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Appendix C. Loop analysis of a matrix population model in a periodic environment.

In this section we demonstrate how the method of loop analysis can be applied for periodic matrix products. Generally, loop analysis is based on the recombination of the elasticity of population growth according to unbranched loops in the life cycle graph. This recombination and the interpretation of loop elasticities as the relative contribution of respective reproductive paths to population growth is based on two mathematical properties of elasticities (van Groenendael et al. 1994):

(1) For each stage in the life cycle graph, the summed elasticity of incoming transitions equals the summed elasticity of outgoing transitions.

(2) The elasticity of a loop is equal to the characteristic elasticity multiplied by the number of transitions in the loop. The elasticities of all loops in a matrix sum to one.

For the periodic matrix model loop analysis is based on the elasticities $e_{ij}^{(h)}$ of the growth rate of the *cycle* matrix **C** to *annual* transition rates of matrices $\mathbf{B}_h$ (cf. main text). To legitimate the interpretation of loop analysis also for periodic matrix models, here we thus discuss these properties in regard to the elasticities $e_{ij}^{(h)}$.

Periodic matrix products

Consider the population dynamics in a cyclic environment of period r being described by a matrix model as

$$\mathbf{n}_h(t+r)=\mathbf{C}_h\mathbf{n}_h(t) \tag{C.1}$$

with $\mathbf{C}_h = \mathbf{B}_{h-1}\mathbf{B}_{h-2}\ldots\mathbf{B}_1\mathbf{B}_r\mathbf{B}_{r-1}\ldots\mathbf{B}_{h+1}\mathbf{B}_h$

where the index h denotes the position in the periodic cycle. It is given as subscript for matrices and as superscript for matrix entries. In case of annual matrices $\mathbf{B}_h$ or respective elements $b_{ij}^{(h)}$, h identifies the matrix position itself. In case of $\mathbf{C}_h$ and other symbols referring to the entire cycle of r years, h denotes the respective cyclic permutation of $\mathbf{C}$ that begins with $\mathbf{B}_h$.

While the eigenvalue λ of **C** is independent of the cyclic permutation, both the stable stage structure vector **w** (right eigenvector of **C**) and the reproductive value vector **w** (left eigenvector of **C**) depend on h and satisfy

$$\mathbf{C}_h\mathbf{w}_h = \lambda\mathbf{w}_h \tag{C.2}$$

and $$\mathbf{v}_h^{\mathrm{T}}\mathbf{C}_h = \lambda\mathbf{v}_h^{\mathrm{T}} \tag{C.3}$$

(Note: In this section λ, **v** and **w** always denote the dominant eigenvalue λ_1 of **C** and associated eigenvectors, respectively) At the asymptotic stable state where we conduct the loop analysis, from $\mathbf{n}_{h+1} = \mathbf{B}_h\mathbf{n}_h$ it follows that $\mathbf{w}_h$ and $\mathbf{v}_h$, respectively, can be scaled to satisfy

$$\mathbf{w}_{h+1} = \mathbf{B}_h\mathbf{w}_h \tag{C.4}$$

and $$\mathbf{v}_h^{\mathrm{T}} = \mathbf{v}_{h+1}^{\mathrm{T}}\mathbf{B}_h \tag{C.5}$$

The scalar product $\langle \mathbf{v}_h, \mathbf{w}_h \rangle$ of such scaled vectors is equal for all cyclic permutations of **C**. Examples of different cyclic permutations of **C** and respective eigenvectors are given in Table C1.

Elasticities

The elasticity of λ to annual transition rates $b_{ij}^{(h)}$ is defined as

$$\begin{aligned}\mathbf{E}_{\mathbf{B}_h} &= \left(e_{ij}^{(h)}\right) = \left(\frac{b_{ij}^{(h)}}{\lambda}\frac{\partial\lambda}{\partial b_{ij}^{(h)}}\right)\\ &= \frac{1}{\lambda}\mathbf{B}_h \circ \mathbf{S}_{\mathbf{B}_h}\end{aligned} \tag{C.6}$$

where $\mathbf{S}_{\mathbf{B}h}$ denotes the sensitivity of λ to annual transition rates $b_{ij}^{(h)}$. Following Caswell and Trevisan (1994) this sensitivity can be calculated as

$$\mathbf{S}_{\mathbf{B}_h} = \mathbf{D}_h^{\mathrm{T}} \mathbf{S}_{\mathbf{C}_h} \quad \text{with} \qquad \mathbf{S}_{\mathbf{C}_h} = \frac{\mathbf{v}_h \mathbf{w}_{\mathrm{h}}^{\mathrm{T}}}{\langle \mathbf{v}, \mathbf{w} \rangle} \tag{C.7}$$

and matrix $\mathbf{D}_h$ being defined as

$$\mathbf{D}_h = \mathbf{B}_{h-1} \mathbf{B}_{h-2} \ldots \mathbf{B}_1 \mathbf{B}_r \mathbf{B}_{r-1} \ldots \mathbf{B}_{h+1}$$

so that $\mathbf{C}_h = \mathbf{D}_h \mathbf{B}_h$

and $$c_{kl}^{(h)} = \mathbf{d}_{k\cdot}^{(h)} \mathbf{b}_{\cdot l}^{(h)} \tag{C.8}$$

With C.8 elasticity (C.7) then is given by

$$\mathbf{E}_{\mathbf{B}_h} = \frac{1}{\lambda} \mathbf{B}_h \circ \mathbf{D}_{\mathrm{h}}^{\mathrm{T}} \frac{\mathbf{v}_h \mathbf{w}_{\mathrm{h}}^{\mathrm{T}}}{\langle \mathbf{v}, \mathbf{w} \rangle} \tag{C.9}$$

Property 1

In the periodic matrix model, for stage $n_i^{(h)}$ we can find the incoming transitions $b_{ij}^{(h\text{-}1)}$, for all j, and the outgoing transitions $b_{ji}^{(h)}$, for all j. Thus, from C.9 summed elasticities for stage i at position h are

incoming $$\sum_{j=1}^{m} e_{ij}^{(h-1)} = \frac{1}{\lambda \langle \mathbf{v}, \mathbf{w} \rangle} \sum_{j=1}^{m} \sum_{k=1}^{m} b_{ij}^{(h-1)} d_{ki}^{(h-1)} v_k^{(h-1)} w_j^{(h-1)} \tag{C.10}$$

outgoing $$\sum_{j=1}^{m} e_{ji}^{(h)} = \frac{1}{\lambda \langle \mathbf{v}, \mathbf{w} \rangle} \sum_{j=1}^{m} \sum_{k=1}^{m} b_{ji}^{(h)} d_{kj}^{(h)} v_k^{(h)} w_i^{(h)} \tag{C.11}$$

where $m \times m$ is the dimension of the square matrices $\mathbf{B}_h$.

To demonstrate that property (1) is fulfilled for elasticities $e_{ij}^{(h)}$, we show the equivalence of C.10 and C.11. From C.4 we get

$$w_i^{(h)} = \sum_{j=1}^{m} b_{ij}^{(h-1)} w_j^{(h-1)}$$

and C.9 can be written as

$$\sum_{j=1}^{m} e_{ij}^{(h-1)} = \frac{w_i^{(h)}}{\lambda\langle \mathbf{v}, \mathbf{w}\rangle} \sum_{k=1}^{m} d_{ki}^{(h-1)} v_k^{(h-1)} \tag{C.12}$$

From C.5 we get

$$v_k^{(h-1)} = \sum_{l=1}^{m} v_l^{(h)} b_{lk}^{(h-1)}$$

and C.12 can be written as

$$\sum_{j=1}^{m} e_{ij}^{(h-1)} = \frac{w_i^{(h)}}{\lambda\langle \mathbf{v}, \mathbf{w}\rangle} \sum_{k} \sum_{l} d_{ki}^{(h-1)} b_{lk}^{(h-1)} v_l^{(h)}$$

With C.8 and C.3 this gives

$$\sum_{j=1}^{m} e_{ij}^{(h-1)} = \frac{w_i^{(h)}}{\lambda\langle \mathbf{v}, \mathbf{w}\rangle} \sum_{l} c_{li}^{(h)} v_l^{(h)}$$

$$= \frac{w_i^{(h)}}{\lambda\langle \mathbf{v}, \mathbf{w}\rangle} \lambda v_i^{(h)} = \frac{w_i^{(h)} v_i^{(h)}}{\langle \mathbf{v}, \mathbf{w}\rangle}$$

Applying C.8 and C.3 we also can write C.11 as

$$\sum_{j=1}^{m} e_{ji}^{(h)} = \frac{w_i^{(h)}}{\lambda\langle \mathbf{v}, \mathbf{w}\rangle} \sum_{j} \sum_{k} d_{kj}^{(h)} b_{ji}^{(h)} v_k^{(h)}$$

$$= \frac{w_i^{(h)}}{\lambda\langle \mathbf{v}, \mathbf{w}\rangle} \sum_{k} v_k^{(h)} c_{ki}^{(h)}$$

$$= \frac{w_i^{(h)}}{\lambda\langle \mathbf{v}, \mathbf{w}\rangle} \lambda v_i^{(h)} = \frac{w_i^{(h)} v_i^{(h)}}{\langle \mathbf{v}, \mathbf{w}\rangle}$$

Thus, both sums of elasticities are equal to the sensitivity of λ to $c_{ii}^{(h)}$ (cf. Eq. C.7), as they are in case of a time-invariant matrix model (cf. van Groenendael et al. 1994). Further, it follows that the elasticity of each transition can be thought as being build up by the elasticities of loops passing through that transition. Thus, in each loop all transitions that belong exclusively to this loop have the same elasticity, i.e., this loop's "characteristic elasticity" (van Groenendael et al. 1994; cf. Fig. C.1).

Property 2

The second property is fulfilled if the first property is true and if all elasticities sum to one (Claessen 2005). In case of constant matrix models it can be shown that elasticities e_{ij} sum to one (de Kroon et al. 1986, Mesterton-Gibbons 1993). However, this is not the case for periodic matrix products.

From C.2 it follows that λ is a homogeneous function of the $b_{ij}^{(h)}$ of degree r, i.e.,

$$(c\mathbf{B}_r)(c\mathbf{B}_{r-1})\ldots(c\mathbf{B}_1)\mathbf{w}_1 = c^r \lambda \mathbf{w}_1$$

Thus, Euler´s theorem on homogeneous functions (cf. Mesterton-Gibbons 1993) states that

$$\sum_{ijh} b_{ij}^{(h)} \frac{\partial \lambda}{\partial b_{ij}^{(h)}} = r\lambda$$

and $$\sum_{ijh} e_{ij}^{(h)} = \sum_{ijh} \frac{b_{ij}^{(h)}}{\lambda} \frac{\partial \lambda}{\partial b_{ij}^{(h)}} = r \quad .$$

For periodic matrix products elasticities $e_{ij}^{(h)}$ thus do not sum to one but to the period r. According to this, loop elasticities of periodic matrix models are calculated by multiplying the loop's characteristic elasticity with the length of the loop l, i.e., the number of transitions it contains, divided by r. In other words, the "effective length" l/r of a loop is its length in units of the projection interval $\Delta t = r$ of the periodic matrix product **C** (cf. Eq. C.1).

Besides the difference in calculating loop elasticities, i.e. the need to relate the length of loops to the time step of matrix **C** to which the growth rate λ refers, the discussion of elasticities $e_{ij}^{(h)}$ corresponds to the fundamentals of the method given by van Groenendael et al. (1994). It, thus, can be stated that loop analysis can be conducted and interpreted for periodic matrix products, as well.

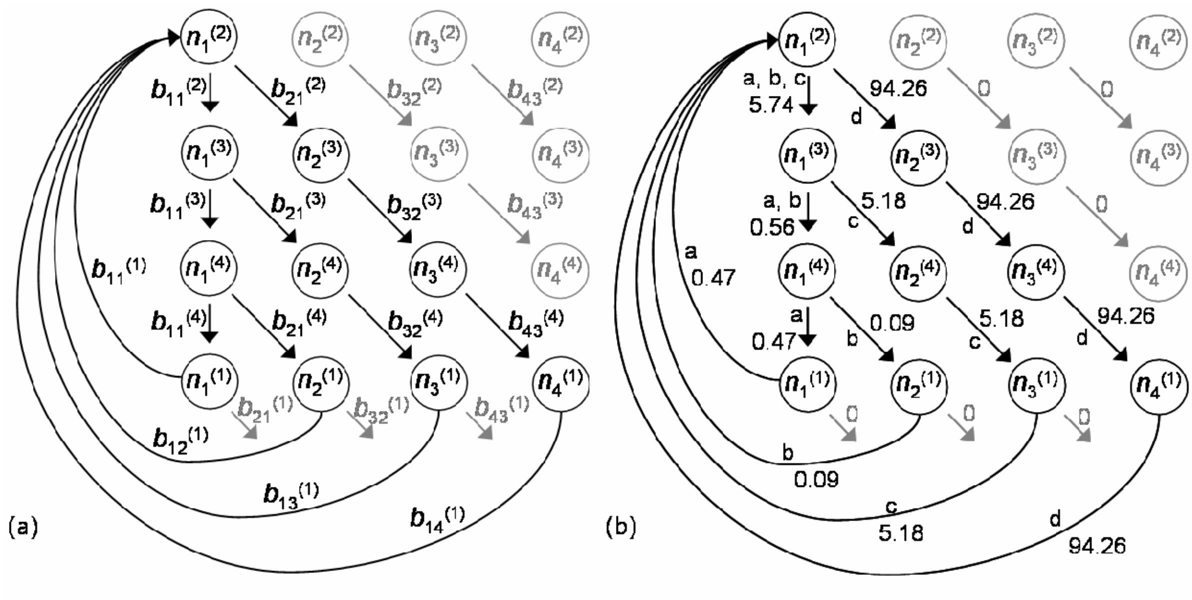

FIG. C1. Life cycle graph for *Thlaspi perfoliatum* in a cyclic environment with period r = 4 yrs.

(a) Population stages $n_{ij}^{(h)}$ and annual transitions $b_{ij}^{(h)}$ at different positions h in the cycle. Stages and corresponding transitions that do not contribute to population growth and are, thus, not considered in loop analysis are displayed gray.

(b) Loops derived from the graph and elasticities of the dominant eigenvalue of the cycle matrix **C** to annual transitions. The loops a–d represent life history pathways of pure annual vegetation cycles (a) and with residence times in the soil seed bank of 1 year (b), 2 years (c) or 3 years (d), respectively. Numbers at the arcs give the elasticities $e_{ij}^{(h)}$ in %. It can be seen that the elasticity of each transition is build up by the elasticities of loops passing through that transition. Transitions that are unique to a certain loop have the same elasticity that is equal to the “characteristic elasticity” of this loop.

TABLE C1. Cyclic permutations of the matrix product **C** and respective annual transition matrices, eigenvectors, and elasticities.

$\mathbf{C}_1$ =				$\mathbf{C}_2$ =				$\mathbf{C}_3$ =				$\mathbf{C}_4$ =			
0.0047	0.0068	0.0068	0.0068	1	0	0	0	0.0574	0.1646	0	0	0.0056	0.0048	0.0032	0
0.0006	0.0009	0.0009	0.0009	0	0	0	0	0.3289	0.9426	0	0	0.0608	0.0518	0.0345	0
0.0362	0.0518	0.0518	0.0518	0	0	0	0	0.0013	0	0	0	1.6588	1.4138	0.9426	0
0.6583	0.9426	0.9426	0.9426	0	0	0	0	0.0004	0	0	0	0.0431	0	0	0
$\mathbf{B}_1$ =				$\mathbf{B}_2$ =				$\mathbf{B}_3$ =				$\mathbf{B}_4$ =			
11.073	15.855	15.855	15.855	0.0277	0	0	0	0.0146	0	0	0	1.0604	0	0	0
0.1083	0	0	0	0.1585	0	0	0	0.1537	0	0	0	0.1394	0	0	0
0	0.4031	0	0	0	0.75	0	0	0	0.75	0	0	0	0.75	0	0
0	0	0.2687	0	0	0	0.5	0	0	0	0.5	0	0	0	0.5	0
$\mathbf{D}_1$ =				$\mathbf{D}_2$ =				$\mathbf{D}_3$ =				$\mathbf{D}_4$ =			
0.0004	0	0	0	2.0747	5.9457	0	0	0.3863	0.3292	0.2195	0	0.0045	0.0064	0.0064	0.0064
0.0001	0	0	0	0.0017	0	0	0	2.2117	1.8851	1.2567	0	0.0482	0.0691	0.0691	0.0691
0.0033	0	0	0	0.0008	0	0	0	0.0861	0	0	0	1.3165	1.8851	1.8851	1.8851
0.0594	0	0	0	0.0317	0	0	0	0.0281	0	0	0	0.0406	0	0	0
$\mathbf{w}_1$ =		$\mathbf{v}_1$ =		$\mathbf{w}_2$ =		$\mathbf{v}_2$ =		$\mathbf{w}_3$ =		$\mathbf{v}_3$ =		$\mathbf{w}_4$ =		$\mathbf{v}_4$ =	
23.1		0.374		53858		0.0338		1491.1		0.071		21.8		0.4712	
3		0.5355		3		0		8538		0.2008		234.6		0.4016	
176		0.5355		1		0		1.9		0		6403.5		0.2677	
3201.8		0.5355		47		0		0.6		0		0.9		0	
$\langle \mathbf{v}_1, \mathbf{w}_1 \rangle = 1818.9$				$\langle \mathbf{v}_2, \mathbf{w}_2 \rangle = 1818.9$				$\langle \mathbf{v}_3, \mathbf{w}_3 \rangle = 1818.9$				$\langle \mathbf{v}_4, \mathbf{w}_4 \rangle = 1818.9$			
$\mathbf{E}_{\mathbf{B}1}$ [%] =				$\mathbf{E}_{\mathbf{B}2}$ [%] =				$\mathbf{E}_{\mathbf{B}3}$ [%] =				$\mathbf{E}_{\mathbf{B}4}$ [%]=			
0.47	0.09	5.18	94.26	5.74	0	0	0	0.56	0	0	0	0.47	0	0	0
0	0	0	0	94.26	0	0	0	5.18	0	0	0	0.09	0	0	0
0	0	0	0	0	0	0	0	0	94.26	0	0	0	5.18	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	94.26	0

All matrices are evaluated for populations in the stable state under a rototilling return interval of 4 years. For notation see the text.

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