Part I: What is Systems Ecology?

An Introductory Overview

1. WHAT IS SYSTEMS ECOLOGY?

Defining systems ecology by “subject matter”: Systems ecology is

- a subdiscipline of ecology (studying interactions between organisms and their biotic and abiotic environment)
- synecological (cf. Schwerdtfeger, 1975), i.e. emphasis is on ecosystems
- not limited to certain taxa, habitats, or functions
- includes human activities and impacts on ecosystems

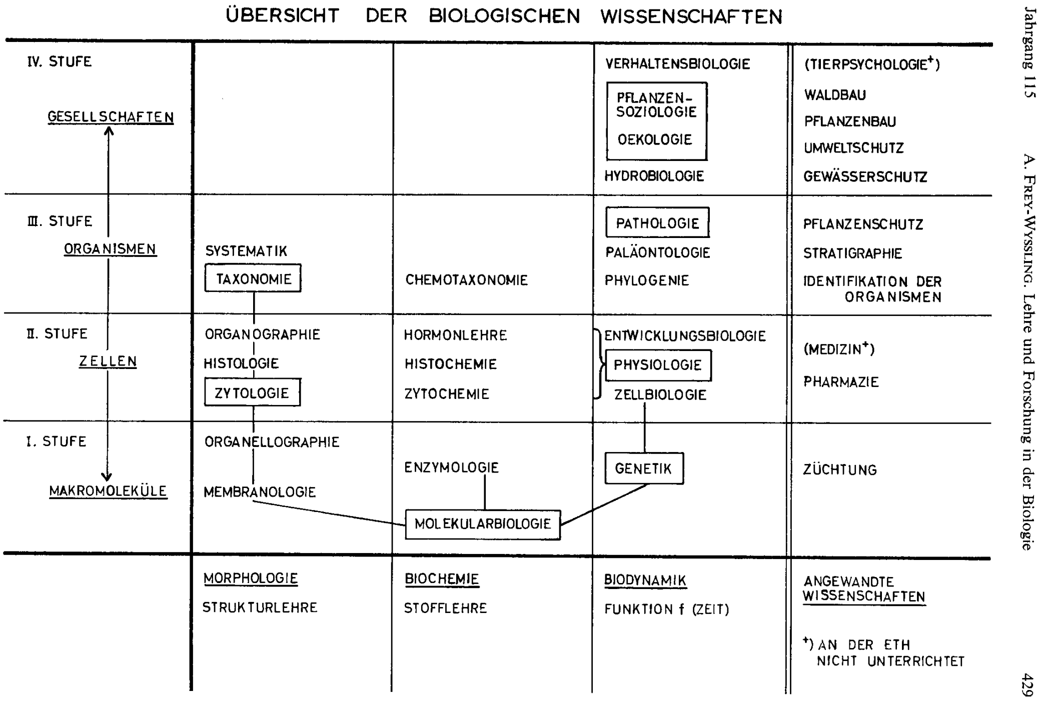
Defining systems ecology by methodology: Systems ecology emphasizes

- application orientation including actual solving of environmental problems
- modelling and the use of models is pivotal
- systems approaches and is based on systems theory
- complex models and is not constrained by "classical" mathematics

The following explains these points:

1.1. Classification by subject matter

Systems ecology is a subdiscipline of ecology. As ecology, it is usually considered to be a biological science (Fig. I-1).



ÜBERSICHT DER BIOLOGISCHEN WISSENSCHAFTEN

IV. STUFE GESELLSCHAFTEN			VERHALTENSBIOLOGIE PFLANZEN-SOZIOLOGIE OEKOLOGIE HYDROBIOLOGIE	(TIERPSYCHOLOGIE+) WALDBAU PFLANZENBAU UMWELTSCHUTZ GEWÄSSERSCHUTZ
III. STUFE ORGANISMEN	SYSTEMATIK TAXONOMIE	CHEMOTAXONOMIE	PATHOLOGIE PALÄONTOLOGIE PHYLOGENIE	PFLANZENSCHUTZ STRATIGRAPHIE IDENTIFIKATION DER ORGANISMEN
II. STUFE ZELLEN	ORGANOGRAPHIE HISTOLOGIE ZYTOLOGIE	HORMONLEHRE HISTOCHEMIE ZYTOCHEMIE	ENTWICKLUNGSBIOLOGIE PHYSIOLOGIE ZELLBIOLOGIE	(MEDIZIN+) PHARMAZIE
I. STUFE MAKROMOLEKÜLE	ORGANELLOGRAPHIE MEMBRANOLOGIE	ENZYMOLOGIE MOLEKULARBIOLOGIE	GENETIK	ZÜCHTUNG
	MORPHOLOGIE STRUKTURLEHRE	BIOCHEMIE STOFFLEHRE	BIODYNAMIK FUNKTION f (ZEIT)	ANGEWANDTE WISSENSCHAFTEN +) AN DER ETH NICHT UNTERRICHTET

Fig. I-1: Systems ecology is a subdiscipline of ecology and with ecology considered to belong to the biological sciences, although this is actually not really appropriate. The graph illustrates earlier understanding of ecology and how Frey-Wissling, who was an influential professor at ETH Zurich, embedded ecology within its neighbouring disciplines (Frey-Wissling, 1970). Frey-Wissling used the criteria (i) organizational or hierarchical level, (ii) applied vs. fundamental sciences (angewandte vs. Grundlagenforschung), (iii) science of structure, of matter, and of functioning (Struktur-, Stoff- sowie Funktionslehre).

During the last century ecology has matured and represents now a large field consisting of many specialisations. The following subdivides ecology into special fields. Classifications are listed by the underlying criterion:

1.1.1. CLASSIFICATION BY ORGANIZATIONAL LEVEL

Ecology can be subdivided according to the level at which the studied object is found within the biological hierarchy. Traditionally three main levels are distinguished:

- **Autecology** (Autökologie), sometimes also called organismal ecology, where the focus is on the individual organism of a particular species (Schwerdtfeger, 1963).
- **Population ecology** (Populationsökologie, Demökologie) where the focus is on the population of a single species (Demozön) (Schwerdtfeger, 1968).

- **Synecology** (Synökologie) where the focus is on the multispecies ecological system (Schwerdtfeger, 1975). Community ecology and synecology are closely related, but not quite the same. Synecology as originally devised by Schwerdtfeger actually overarches community ecology (focus on a multispecies community of organisms living together), ecosystem ecology, and landscape ecology. Yet, Schwerdtfeger largely ignored the global scale (global ecology).

Systems ecology, today often also called ecosystem ecology, studies primarily ecosystems (see e.g. Fig I-2) and is a synecological ecology.

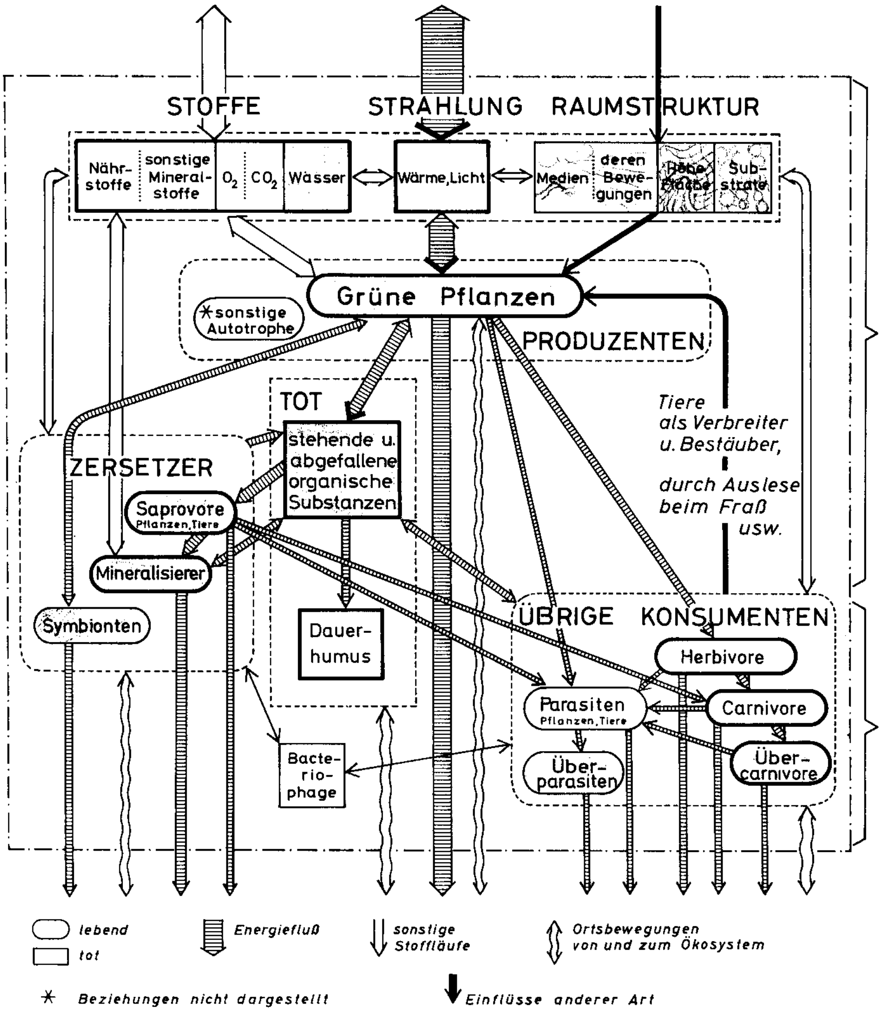


Fig. I-2: Schematic model of an ecosystem (Ellenberg, 1973) emphasizing energy flow, which determines functional groups of organisms such as primary producers, consumers or decomposers. Ellenberg was in Europe a very prominent and influential ecologist, who also taught for a while at ETH Zurich. A similar role played Eugene Odum for the North American continent, notably with his influential text book (Odum, 1971, cf. Fig. I-3).

Terminology: Stoffe/ inputs; Nährstoffe/ nutrients; Mineralstoffe/ minerals; Wasser/ water; Strahlung/ radiation; Wärme/ heat; Licht/ light; Raumstruktur/ space structure; Bewegung/ motion; Höhe/ altitude; Fläche/ area; Grüne Pflanzen/ green plants; Produzent/ producer; Zersetzer bzw. Mineralisier / decomposer; tot/ dead; stehende und abgefallene organische Substanzen/ living and dead organic matter; Dauerhumus/ permanent humus; Tiere als Verbreiter und Bestäuber/ animals as dispersers and pollinators; durch Auslese beim Frass / through food-selection; lebend/ living; Energiefluss/ energy flux; Sonstige Stoffläufe/ other fluxes; Ortsbewegungen von und zum Ökosystem/ migration from and to the ecosystem; Einflüsse anderer Art/ other influences.

1.1.2. CLASSIFICATION BY HABITAT (TOPICAL UNIT)

Examples are marine ecology, limnology or freshwater ecology, terrestrial ecology, arctic or tropical ecology etc. Classification by habitat is of no relevance in systems ecology.

1.1.3. CLASSIFICATION BY TAXA (BIOTIC UNIT)

Examples are microbial ecology, plant ecology, animal ecology, insect ecology, etc. Classification by taxa is of no relevance in systems ecology.

1.1.4. CLASSIFICATION BY FUNCTION

Production ecology is a branch of ecology focussing on certain functions such as primary production (Fig. I-3) or decomposition, both the pathways along which energy and matter flow within ecosystems.

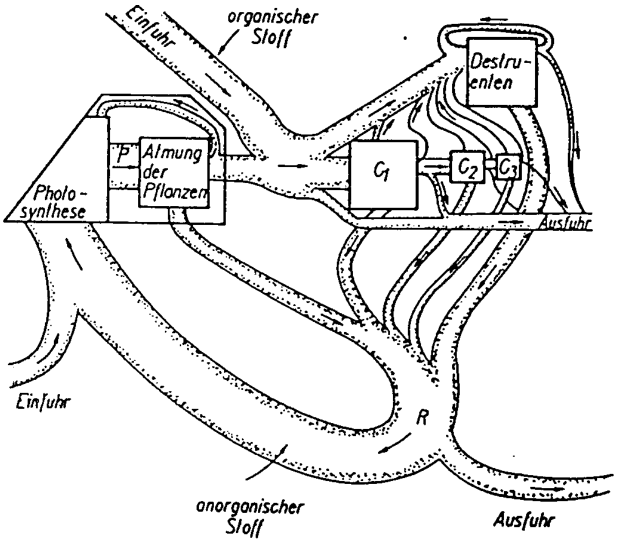


Fig. I-3: Energy flows in an ecosystem by H.T. Odum 1960.

Systems ecology does not favour some functions over others.

1.1.5. CLASSIFICATION BY TIME

Palaeoecology focuses on the ecology of the past, where neoecology focusses on the present. Fig. I-4 illustrates the role of criterion time, but depicts in addition the use of other criteria (hierarchy, space) for subdividing ecology.

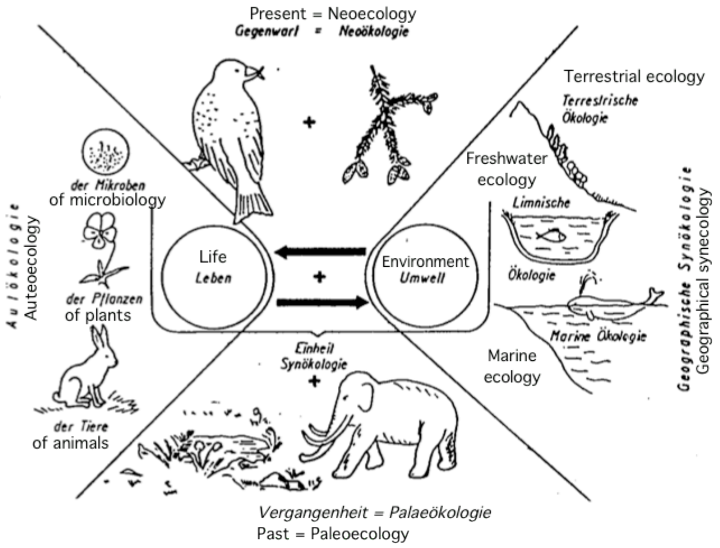


Fig. I-4: Classification of ecology by the time criterion (vertical), the organizational level (horizontal, left) and the topical (geographical or spatial) criterion (right) (Stugren, 1979).

The criterion time is not important for defining systems ecology.

1.2. Classification by methodology

Methodological criteria are important for systems ecology. The methodological criterion lets us distinguish among e.g. *experimental ecology* and systems ecology. In experimental ecology, the emphasis is on experimental methods, i.e. laboratory- and field experiments whereas systems ecology emphasizes an approach that focuses on the system properties of the studied object or problem in a holistic manner.

1.2.1. APPLICATION ORIENTED

Systems ecology has a tradition of being strongly application oriented. This is perhaps the most important distinction between the term systems ecology, as it used to be understood, vs. the currently more often heard term ecosystem ecology. Note, apart from this minor difference they can be considered synonyms.

In the past systems ecology has contributed to solve many environmental problems (e.g. Shugart & O'Neill, 1979). Examples: Plant protection, environmental pollution, pest management (see our 2nd case study featuring the larch bud moth population system), management of naturally renewable resources, and landscape management.

It was always a strength of systems ecology to be holistic and therefore include anthropogenic components of ecological and environmental systems in an integrative manner.

2. SYNOPSIS OF SYSTEMS ECOLOGY

The methodology of systems ecology is based on certain procedures and theoretical principals. These include systems theory, particularly systems analysis and mathematical modelling, or simply modelling, and finally simulation.

2.1. Modelling

Since systems ecology focuses on investigating complex subject matters, e.g. whole ecosystems, modelling plays a particularly important role. Complexity can be mind boggling, but modelling helps us, amongst other things, to maintain an overview and to upheld scientific rigor and consistency despite high degrees of complexity.

Models represent on purpose only an “excerpt of reality” (Ausschnitt der Wirklichkeit). They are only a model that is modelled after a “real system”. Models are studied in lieu of the real system, possibly to avoid intolerable damage or high risks (e.g. failure of a nuclear power plant) or to make projections into the future (possibly to avoid that future). Typically a given real system can be modelled in more than one way: Depending on the purpose of the study another “excerpt of reality” is chosen. This is abstraction, which facilitates the study of a system by focusing only on those aspects of the system that matter in a particular context the most. Abstraction is typically determined by the problem motivating the study or whatever question the researcher is most interested in.

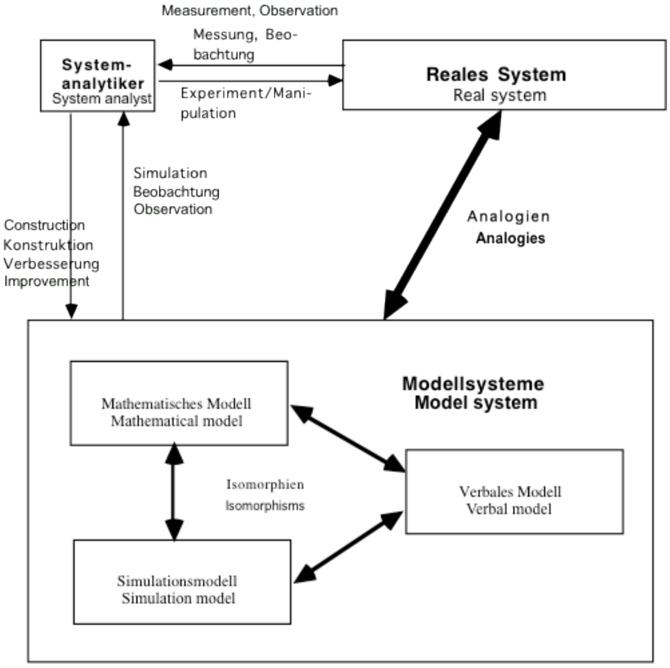


Fig. I-5: Basic epistemological situation in modelling and analysis of existing systems such as ecosystems or population systems.

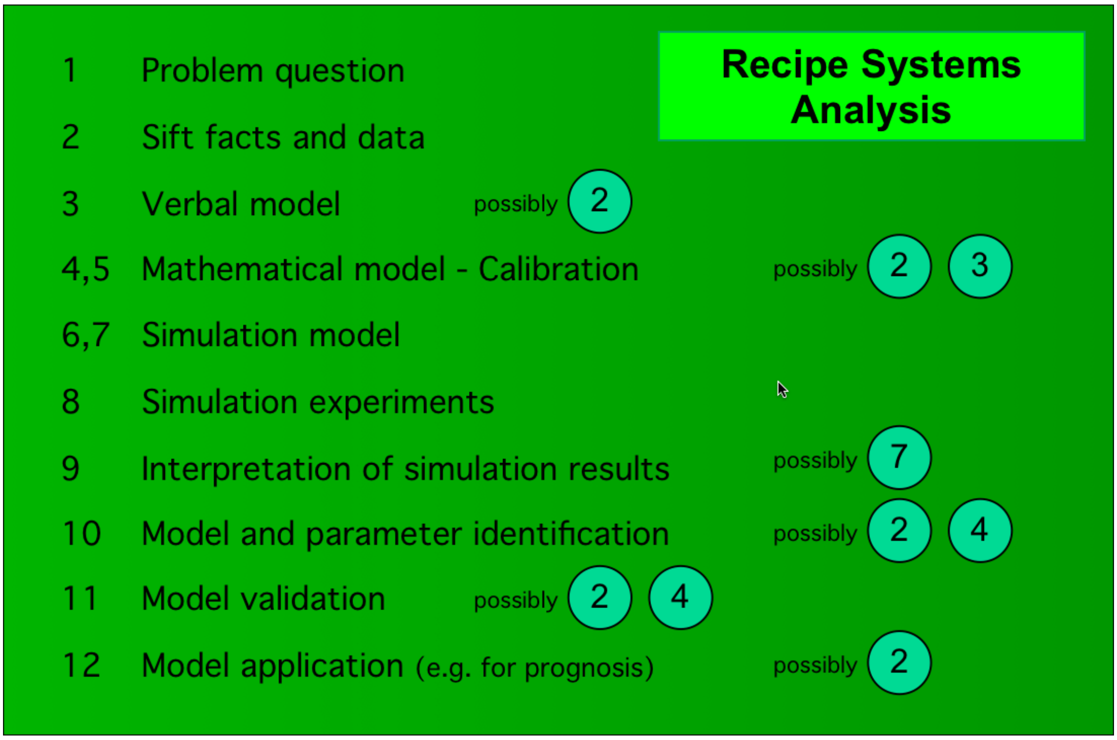
2.2. Systems analysis

Ecological systems such as ecosystems, population systems or ecological processes, are understood to have evolved naturally. This fact makes a difference in the context of systems analysis, despite the fact that almost all ecosystems are today exposed to significant direct and indirect human influences.

Systems analysis stands out whenever we are confronted with a given, non-man-made system. This situation contrasts with that when we deal with a human-made system, such as a machine, some human infrastructure, or a social organisation, e.g. an enterprise. Most parts of such a system are basically known, since they are human designed from the beginning. Whereas all ecological systems, together with many other natural, i.e. non-man-made, systems are initially unknown and their structure and functioning requires first of all a careful and meaningful analysis before they can be understood let alone managed.

In systems ecology the purpose of systems analysis is to gather the system character of the studied ecological system, e.g. an ecosystem such as a forest or a lake. This is best done by building a model, i.e. modelling. Through such an analysis we can improve our understanding of the structure and the functioning of complex ecological phenomena.

Some claim systems analysis can be done in many ways, including informal ones. Indeed we analyze systems all the time and there is more than one way to skin a cat. However, to be economic and successful, systems analysis is best done in a system theory based manner (see below "systems theory") and is almost never done without some form of modelling (see below "modelling"). Despite the many approaches you may find, I recommend to follow always the very same comprehensive procedure during any systems analysis of any ecological system:



Recipe Systems Analysis

1 Problem question
2 Sift facts and data
3 Verbal model possibly ②
4,5 Mathematical model - Calibration possibly ② ③
6,7 Simulation model
8 Simulation experiments
9 Interpretation of simulation results possibly ⑦
10 Model and parameter identification possibly ② ④
11 Model validation possibly ② ④
12 Model application (e.g. for prognosis) possibly ②

Circled numbers on the right mean return to a previously listed step

2.3. Systems theory

Systems theory originated from control engineering (Regelungstechnik). The basic idea is to maintain a wanted state or more sophisticated a wanted system behavior (erwünschtes Systemverhalten) of the controlled system (Regelstrecke) under any set of conditions and influences. In many situations it is hopeless to anticipate all possible perturbations

(Störeinflüsse) a system might be exposed to during its existence. Thus control engineering gives up on preparing a system for all possible influences. Instead it cleverly designs control systems such that their response to a perturbation becomes independent from a particular kind of perturbation. Such a system responds to all perturbations by looking only at the deviation of the variable of interest (control variable, Regelgrösse) from the wanted state (Sollwert der Regelgrösse), regardless of the cause of the perturbation. This introduces a control loop or feedback loop (Rückkopplung). Historically the very first controller based on such a principle emerged from sailing, i.e. the desire to keep a ship on a wanted course (Sollwert) despite ever-changing winds (Störungen) lead to such a solution.

Since not human-made, ecosystems are not control systems in a strict sense. However, they share several properties with control systems: They are "very" open systems, which are exposed to many environmental influences and most importantly they contain many feedbacks. For evolutionary reasons ecological systems "wish"[1] often also to maintain some optimal state (note, "wish" **must not** be understood from a human perspective).

Not every part of the system of interest needs to be known. It may suffice to control the course of a sailing ship or to regulate the temperature of your body by focusing only on those variables, while ignoring all other body parts, i.e. leave everything else alone. Control focuses on the variables of interest, the control variables (Regelgrössen), which are often also output variables (Ausgangsvariablen). We will see later why variables got their names; they make sense only in a systems theoretical context. Once the extant system has been analyzed (Systemanalyse), typically by building a model, the next step is the systems synthesis (Systemsynthese). The latter means you design a new system (Reglerentwurf) consisting of the controlled system (Regelstrecke) and the controller (Regelstrecke + Regler) such that the new enhanced system shows the desired behaviour.

Linear systems theory is the cornerstone of all systems theory. Although applicable only to a limited class of systems, it can nevertheless also be used in many other instances as well, e.g. in the essential stability analysis of non-linear systems.

Fundamental is the **system concept**: It is best explained with the illustrative example of a linear system (Fig. I-6). To be as general as possible, we assume here that every system component (Systemelement) is connected to every other. There are many kinds of system components.

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[1] Here we have to be careful and should avoid any so-called teleological thinking. Ecosystems do of course not have any "wishes", have no "will" nor "desire" to be in a particular state. However, evolution has produced many biological systems, including organisms, that function only within certain environmental conditions. Then it is of an evolutionary advantage to an organism to be able to gain at least partial control over the environment and regulate it such that the organism can enjoy that environment during a longer time or access more of those favourable conditions. See also the Gaia hypothesis, proposed by James Lovelock for the global scale (e.g. Fischlin, 1990; Lovelock, 1990).

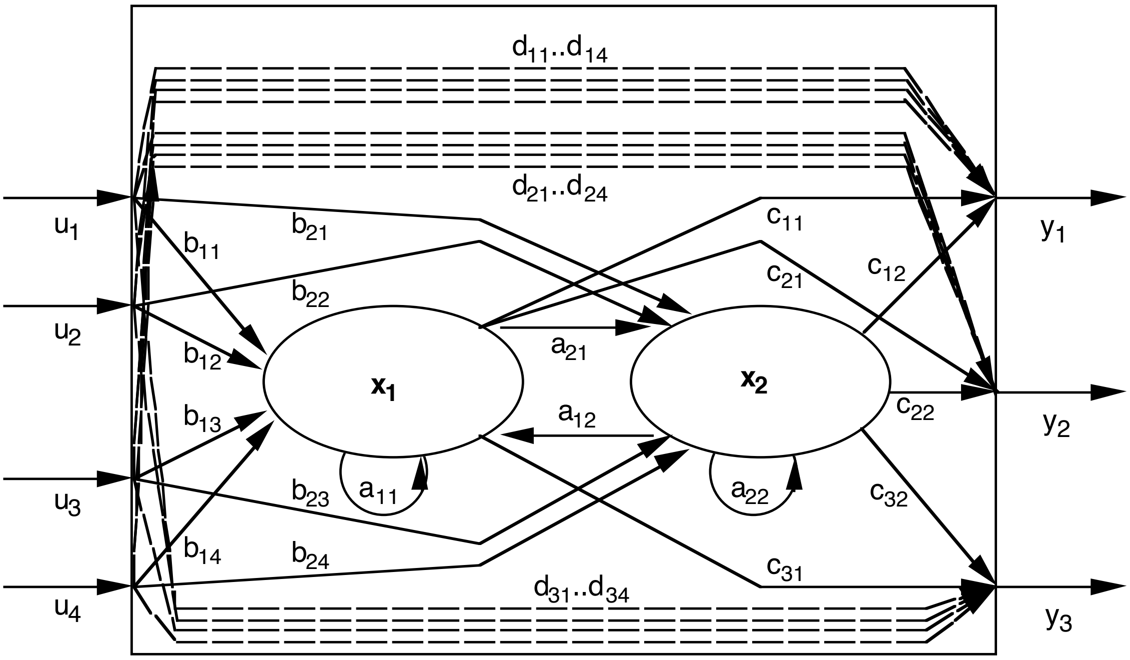

Fig. I-6: Example of a 2nd order system with 4 inputs and 3 outputs. Arrows designate a cause-effect relationship between system components.

2nd order system	2 **state variables** (**Zustandsvariablen**) $[x_1\ x_2]'$, i.e. the system consists of 2 components (Systemelementen), e.g. pest- and host plant populations. They determine the internal state of the system (memory) at any given point in time.
4 inputs	Time-dependent **input variables** (Eingangsgrössen, **Eingangsvariablen**) $[u_1\ u_2\ u_3\ u_4]'$. They represent four different environmental factors, e.g. temperature, precipitation, fertilizer, and insecticide treatment.
3 outputs	System state dependent **output variables** (Ausgangsgrössen, **Ausgangsvariablen**) $[y_1\ y_2\ y_3]'$. They are the available or interesting information about the system's internal current state, e.g. pest caused damage, yield, and profit.

Arrows (Pfeile, Kanten) represent cause-and effect relationships between system elements (Knoten, Punkte). Notably input variables $\underline{u}$ (input vector) influence state variables $\underline{x}$ (state vector) and they influence the output variables $\underline{y}$ (output vector). Since all variables affect each other in any direction ("all is connected"), it arises a complicated cause-effect structure (Wirkungsgefüge) (Fig. I-6). However, an important system theoretical restriction applies (by definition): Neither state nor output variables may feedback (Rückkopplung) to input variables and output variables may not feedback to any state or input variables.

Arrows are marked with the symbols $a_{..}$, $b_{..}$, $c_{..}$ and $d_{..}$. In the linear case, such a relationship between cause x and effect y describes precisely a multiplication using a time independent constant c: $y = c \cdot x$.

The following system equations hold assuming linearity throughout the system:

$$dx_1/dt = a_{11} \cdot x_1 + a_{12} \cdot x_2 + b_{11} \cdot u_1 + b_{12} \cdot u_2 + b_{13} \cdot u_3 + b_{14} \cdot u_4 \quad (1)$$

$$dx_2/dt = a_{21} \cdot x_1 + a_{22} \cdot x_2 + b_{21} \cdot u_1 + b_{22} \cdot u_2 + b_{23} \cdot u_3 + b_{24} \cdot u_4 \quad (2)$$

$$y_1 = c_{11} \cdot x_1 + c_{12} \cdot x_2 + d_{11} \cdot u_1 + d_{12} \cdot u_2 + d_{13} \cdot u_3 + d_{14} \cdot u_4 \quad (3)$$

$$y_2 = c_{21} \cdot x_1 + c_{22} \cdot x_2 + d_{21} \cdot u_1 + d_{22} \cdot u_2 + d_{23} \cdot u_3 + d_{24} \cdot u_4 \quad (4)$$

$$y_3 = c_{31} \cdot x_1 + c_{32} \cdot x_2 + d_{31} \cdot u_1 + d_{32} \cdot u_2 + d_{33} \cdot u_3 + d_{34} \cdot u_4 \quad (5)$$

(1) and (2) are called the **dynamic equations** (**Dynamikgleichungen**). They consist here of 2 linear, continuous-time differential equations, which describe the system dynamics and model the dependence of the internal system elements on the environment and on the internal system state itself (**feedback loops**). (3) – (5) are called **output equations** (**Ausgangsgleichungen**). They represent the dependence of the system's outputs from the internal system state and indirectly from the inputs (terms with coefficients $c_{..}$). Moreover, output variables may also directly depend on influences from the system's environment, i.e. the input variables (terms with coefficients $d_{..}$).

By definition applies:

$\underline{x} = \begin{bmatrix} x_1 \\ x_2 \end{bmatrix}$ State vector (Zustandsvektor)

$\underline{\dot{x}} = \begin{bmatrix} \dot{x}_1 \\ \dot{x}_2 \end{bmatrix}$ Derivative vector (Ableitungsvektor)

$\underline{u} = \begin{bmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \end{bmatrix}$ Input vector (Eingangsvektor)

$\underline{y} = \begin{bmatrix} y_1 \\ y_2 \\ y_3 \end{bmatrix}$ Output vector (Ausgangsvektor)

$A = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$ System matrix (Systemmatrix)

$B = \begin{bmatrix} b_{11} & b_{12} & b_{13} & b_{14} \\ b_{21} & b_{22} & b_{23} & b_{24} \end{bmatrix}$ Input matrix (Eingangsmatrix)

$C = \begin{bmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \\ c_{31} & c_{32} \end{bmatrix}$ Output matrix (Ausgangsmatrix)

$$D = \begin{bmatrix} d_{11} & d_{12} & d_{13} & d_{14} \\ d_{21} & d_{22} & d_{23} & d_{24} \\ d_{31} & d_{32} & d_{33} & d_{34} \end{bmatrix}$$

Input-output matrix (Eingangs-Ausgangskopplungsmatrix)

The vector notation shown above allows us to use the following matrix representation to elegantly describe the entire set of equations (1) .. (5) with only following two matrix equations:

$$\begin{aligned} \underline{\dot{x}} &= A \cdot \underline{x} + B \cdot \underline{u} \\ \underline{y} &= C \cdot \underline{x} + D \cdot \underline{u} \end{aligned}$$

If some cause-effect relationships are absent, corresponding coefficients are set to zero. For example, the interactions between the two state variables are omitted in following system matrix:

$$A = \begin{bmatrix} a_{11} & 0 \\ 0 & a_{22} \end{bmatrix}$$

In this case the two state variables are decoupled from each other. Often there is no direct dependency between inputs and outputs, which is expressed by setting $D = \underline{0}$, i.e. the output equations become $\underline{y} = C \cdot \underline{x}$.

Nonlinear, continuous-time systems can be represented in a similar manner, however, usually a matrix notation is no longer possible. General form:

$$\begin{aligned} \underline{\dot{x}} &= \underline{f}(\underline{x}, \underline{u}) \\ \underline{y} &= \underline{g}(\underline{x}, \underline{u}) \end{aligned}$$

Here arise the additional function vectors $\underline{f}$ and $\underline{g}$. The equations describing the dynamics of the system (Dynamikgleichungen) then represent a nonlinear, coupled differential equation system (**DESS** – Differential Equation System Specification).

2.4. Mathematics and simulation

Mathematical ecology emphasizes "classical", mathematical approaches to model ecological systems. E.g. bisystems, suc as predator-prey systems, are very important in mathematical ecology. Systems ecology builds on mathematical ecology. However, because of its application orientation systems ecology requires often a degree of realism, which can rarely be achieved through the strategic models so emphasized by mathematical ecology. The models used in systems ecology are typically much more complex and require tools and approaches beyond classical mathematics.

Ecological systems are not only inherently non-linear, they typically are very dynamic and piece-wise linear approximations are rarely of much interest. Consequently systems ecology is pervaded by non-linear systems. However, the price to pay is that analytical solutions are very rarely possible. In general non-linear systems are analytically intractable. What follows is that simulation models are needed to solve those non-linear systems at least numerically, today using digital computers.

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