can support population managers in decision-making under scarce demographic information. Second, we show how to identify candidates for invariant trade-offs in evolutionary optimal life cycles. The method extends to the elasticity analysis of non-dominant eigenvalues, of the stochastic growth rate and, in next-generation matrices, of the basic reproduction number.

Keywords Eigenvalues · Life cycles · Matrix models · Population management · Trade-offs

Introduction

Matrix models are key tools to study the ecology and evolution of stage-structured populations (Caswell 2001). A matrix model contains all information about the life cycle in the population, i.e., transition probabilities and fertilities at all stages. The dominant eigenvalue of a matrix model $\boldsymbol{A} = [a_{i,j}]$ corresponds to the asymptotic geometric growth of the population when its dynamics are governed by the linear recurrence $\boldsymbol{x}(t+1) = \boldsymbol{A}\boldsymbol{x}(t)$, where $\boldsymbol{x}(t)$ is the vector of stage abundances and $a_{i,j}$ is the number of individuals in stage i at $t+1$ per individual in stage j at t.

The elasticity $e_{i,j}$ of the dominant eigenvalue of a matrix model to an entry $a_{i,j}$ gives the slope of the natural logarithm of the dominant eigenvalue plotted against the natural logarithm of $a_{i,j}$ (Caswell 2001). Elasticity analysis studies the effects of small modifications of the life cycle on population growth (de Kroon et al. 1986). Ecologically, such modifications may be due to environmental variation or to population management decisions. Often it is of interest to forecast the ensuing population growth. Elasticity analysis has proven a highly valuable tool to understand how population dynamics may react depending on which life cycle traits are targeted in proportional interventions (de Kroon et al. 1986; Silvertown et al. 1996; Benton and Grant 1999; Caswell 2000). Understanding the effect of life cycle modifications is also relevant to the study of evolution: Can a mutant subpopulation with a different allocation of resources over its life cycle grow faster than the resident population? Elasticities can help us to answer this question, too (van Tienderen 1995, 2000)

Intriguingly, in any matrix model, elasticities of the dominant eigenvalue to entries in row i of the model and elasticities of the dominant eigenvalue to entries in column i add up to the same number (van Groenendael et al. 1994). This is here called the row–column symmetry. This symmetry is foundational to loop analysis (van Groenendael et al. 1994), which explores the relative importance to population growth of the different pathways an individual can take through the life cycle stages. More generally, mathematical regularities like the row–column symmetry can always be exploited in model analysis and additional such regularities are eagerly looked for (Carslake et al. 2009). So far, there are two main applications of the row–column symmetry outside the literature on loop analysis: (i) classifying species with minimal demographic data for management purposes based on how elastic their population growth is to basic life

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cycle traits (Heppell et al. 2000) and (ii) studying the linear relationships between subsets of elasticities of the dominant eigenvalue in specific matrix models of plants (de Matos and Silva Matos 1998).

The potential of this symmetry has not been fully appreciated, we suggest. In this note, we propose an alternative form of regularity based on the row–column symmetry that lends itself to visual reasoning. Two new applications of the symmetry are then explored. First, several regularities about elasticities of the dominant eigenvalue to matrix entries were conjectured with the aim of providing a rough guide for population management under scarce demographic information (Carslake et al. 2009). We prove these regularities, which were based on purely numerical results, mathematically by applying the alternative form of the row–column symmetry. Second, we show how this can also assist one in finding candidates for so-called invariant trade-offs in life cycle evolution (Charnov 1997). In the study of optimal life cycles, these trade-offs are of special importance, because their properties at fitness optima are independent of most specifics of the life cycle.

An alternative form of the row–column symmetry

Consider an eigenvalue λ of a $n \times n$ matrix model $\boldsymbol{A}$ with corresponding right eigenvector $\boldsymbol{u}$ and left eigenvector $\boldsymbol{v}$. It is a classic result (Caswell 2001) that the sensitivity of λ to $a_{i,j}$ is

$$\frac{\partial \lambda}{\partial a_{i,j}} = \frac{v_i^* u_j}{\langle \boldsymbol{u}, \boldsymbol{v} \rangle}, \tag{1}$$

where $\langle \bullet, \bullet \rangle$ gives the inner product of two vector arguments and v_i^* is the complex conjugate of the ith component of $\boldsymbol{v}$. The elasticity $e_{i,j}$ of λ to $a_{i,j}$ is a relative sensitivity (Caswell 2001, p. 226):

$$e_{i,j} = \frac{a_{i,j}}{\lambda} \frac{\partial \lambda}{\partial a_{i,j}} = \frac{a_{i,j} v_i^* u_j}{\lambda \langle \boldsymbol{u}, \boldsymbol{v} \rangle}. \tag{2}$$

When λ is the dominant eigenvalue, this is guaranteed real and positive and the components of corresponding eigenvectors are nonnegative by mild assumptions about $\boldsymbol{A}$, e.g., it is nonnegative and irreducible. Then, we can write Eq. 2 as $e_{i,j} = \partial \log \lambda / \partial \log a_{i,j} \geq 0$ (Caswell 2001). Using the eigenvector equations $\lambda \boldsymbol{u} = \boldsymbol{A}\boldsymbol{u}$ and $\lambda \boldsymbol{v}^* = \boldsymbol{v}^* \boldsymbol{A}$, where $\boldsymbol{v}^*$ is the conjugate tranpose of $\boldsymbol{v}$,

$$\sum_j e_{i,j} = \sum_j \frac{a_{i,j} v_i^* u_j}{\lambda \langle \boldsymbol{u}, \boldsymbol{v} \rangle} = \frac{v_i^* u_i}{\langle \boldsymbol{u}, \boldsymbol{v} \rangle} = \sum_j \frac{a_{j,i} v_j^* u_i}{\lambda \langle \boldsymbol{u}, \boldsymbol{v} \rangle} = \sum_j e_{j,i}. \tag{3}$$

This implies that the elasticities of λ to matrix entries obey the row–column symmetry:

$$\sum_j e_{i,j} = \sum_j e_{j,i}, \qquad i = 1, \ldots, n, \tag{4}$$

as first shown by van Groenendael et al. (1994) assuming that λ is the dominant eigenvalue.

For an alternative form of this symmetry, partition the n stages into an arbitrary, nonempty subset X and its complement X^{c}. Add the row–column symmetry for each stage in X to obtain

$$\sum_{i \in X} \sum_j e_{i,j} = \sum_{i \in X} \sum_j e_{j,i}. \tag{5}$$

Subtracting from this equation redundant terms, i.e., $e_{k,l}$ for which both k and l are in X, we get

$$\sum_{\substack{i \in X \\ j \in X^{\mathrm{c}}}} e_{i,j} = \sum_{\substack{i \in X^{\mathrm{c}} \\ j \in X}} e_{i,j}. \tag{6}$$

This alternative form of the symmetry is easily visualized. In a life cycle graph, nodes are stages and $a_{i,j}$ is the weight on the arrow from node j to node i. By substituting $e_{i,j}$ for $a_{i,j}$, one gets the corresponding elasticity graph. A bipartition of the stages is a cut through this graph that separates the stages into two complementing parts. By Eq. 6, the flow of elasticities traversing the cut in one direction balances the flow of elasticities traversing the cut in the opposite direction. This reasoning about symmetry is illustrated in Fig. 1.

Applications

Proving conjectures

In a computational study, Carslake et al. (2009) generated a large number of matrix models with random, positive entries that were following several possible patterns. For each matrix, Carslake et al. (2009) compared the elasticities of the dominant eigenvalue to matrix entries pairwise, thereby obtaining inequalities of the form $e_{i,j} \geq e_{k,l}$. Extracting those inequalities that were true across all generated matrices with the same pattern of positive entries irrespective of the matrix dimensions, Carslake et al. (2009) conjectured the existence of some general rules. These rules were meant to show that the stage structure alone, as represented by a given pattern of positive matrix entries, may suffice to rank demographic contributions to be targeted in a proportional intervention aimed at modifying population growth. Crucially, this would be possible even if the actual magnitude of some of these contributions

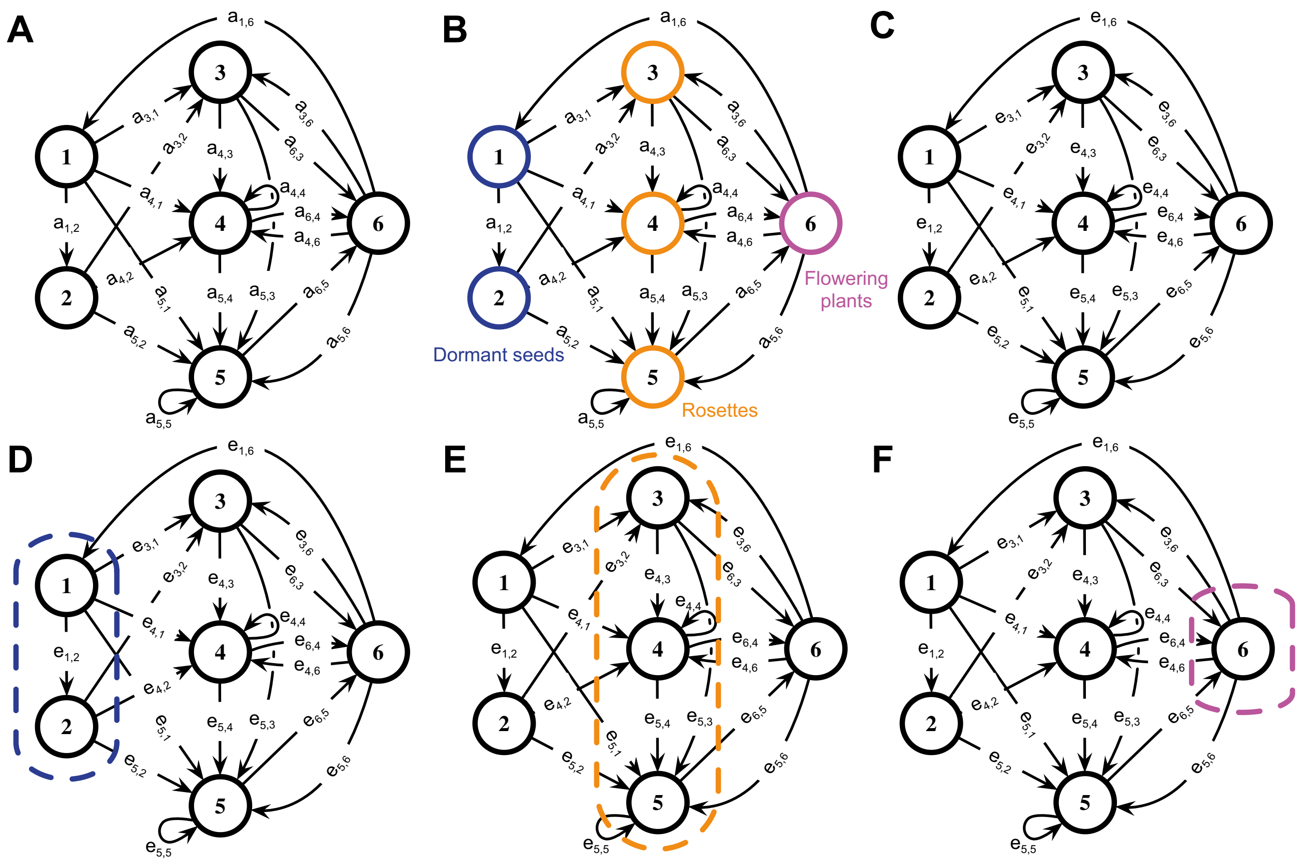

Fig. 1 Applications of a general symmetry about elasticities of matrix models. **A**–**B**, the life cycle graph of the flowering plant *Dipsacus sylvestris* (Caswell 2001). (**C**), elasticity graph of this model. **D**–**F**, the elasticity graph is cut in three different ways. The flow of elasticities out of dormancy stages equals the flow of elasticities into dormancy stages (**D**); the flow of elasticities out of rosette stages equals the flow of elasticities into rosette stages (**E**); the flow of elasticities out of the flowering stage equals the flow of elasticities into the flowering stage (**F**). The symmetry holds for any possible cut of the graph into a subset of stages and its complement and applies to elasticities of any eigenvalue of the matrix model

are unknown, a situation that is typical of the lack of demographic information that population managers often face (Conde et al. 2019). For example, in age-classified matrix models, the magnitude of the elasticity of the dominant eigenvalue to adult survival declines with adult age (Hamilton 1966). Carslake et al. (2009) argued that the numerical finding that in a conservation plan for an endangered species, survival earlier in adult life should be preferentially preserved compared to later survival (Grenier et al. 2007) may be predicted a priori ignoring the species exact life table.

Carslake et al. (2009) report a total of 12 putative rules about elasticities, which are summarized in Table 1. Some are known, yet others have remained putative so far, as no proof of them has been given yet. Rules E1, E3, E4, E6, E7, E9, E10, and E11 in this table can be proven directly from the row–column symmetry in its original form. The four remaining rules (E2, E5, E8 and E12), which are new (Carslake et al. 2009), are all about matrix models with the following pattern

$$\boldsymbol{A} = \begin{pmatrix} + & + & \dots & \dots & + \\ + & * & * & \dots & * \\ 0 & + & * & \dots & * \\ 0 & 0 & \ddots & \ddots & \vdots \\ 0 & 0 & 0 & + & * \end{pmatrix}. \tag{7}$$

where + indicates a positive entry and $*$ indicates a non-negative entry. For brevity, we combined in this one pattern several distinct patterns considered by Carslake et al. (2009) (see Table 1), who also added some bounds on the entry values, but these bounds play no relevant role here. The conjectured rules about matrix models with the above pattern can be summarized as

$$e_{i,i-1} \geq e_{k,l}, \qquad i = 2, \dots, n, \quad k \leq i-1, \quad l \geq i, \tag{8}$$

i.e. each entry $(i, i-1)$ in the subdiagonal of the elasticity matrix is greater than or equal to any entry in the block stretching from the corresponding superdiagonal entry

Table 1 Elasticities patterns conjectured by Carslake et al. (2009)

Matrix Name	Pattern[a]	Conjectured Rules
Leslie	$a_{1,j} > 0$	E1: $e_{i,i-1} \geq e_{k>i,k-1}$
	$a_{i,i-1} > 0$	E2: $e_{i,i-1} \geq e_{1,l\geq i}$
		E3: $e_{n,n-1} = e_{1,n}$
Leslie+	$a_{1,j} > 0$	E4: $e_{i,i-1} \geq e_{k>i,k-1}$
	$a_{i,i-1} > 0$	E5: $e_{i,i-1} \geq e_{1,l\geq i}$
	$a_{n,n} > 0$	E6: $e_{n,n-1} = e_{1,n}$
Progression	$a_{1,j} > 0$	E7: $e_{i,i-1} \geq e_{k>i,k-1}$
	$a_{i,i-1} > 0$	E8: $e_{i,i-1} \geq e_{1,l\geq i}$
	$a_{i,i} > 0$	E9: $e_{n,n-1} = e_{1,n}$
Growth	$a_{1,j} > 0$	E10: $e_{2,1} \geq e_{k\neq 2,2}$
	$a_{i,j\leq i} > 0$	E11: $e_{1,n} \geq e_{n,l<n}$
Leslie(R)	$a_{1,j} > 0$	E12: $e_{i,i-1} \geq e_{k<i,l>i-1}$
	$a_{i,j\geq i-1} > 0$	

This table recapitulates Table 3 in Carslake et al. (2009)

[a] Unspecified matrix entries are set to 0

$(i-1, i)$ to the entry $(1, n)$. This inequality can be proven using the suggested visual approach on elasticity graphs. As Fig. 2 shows, for matrix models with a pattern like in Eq. 7, not only an inequality must hold, but instead the equation

$$e_{i,i-1} = \sum_{k\leq i-1, l\geq i} e_{k,l}, \qquad i = 2, \ldots, n, \tag{9}$$

i.e., the elasticity of λ to $a_{i,i-1}$ equals the sum of the elasticities of λ taken over all entries that are both in columns on the right of $a_{i,i-1}$ and in rows above $a_{i,i-1}$. Since elasticities of the dominant eigenvalue to matrix entries are nonnegative, Eq. 9 proves Eq. 8 for any matrix model with the pattern in Eq. 7.

Looking for invariant trade-offs in evolution

Life cycles are usually subject to trade-offs, i.e., constraints to the independent increment of different traits (Stearns 1992; Roff 1992). For example, there may be a quality-quantity trade-off in offspring production: big-sized newborns could be more likely to survive through their first year, yet parents can only have fewer of them. Selection is supposed to lead to the evolution of optimal life cycles, i.e. they attain maximum fitness within the constraints. In the context of matrix models, the dominant eigenvalue is usually taken as the maximand of selection (Stearns 1992; Roff 1992), albeit with some caveats (Metz et al. 2008). Trade-offs may be envisaged between matrix entries (van Tienderen 1995). For example, using a Leslie matrix model,

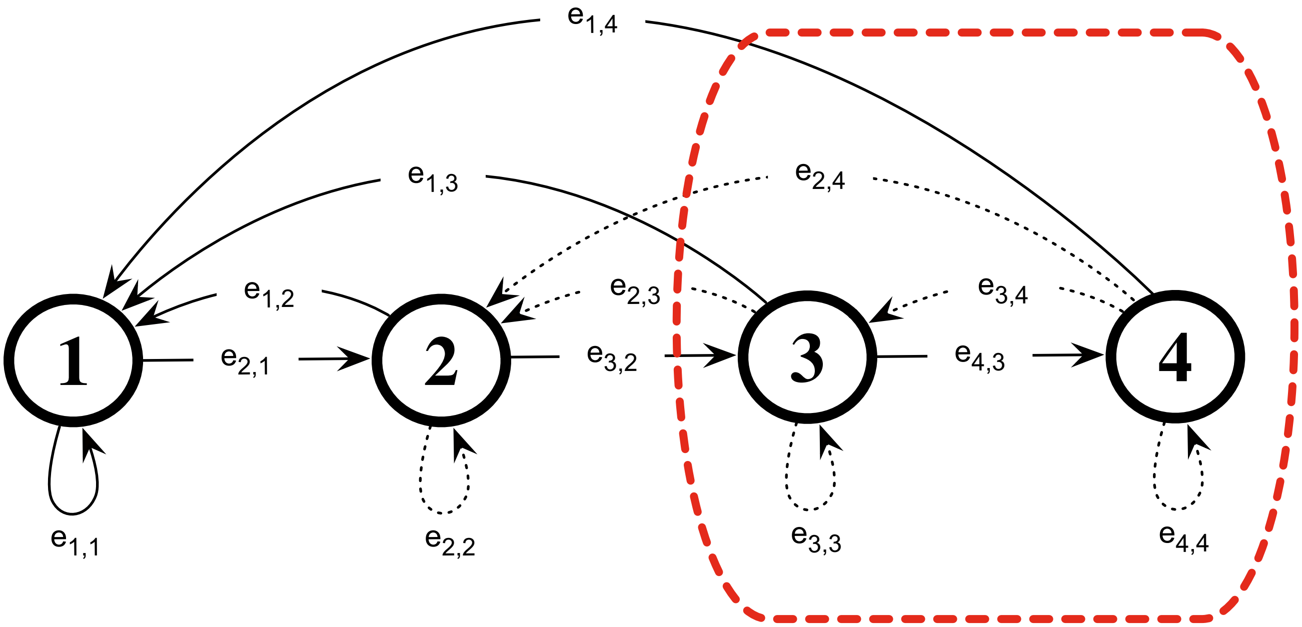

Fig. 2 Elasticity graph of a matrix model with growth only into the next stage, retrogression or reproduction to any earlier stage and stasis in the current stage. Solid arrows indicate positive entries in the matrix model, dotted arrows indicate nonnegative entries, see Eq. 7 in the main text. Here an example with $n = 4$ stages. The graph is cut (red dashed line) to separate the first 2 stages from the rest. By symmetry, elasticities traversing the cut in one direction balance elasticities traversing the cut in the opposite direction. Therefore, the elasticity $e_{3,2}$ of λ to growth into stage 3 equals the sum of all elasticities $e_{k,l}$ of λ to retrogression or reproduction from any stage $l \geq 3$ into any stage $k \leq 2$, e.g. $e_{3,2} = e_{1,3} + e_{1,4} + e_{2,3} + e_{2,4}$. When dotted arrows are removed, growth is interpreted as survival and arrows towards the first stage as fertility, the elasticity graph of an age classified population is obtained. In this special case, the elasticity of λ to survival from an age to the next equals the sum of elasticities of λ to fertility at any later age, e.g., $e_{3,2} = e_{1,3} + e_{1,4}$

Caswell (1982) studied a possible trade-off between fecundity at some age and survival from that age to the next.

Generally, constrained optima of fitness display some dependence on life cycle details. For example, in a log–log plot the constraint curve that bounds the feasible combinations between overall survival and overall fertility in a life cycle has a slope at the maximum attainable fitness that is equal to 1 minus the generation time of the optimal life cycle (Giaimo and Traulsen 2019). Invariant trade-offs are special in this respect. Charnov (1997) originally used the term 'trade-off-invariant rules' to refer to those trade-offs for which the slope of the constraint curve at an optimum between two traits in a log-log plot is always -1.

Invariant trade-offs are typically identified by working with the characteristic equation of the matrix model, e.g., (Charnov 1997; Giaimo and Traulsen 2019). For age-structured life cycles, this is the Euler–Lotka equation, which is well understood. Unfortunately, equally intelligible characteristic equations are not known for most matrix models. This complicates the discovery of invariant trade-offs, which in fact appear to be known by and large only for the age-structured case. Here is where the symmetry in Eq. 6 can assist us.

Parametrize a matrix model $\boldsymbol{A}$ so that $a_{i,j} = b_{i,j}$ when both i and j are in X or neither is, $a_{i,j} = \theta_1 b_{i,j}$ when j is in X and i is not, and $a_{i,j} = \theta_2 b_{i,j}$ when i is in X and j is not. The $b_{i,j}$ are positive constants. The positive parameters θ_1 and θ_2 control the demographic contributions from stages in X to stages out of X and in the opposite direction. The elasticity of the dominant eigenvalue λ of $\boldsymbol{A}$ to these two parameters are

$$e_{\theta_1} = \frac{\partial \log \lambda}{\partial \log \theta_1} = \frac{\theta_1}{\lambda}\frac{\partial \lambda}{\partial \theta_1} = \frac{\theta_1}{\lambda}\sum_{\substack{i\in X^c\\ j\in X}} \frac{\partial a_{i,j}}{\partial \theta_1}\frac{\partial \lambda}{\partial a_{i,j}} = \frac{\theta_1}{\lambda}\sum_{\substack{i\in X^c\\ j\in X}} b_{i,j}\frac{\partial \lambda}{\partial a_{i,j}} = \sum_{\substack{i\in X^c\\ j\in X}} e_{i,j}, \tag{10}$$

$$e_{\theta_2} = \frac{\partial \log \lambda}{\partial \log \theta_2} = \frac{\theta_2}{\lambda}\frac{\partial \lambda}{\partial \theta_2} = \frac{\theta_2}{\lambda}\sum_{\substack{i\in X\\ j\in X^c}} \frac{\partial a_{i,j}}{\partial \theta_2}\frac{\partial \lambda}{\partial a_{i,j}} = \frac{\theta_2}{\lambda}\sum_{\substack{i\in X\\ j\in X^c}} b_{i,j}\frac{\partial \lambda}{\partial a_{i,j}} = \sum_{\substack{i\in X\\ j\in X^c}} e_{i,j}. \tag{11}$$

for all positive values of θ_1 and θ_2. Consider then a log–log plot of θ_2 against θ_1. The implicit function theorem and Eqs. 6, 10 and 11 imply that the slope of any level curve of constant $\log \lambda$ in this plot is

$$-\frac{\partial \log\lambda}{\partial \log\theta_1} \Big/ \frac{\partial \log\lambda}{\partial \log\theta_2} = -e_{\theta_1}/e_{\theta_2} = -1. \tag{12}$$

Suppose θ_1 and θ_2 are under selection, and there is a trade-off between them. Since the dominant eigenvalue is an increasing function of matrix entries, fitness is an increasing function of θ_1 and θ_2. Both these parameters then tend to increase. Yet not all combinations of θ_1 and θ_2 are feasible. Eventually, a constraint is hit and to an increment in θ_1 there corresponds a decrement in θ_2 and vice versa. We think of this constraint as a smooth curve that separates what is feasible from what is not in the $\log \theta_1$-$\log \theta_2$ plane. We restrict attention to evolution along this curve. Assume that a constrained local maximum $\log \lambda^*$ of fitness is on the constraint curve at $(\log \theta_1^*, \log \theta_2^*)$. This optimum also belongs to a level curve of constant fitness, i.e. the set of all points $(\log \theta_1, \log \theta_2)$ at which fitness takes value $\log \lambda^*$. As shown above, Eq. 12, any such level curve actually is a straight line with slope -1. Focus then on a sufficiently small neighborhood around $(\log \theta_1^*, \log \theta_2^*)$ so that the constraint curve is well approximated by its tangent at such optimum. If this tangent has a slope different from -1, then it intersects the level line of optimal fitness exactly once at the optimum. A segment of the tangent not including the optimum remains above the line of optimal fitness. Since fitness increases both in θ_1 and in θ_2, this segment contains points that have greater than optimal fitness. These points are also feasible, as they lie on the curve and, therefore, satisfy the constraint. Moreover, we can always find such feasible points at any arbitrarily small distance from the optimum $(\log \theta_1^*, \log \theta_2^*)$. But this contradicts the fact that this optimum is a local maximum of fitness. Therefore, the tangent of the constraint curve at the optimum must have slope -1. We can then conclude that if there is a trade-off across a bipartition of the life cycle stages, then it is an invariant trade-off.

Visual reasoning about the elasticity graph helps us to apply this result. For example, the invariant trade-off between present survival and future reproduction that was laboriously derived from the characteristic equation of the matrix in Giaimo and Traulsen (2019) can be proven much more easily as follows. Keep only the solid arrows in the graph in Fig. 2 to get the elasticity graph of the age-classified (Leslie) matrix model, i.e. arrows ending in 1 indicate fertilities and arrows from one node (age class) to the next indicate survival. By cutting the elasticity graph to separate the first k age classes from the remaining ones, the elasticity of survival at age class

k (into the next age class) balances the elasticities of fertility at all subsequent age classes ($> k$). Therefore, if there is a trade-off between survival at age class k and fertility in all subsequent age classes, then this trade-off is invariant.

Discussion

The row–column symmetry has been helpful to classify species with minimal demographic information for conservation purposes (Heppell et al. 2000). In order to extend the repertoire of useful mathematical rules about elasticities for population management in the absence or scarcity of demographic data, Carslake et al. (2009) have developed a numerical approach that yielded a number of putative such rules. Our work shows that these rules, which can be applied by only knowing the stage structure of the population while ignoring its exact demographics, can be proven analytically as special cases of the row–column symmetry using an alternative form of it. The eventual usefulness of these rules remains conditional to the known limitations of elasticity analysis (Benton and Grant 1999; Mills et al. 1999; de Kroon et al. 2000).

In the study of optimal life cycles, using symmetry to reason about invariant trade-offs vastly expands upon the original approach by Charnov (1997). He expressed fitness as a product of only three aggregate life cycle traits and looked at trade-offs among them: the probability of surviving to the age of first breeding, the average rate of offspring production over the adult lifespan, and the average length of the adult lifespan. To get to this formulation, Charnov (1997) limited attention to the case where stages are age classes and the population is stationary, i.e. the dominant eigenvalue of the matrix model is 1. These restrictions are not required in our approach. Stages need not be age classes and the matrix model can represent any demography. By bipartitioning n stages, there are up to $2^{n-1} - 1$ ways of aggregating matrix entries into two traits which, if related by a trade-off, would display invariance. Fitness as given by the dominant eigenvalue of the matrix model will generally be a nonlinear function of these possible traits (Hodgson et al. 2006). But this adds no further complication and the population can grow, shrink or stay constant in size.

However, an important caveat should be stated. Symmetries of elasticities deliver a quick method to check for invariance of a trade-off between certain subsets of matrix entries. But this method is silent as to whether a trade-off exists in the first place. It is unclear whether a given bipartition of the set of stages identifies a trade-off between demographic contributions from one part into the other and vice versa. More generally, an arbitrary bipartition-induced grouping of matrix entries may fail to single out two biologically meaningful traits.

Our results were derived with reference to the elasticities of the dominant eigenvalue to the entries of a matrix model that governs time-homogeneous population dynamics of the form $\boldsymbol{x}(t) = \boldsymbol{A}^t \boldsymbol{x}(0)$. In such scenario, this eigenvalue corresponds to asymptotic population growth (i.e. $t \to \infty$) and fitness for a density-independent population in a constant environment. However, the scope of our results extends to more general scenarios. Here, we discuss three of them.

First, in the study of transient population dynamics (i.e. small t), nondominant eigenvalues matter (Stott et al. 2011). The ratio between the dominant eigenvalue and the modulus of the subdominant eigenvalue of the matrix model determines the rate of convergence to the stable state (Caswell 2001). More generally, all eigenvalues of the matrix model, along with the initial population state, influence dynamics before the population reaches the asymptotic phase and they may induce overshoots, undershoots and oscillations that, however transient, need to be accounted for in population management (Koons et al. 2005). Since natural or human-induced disturbances on a population tend to displace this from equilibrium, transient dynamics are of direct relevance to conservation biology and applied ecology, as these dynamics operate on roughly the same time scale as many population management plans (Ezard et al. 2010). The elasticity of the population state outside of demographic equilibrium to matrix entries can be analyzed (Fox and Gurevitch 2000; Caswell 2007). In particular, Fox and Gurevitch (2000) propose an analysis that requires the computation of the elasticities of all matrix eigenvalues to matrix entries. Our derivation and re-elaboration of the row–column symmetry in Eq. 3 apply to any eigenvalue of $\boldsymbol{A}$. Thus, symmetries extend to elasticities of nondominant eigenvalues to matrix entries. In the study of transient dynamics, these symmetries may be leveraged to facilitate some computations or gain some insights. However, it should be kept in mind that elasticities of non-dominant eigenvalues may be negative. This means, for example, that while our Eq. 9 holds for any eigenvalue, the inequality in Eq. 8 does not.

Second, populations rarely live in a constant environment. More often, they experience varying environmental conditions. To capture the effect of these on life cycle traits, a time-dependent matrix model for population dynamics of the form $\boldsymbol{x}(t) = \boldsymbol{A}_{t-1} \dots \boldsymbol{A}_1 \boldsymbol{A}_0 \boldsymbol{x}(0)$ is used (Caswell 2001). In this model, matrix $\boldsymbol{A}_\tau$ contains the vital rates that are induced to the population by the environment that is experienced at time τ. When the matrix sequence is governed by a stochastic process, under mild assumptions about the process and the matrices in the sequence, long run populations dynamics are characterized by a stochastic growth rate $\log \lambda_s$ (Cohen 1977a, b; Tuljapurkar 1990), which also serves as a measure of fitness (Tuljapurkar 1990). Since the $a_{i,j}$ vary randomly, it is possible to define different elasticities of λ_s to matrix entries depending on which feature of the distribution of these entries is perturbed (Tuljapurkar et al. 2003).

However, it is customary to refer to a perturbation of both the mean and the standard deviation of $a_{i,j}$ in the same proportion for all matrices in the sequence as “the” stochastic elasticity of λ_s (Caswell 2001; Tuljapurkar et al. 2003). Stochastic elasticities were crucial in assessing the impact of harvest intensity on population persistence of *Khaya* (Gaoue et al. 2011) and in investigating fitness differences between genetic variants at a polymorphism under variable environments (Smallegange and Coulson 2011). Interestingly, stochastic elasticities are nonnegative and they also obey the row–column symmetry (Claessen 2005). Therefore, when stochastic elasticities are the relevant ecological and evolutionary quantities, our results extend to stochastically fluctuating environments and could be used to predict a priori some findings of elasticity analysis solely on the basis of the matrix structure.

Third, elasticity analysis has lately been extended to next-generation matrices (Hartemink et al. 2008; Matser et al. 2009; Davis and Bent 2011; Polo et al. 2018). Matrix models discussed in the present work demographically project the population over time steps of conveniently chosen length, e.g. a day, one year or five years. Next-generation models, instead, project the population over generations. In this context, a single generation is the time needed for the population to grow by its basic reproductive number R_0, which corresponds to the dominant eigenvalue of the next-generation matrix. The elasticity of R_0 to entries of the next-generation matrix and their underlying parameters has been employed to understand infectious disease ecology (Hartemink et al. 2008; Matser et al. 2009). Here, R_0 measures how the number of infected hosts tends to grow in the long run, while matrix entries quantify processes of pathogen transmission through hosts. Elasticity analysis has been pivotal in comparing the importance of different transmission routes for distinct tick-borne infections (Matser et al. 2009). The eigenvalue perturbation machinery required to get the elasticities of R_0 for next-generation matrices is the same as that for the elasticities of λ. Therefore, the row–column symmetry and our derived results carry over smoothly to the elasticity analysis of next-generation matrices in ecology.

For future work it would be interesting to systematically review the literature on elasticity analysis to apply our results. We can foresee that several findings, i.e. some elasticities being equal to or larger than others, may be found therein that would appear as empirical because they emerge from the analysis of specifically parametrized matrix population models. However, some of these findings could instead be instances of more general regularities that are to be expected solely in virtue of the matrix structure.

The row–column symmetry has long been known. But some relevant applications of it have not been discussed yet. Here, we have proposed a different way of formulating and using this symmetry that, in some contexts, seems to be more revealing than the original one. More generally, our work highlights the importance of exploring different ways of looking at already known results to fully understand all their implications.

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Declarations

Ethical approval No ethical approval was required for this research.

Consent to participate No subject were recruited for this research, whence no consent to participate was obtained.

Consent to publication No subject were recruited for this research, whence no consent to publish their data was obtained. Both authors give the Publisher the permission to publish this work if eventually accepted by the journal.

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