Ecological Applications of Matrices and Graphs,

a 3-lecture course to be given by
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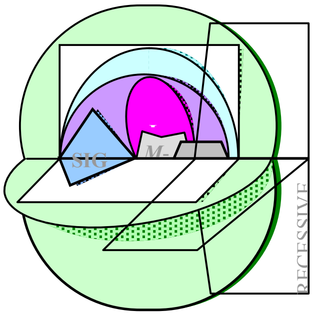

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Matrices and graphs, as general mathematical tools, apply everywhere a system under study has two or more components in its structure. Impressive ecological applications are those exploiting a fundamental link between any $n \times n$ matrix $\boldsymbol{A} = [a_{ij}]$ and its n-node *directed graph* $\Gamma(\boldsymbol{A})$ *associated* to the matrix by the following rule: there is an arc directed from node j to node i if and only if the matrix element $a_{ij} \neq 0$ $(i, j = 1,\ldots, n)$. Besides a visualization of the system structure, the *digraph* Γ provides for a means to verify certain matrix properties such as *indecomposability* (*irreducibility* in some texts) and *primitivity*/*imprimitivity*, which are crucial in matrix analysis.

As a function of which particular field of ecology gives rise to a graph representation of the system, one can specify at least three directions for the use of matrix analysis in ecology, each harbouring attractive mathematical problems motivated by various kinds of uncertainty in data, each deserving of an introductory lecture. Each of three lectures will introduce basic notions in the filed and illustrate applications with particular projects of ecological modelling.

Participants are supposed to be familiar with elementary notions of linear algebra such as linear spaces, transformations, eigenvalues, eigenvectors, etc.

Lecture 1

- *Matrix* models of *discrete-structured population dynamics*, one of the basic tools in modern demography and population ecology. The digraph Γ represents a *life cycle graph*, a scheme of *life history* for individuals of a particular biological species formalized in the terms of discrete ontogenetic stages the organisms pass through when being born, growing, reproducing, and senescing. The population thus consists of several age/stage classes whose population sizes or densities constitute a n-vector, $\boldsymbol{x}(t)$. The life cycle graph associates to a *projection matrix* $\boldsymbol{L}$, the matrix elements serving as demographic parameters, or *vital rates*, and population dynamics, registered at discrete moments of time, obey the difference equation $\boldsymbol{x}(t+1) = \boldsymbol{L}\,\boldsymbol{x}(t)$. The mathematics of matrix population models was studied comprehensively last century, the outcome substantiating the dominant eigenvalue $\lambda_1(\boldsymbol{L}) >$ as a multi- dimensional analogue for a scalar population growth rate, i.e., a quantitative measure of population adaptation. Current ecological practice motivates new problems, e.g, the calibration of $\boldsymbol{L}$ under "reproductive uncertainty" in the data for a single time step as a nonlinear maximization problem under constraints.

Lecture 2

- *Lotka–Volterra* and other *nonlinear* ODE models of *community dynamics*, a framework to study many problems of theoretical population ecology including "stability-vs.-complexity" issues in multi-species communities. The digraph Γ now represents a structure of inter- and intra-species relations in the community, the arc $j \rightarrow i$ acquiring also the sign of the effect the species j exerts upon species i $(i, j = 1,\ldots, n)$. The *signed digraph* thus associates to the *Jacobi matrix* $\boldsymbol{A}$ calculated at an equilibrium point of the ODE system and called the *community matrix* in these contexts. Besides representing a structure of biological interactions, it serves also as a tool to analyze community stability through the localization of the matrix spectrum (Re $\lambda(\boldsymbol{A}) < 0$). An eternal issue of how the community structure effects the community stability gets a variety of formulations, which give rise to special, *stronger-than-Lyapunov*, notions of matrix stability motivated by various kinds of data uncertainty. To characterize a particular stability notion in the matrix or/and signed digraph terms represents a challenging problem, and a logical hierarchy of inclusion relations among the corresponding subsets in the space of real $n \times n$ matrices (*Matrix Flower*) helps solve these problems.

Lecture 3

- <u>*Markov-chain* models of ecological *succession*</u>, a long-term process of ecosystem development where successive species substitutions result in directed movement from the pioneer stage of succession to its final (*climax*) one (s). The digraph Γ represents here a known scheme of transitions among the specified stages, and it associates to the *transition matrix* ***P***, a (column-stochastic) matrix of transition probabilities for a certain time step (e.g., 1, 5, or 10 years), while stochasticity appears due to the uncertainty in whether a transition event does or does not occur. An *ergodic hypotheses* helps calibrate matrix ***P*** from either *temporal*, or *spatial* data, and the matrix algebra of Markov-chain theory yields quantitative forecasts on the outcomes of succession such as the final compositions of stages, the mean time till absorption at a final stage, etc. In a new generation of Markov-chain models – time-*inhomogeneous chains* – transition probabilities are considered to be some functions of those key environmental variables which effect the course of succession, thus turning the transition matrix into a composite function of time, ***P***(*t*), and linking the model to a potential scenario of climate changes. To expand the elegant formulae of classic theory into the inhomogeneous case is a challenging problem.

LITERATURE RECOMMENDED

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* Available in PDF.