CHAPTER 13

Structurally dynamic models

S.E. Jørgensen

Environmental Chemistry, Copenhagen University, Copenhagen, Denmark.

1 Introduction: why structurally dynamic models?

Models of ecosystems attempt to capture the characteristics of ecosystems. However, ecosystems differ from most other systems by being extremely adaptive, having the ability of self-organization and having a large number of feedback mechanisms. The real challenge to modelling is: How can we construct models that are able to reflect these characteristics. Section 2 will focus on the characteristic of ecosystems we should consider in our modelling approach.

Section 3 is devoted to how to develop what is denoted structurally dynamic models (SDM) or variable parameter models. The section will present the advantages and disadvantages of this model type and where it is most recommendable to consider applying SDM. Sections 4 and 5 present two illustrative examples of SDM.

Both illustrations will be explained in details, while the illustration presented in Section 5 is available on the enclosed CD and can be tested and run by the readers. This model type will most probably be used increasingly in the coming years in our endeavour to make better prognoses, because reliable prognoses can only be made by models with a correct description of ecosystem properties including the ability to change the structure and the properties of key species. If our models do not describe properly adaptation and possible shifts in species composition, the prognoses will inevitably be more or less incorrect; the SDM attempt to overcome these shortcomings.

There is no software available yet that enables using it for a general development of SDM. It is necessary to develop, for instance, a C++ program for development of every SDM. Downloadable models of eutrophication for both deep and shallow lakes and wetlands have been developed for UNEP under the name Pamolare. They are can be found on the home page www.unep.org.jp.

Notice that there are two SDMs of lakes, for a deep lake with thermocline under the name Pamolare 1 together with three other models and for a shallow lake under Pamolare 2.

2 Ecosystem characteristics

Ecology deals with irreducible systems (see Wolfram [1, 2] and Jørgensen [3–9]). We cannot design simple experiments, which will reveal a relationship that can in all detail be transferred
from one ecological situation and one ecosystem to another situation in another ecosystem. That is possible for instance with Newton’s laws of gravity, because the relationship between forces and acceleration is reducible. The relationship between force and acceleration is linear, but growth of living organisms is dependent on many interacting factors, which again are functions of time. Feedback mechanisms will simultaneously regulate all the factors and rates and they also interact and are also functions of time, as pointed out by Straskraba [10, 11].

Table 1 shows the hierarchy of regulation mechanisms, which are operating at the same time. From this example, the complexity alone clearly prohibits the reduction to simple relationships that can be used repeatedly.

An ecosystem has so many interacting components that it is impossible ever to be able to examine all these relationships and even if we could, it would not be possible to separate one relationship and examine it carefully to reveal its details, because the relationship is different when it works in nature with interactions from the many other processes, from when we examine it in a laboratory with the relationship completely separated from the other ecosystem components.

A known phrase in system ecology is ‘everything is linked to everything’ or ‘the whole is greater than the sum of the parts’. It implies that it may be possible to examine the parts by reduction to simple relationships, but when the parts are put together they will form a whole that behaves differently from the sum of the parts. This statement requires a more detailed discussion of how an ecosystem works.

Allen and Starr [12] claim that the latter statement is correct, because of the evolutionary potential that is hidden within living systems. The ecosystem contains within itself the possibilities of becoming something different, i.e. of adapting and evolving. The evolutionary potential is linked to the existence of microscopic freedom, represented by stochasticity and non-average behaviour, resulting from the diversity, complexity and variability of its elements.

Underlying the taxonomic classification is the microscopic diversity, which only adds to the complexity to such an extent that it will be completely impossible to cover all the possibilities and details of the observed phenomena. We attempt to capture at least a part of the reality by use of models. A model seems the only useful tool when we are dealing with irreducible systems. However, we need many models simultaneously to capture a more complete image of reality. It seems our only possibility to deal with the very complex living systems.

This has been acknowledged by the holistic ecology or systems ecology, while the more reductionistic ecology attempts to understand ecological reactions by analysis of one or at the most a

<table>
<thead>
<tr>
<th>Level</th>
<th>Explanation of regulation process</th>
<th>Exemplified by phytoplankton growth</th>
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<tbody>
<tr>
<td>1</td>
<td>Rate by concentration in medium</td>
<td>Uptake of phosphorus in accordance with phosphorus concentration</td>
</tr>
<tr>
<td>2</td>
<td>Rate by needs</td>
<td>Uptake of phosphorus in accordance with intracellular concentration</td>
</tr>
<tr>
<td>3</td>
<td>Rate by other external factors</td>
<td>Chlorophyll concentration in accordance with previous solar radiation</td>
</tr>
<tr>
<td>4</td>
<td>Adaptation of properties</td>
<td>Change in optimal temperature for growth</td>
</tr>
<tr>
<td>5</td>
<td>Selection of other species</td>
<td>Shift to better fitted species</td>
</tr>
<tr>
<td>6</td>
<td>Selection of other food web</td>
<td>Shift to better fitted food web</td>
</tr>
<tr>
<td>7</td>
<td>Mutations, new sexual recombinations and other shifts of genes</td>
<td>Emergence of new species or shifts of species properties</td>
</tr>
</tbody>
</table>
few processes, which are related to one or two components. Both analyses and syntheses are
needed in ecology and the analysis is a necessary foundation for the synthesis, but it may lead to
wrong scientific conclusions to stop at the analysis. Analysis of several interacting processes may
give a right result of the processes under the analysed conditions, but the conditions in ecosys-
tems are constantly changing and even if the processes were unchanged (which they very rarely
are), it is not possible to overview the analytical results of so many simultaneously working proc-
tesses. Our brain simply cannot overview what will happen in a system where for instance only
six interacting processes are working simultaneously.

The reductionistic approach does not consider:

1. The basic conditions determined by the external factors for our analysis are constantly chang-
ing in the real world and the analytical results where only one or a few factors are varied are
therefore not necessarily valid in the system context.
2. The interaction from all the other processes and components may change the processes and the
properties of all biological components significantly in the real ecosystem and the analytical
results are therefore not valid at all.
3. (A direct overview of the many processes simultaneously working is not possible and wrong
conclusions may be the result, if it is attempted.

The conclusion is therefore that we need a tool to overview and synthesize the many interact-
ing processes. The synthesis may in the first instance just be ‘putting together’ the various ana-
lytical results, but afterwards, we need to make changes to account for an additional effect,
resulting from the fact that the processes are working together and thereby become more than the
sum of the parts – they show in other words, a synergistic effect – a symbiosis. By a network
analysis, see Chapters 17 and 18, it is possible to show how important the indirect effects are
compared to the direct effects in an ecological network.

It is clear from this discussion that the complexity of ecosystems has set the limitations for our
understanding and for the possibilities of proper management. We cannot capture the complexity
as such with all its details, but we can understand how ecosystems are complex and we can set
up a realistic strategy for how to get sufficient knowledge about the system – not knowing all the
details, but still understanding and knowing the mean behaviour and the important reactions of
the system. It means that we can only try to reveal the basic properties behind the complexity.

We have no other choice than to go holistic. The results from the more reductionistic ecology
are essential in our effort ‘to go to the root’ of the system properties of ecosystems, but we need
systems ecology, which consists of many new ideas, approaches and concepts, to follow the path
to the roots of the basic system properties of ecosystems. The idea may also be expressed in
another way: we cannot find the properties of ecosystems by analyzing all the details, because
they are simply too many, but only by trying to reveal the system properties of ecosystems by
examination of the entire systems.

The number of feedbacks and regulations is extremely high and makes it possible for the living
organisms and populations to survive and reproduce in spite of changes in external conditions.
These regulations correspond to levels 3 and 4 in Table 1. Numerous examples can be found in the
literature. If the actual properties of the species are changed the regulation is named adaptation.
Phytoplankton is for instance able to regulate its chlorophyll concentration according to the solar
radiation. If more chlorophyll is needed because the radiation is insufficient to guarantee growth,
more chlorophyll is produced by the phytoplankton. The digestion efficiency of the food for many
animals depends on the abundance of the food. The same species may be of different sizes in dif-
f erent environments, depending on what is most beneficial for survival and growth. If nutrients are
scarce, phytoplankton becomes smaller and vice versa. In this latter case the change in size is a result of a selection process, which is made possible because of the distribution in size.

*The feedbacks are furthermore constantly changing, i.e. the adaptation itself is adaptable in the sense that if a regulation is not sufficient, another regulation process higher in the hierarchy of feedbacks – see Table 1 – will take over.* The change in size within the same species is for instance only limited. When this limitation has been reached, other species may take over; see level 5 and 6 in Table 1. It implies that not only the processes and the components, but also the feedbacks can be replaced, if it is needed to achieve a better utilization of the available resources.

*An ecosystem is a very dynamic system. All its components and particularly the biological ones are steadily moving and their properties are steadily modified,* which is why an ecosystem will never return to the same situation again.

Every point is furthermore different from any other point and therefore offering different conditions for the various life forms. This enormous heterogeneity explains why there are so many species on earth. There is, so to say, an ecological niche for ‘everyone’ and ‘everyone’ may be able to find a niche where he is best fitted to utilize the resources.

Margalef [13, 14] claims that ecosystems are anisotropic, meaning that they exhibit properties with different values, when measured along axes in different directions. It means that the ecosystem is not homogeneous in relation to properties concerning matter, energy and information and that the entire dynamics of the ecosystem works towards increasing the differences.

These variations in time and space make it particularly difficult to model ecosystems and to capture the essential features of ecosystems.

*Ecosystems and their biological components, the species, evolve steadily and in the long-term perspective towards higher complexity.*

Darwin’s theory describes the competition among species and states that the species that are best fitted to the prevailing conditions in the ecosystem will survive. Darwin’s theory can, in other words, describe the changes in ecological structure and the species composition, but cannot directly be applied quantitatively, e.g. in ecological modelling; see, however, the next section.

All species in an ecosystem are confronted with the challenge: how is it possible to survive or even grow under the prevailing conditions? The prevailing conditions are considered as all factors influencing the species, i.e. all external and internal factors including those originating from other species. This explains the co-evolution, as any change in the properties of one species will influence the evolution of the other species.

All natural external and internal factors of ecosystems are dynamic – the conditions are steadily changing and there are always many species waiting in the wings, ready to take over, if they are better fitted to the emerging conditions than the species dominating under the present conditions. There is a wide spectrum of species representing different combinations of properties available for the ecosystem. The question is which of these species are best able to survive and grow under the present conditions and which are best able to survive and grow under the conditions one time-step further and two time-steps further and so on? The necessity in Monod’s sense is given by the prevailing conditions – the species must have genes or maybe rather phenotypes (meaning properties) that match these conditions, to be able to survive. But the natural external factors and the genetic pool available for the test may change randomly or by ‘chance’.

Steadily, new mutations (misprints are produced accidentally) and sexual re-combinations (the genes are mixed and shuffled) emerge and give steadily new material to be tested by the question: which species are best fitted under the conditions prevailing just now?

These ideas are illustrated in Fig. 1. The external factors are steadily changed and some even relatively fast – partly at random, such as the meteorological or climatic factors. The species of the system are selected among the species available and represented by the genetic pool, which
again is slowly, but surely changed randomly or by ‘chance’. The selection in Fig. 1 includes the level 4 of Table 1. It is a selection of the organisms that possess the properties best fitted to the prevailing organisms according to the frequency distribution. What is named ecological development is the changes over time in nature caused by the dynamics of the external factors, giving the system sufficient time for the reactions.

Evolution, on the other hand, is related to the genetic pool. It is the result of the relationship between the dynamics of the external factors and the dynamics of the genetic pool. The external factors steadily change the conditions for survival and the genetic pool steadily comes up with new solutions to the problem of survival.

The species are continuously tested against the prevailing conditions (external as well as internal factors) and the better they are fitted, the better they are able to maintain and even increase their biomass. The specific rate of population growth may even be used as a measure for the fitness (see, e.g. Stenseth [15]). But, the property of fitness must, of course, be inheritable to have any effect on the species composition and the ecological structure of the ecosystem in the long run.

Natural selection has been criticized for being a tautology: fitness is measured by survival, and survival of the fittest therefore means survival of the survivors. However, the entire Darwinian theory including the above-mentioned three assumptions, cannot be conceived as a tautology.

**Figure 1:** Conceptualization of how the external factors steadily change the species composition. The possible shifts in species composition are determined by the gene pool, which is steadily changed due to mutations and new sexual re-combinations of genes. The development is, however, more complex. This is indicated (1) by an arrow from ‘structure’ to ‘external factors’ and ‘selection’ to account for the possibility that the species can modify their own environment and thereby their own selection pressure; (2) an arrow from ‘structure’ to ‘gene pool’ to account for the possibilities that the species can, to a certain extent, change their own gene pool. Several mechanisms for this possibility can be found in the literature.
but may be interpreted as follows: the species offer different solutions to survival under given prevailing conditions and the species that have the best combinations of properties to match the conditions also have the highest probability of survival and growth.

*Man-made changes in external factors, i.e. anthropogenic pollution, have created new problems, because new genes fitted to these changes do not develop overnight, whereas most natural changes have occurred many times previously and the genetic pool is therefore prepared and fitted to meet the natural changes. The spectrum of genes is able to meet most natural changes, but not all of the man-made changes, because they are new and untested in the ecosystem.*

The evolution moves towards increasing complexity in the long run. The fossil records have shown a steady increase in species diversity. There may be destructive forces – for instance, man-made pollution or natural catastrophes – for a shorter time, but the probability that (1) new and better genes are developed and (2) new ecological niches are utilized will increase with time. The probability will even – again excluding the short time perspective – increase faster and faster, as the probability is roughly proportional to the amount of genetic material on which the mutations and new sexual re-combinations can be developed.

### 3 Structurally dynamic models

If we follow the modelling procedure proposed in Chapter 2, we will attain a model that describes the processes in the focal ecosystem, but the parameters will represent the properties of the state variables as they are in the ecosystem during the examination period. They are not necessarily valid for another period, because we know that an ecosystem can regulate, modify and change them, if needed, as a response to the change in the prevailing conditions, determined by the forcing functions and the interrelations between the state variables. Our present models have rigid structures and a fixed set of parameters, reflecting that no changes or replacements of the components are possible. We need, however, to introduce parameters (properties) that can change according to changing forcing functions and general conditions for the state variables (components) to optimize continuously the ability of the system to move away from thermodynamic equilibrium.

We will try in this section to answer the question: How can we construct models that are able to reflect the characteristics of ecosystems, particularly the adaptability and the possibilities to change the composition of species corresponding to levels 4–6 in Table 1 and as illustrated in Fig. 1 Models that account for the change in species composition as well as for the ability of the species, i.e. the biological components of our models, to change their properties, i.e. to adapt to the prevailing conditions imposed on the species, are called SDM, to indicate that they are able to capture changes structurally. It could be argued that the ability of ecosystems to replace present species with other (level 6 in Table 1), better fitted species can be considered by construction of models that encompass all actual species for the entire period that the model attempts to cover. This approach has, however, two essential disadvantages. The model becomes first of all very complex, as it will contain many state variables for each trophic level. It implies that the model will contain many more parameters that have to be calibrated and validated. It will inevitably introduce a high uncertainty to the model and will render the application of the model very case-specific (see Nielsen [16, 17]). In addition, the model will still be rigid and not give the model the property of the ecosystems of having continuously changing parameters even without changing the species composition (see Fontaine [18]).

The SDMs can be constructed by two different methods: either by expert knowledge or by introduction of a goal function. If it is known how the properties of the species will change when
the prevailing conditions are changed, it is, of course, possible to introduce this knowledge into
the model, which is possible either by formulation of rules or by artificial intelligence. Rules may
be exemplified by this example: when the phosphorus concentration is in the range $x$ to $y$, then
the growth rate of phytoplankton will be changing gradually from $z$ to $v$. For examples of this
type of SDMs, see Patten [19]. Artificial intelligence is able to find the rules from interpretation
by a computer of a suitable set of observations.

Several goal functions have been proposed as shown in Table 2, but only very few models that
account for change in species composition or for the ability of the species to change their proper-
ties within some limits have been developed.

Bossel [20] uses what he calls six basic orientors or requirements to develop a system model
that can describe the system performance properly. The six orientors are:

1. **Existence.** The system environment must not exhibit any conditions, which may move the
state variables out of its safe range.
2. **Efficiency.** The exergy gained from the environment should exceed over time the exergy
expenditure.
3. **Freedom of action.** The system reacts to the inputs (forcing functions) with a certain variability.
4. **Security.** The system has to cope with the different threats to its security requirement
with appropriate but different measures. These measures either aim at internal changes in the
system itself or at particular changes in the forcing functions (external environment).
5. **Adaptability.** If a system cannot escape the threatening influences of its environment, the one
remaining possibility consists in changing the system itself to cope better with the environ-
mental impacts.
6. **Consideration of other systems.** A system must respond to the behaviour of other systems.
The fact that these other systems may be of importance to a particular system may have to be
considered with this requirement.

Bossel [20] applies maximization of a benefit or satisfaction index based on balancing weighted
surplus orientor satisfactions on a common satisfaction scale. The approach is used to select the
model structure of continuous dynamic systems and is able to account for the ecological struc-
tural properties as presented in Fig. 1. The approach seems very promising, but has unfortunately
not been applied to ecological systems except in three cases.

Straskraba [10, 11] uses a maximization of biomass as the governing principle. The model
computes the biomass and adjusts one or more selected parameters to achieve the maximum

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**Table 2: Goal functions proposed.**

<table>
<thead>
<tr>
<th>Proposed for</th>
<th>Objective function</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Several systems</td>
<td>Maximum useful power or energy flow</td>
<td>Lotka [21–23]</td>
</tr>
<tr>
<td>Several systems</td>
<td>Minimum entropy</td>
<td>Glansdorff and Prigogine [25]</td>
</tr>
<tr>
<td>Networks</td>
<td>Maximum ascendancy</td>
<td>Ulanowicz [26]</td>
</tr>
<tr>
<td>Several systems</td>
<td>Maximum exergy</td>
<td>Mejer and Jørgensen [27]</td>
</tr>
<tr>
<td>Ecological systems</td>
<td>Maximum persistent organic matter</td>
<td>O’Neill et al. [28]</td>
</tr>
<tr>
<td>Ecological systems</td>
<td>Maximum biomass</td>
<td>Margalef [13, 14]</td>
</tr>
<tr>
<td>Economic systems</td>
<td>Maximum profit</td>
<td>Various authors</td>
</tr>
</tbody>
</table>
biomass at every instance. The model has a routine, which computes the biomass for all possible combinations of parameters within a given realistic range. The combination that gives the maximum biomass is selected for the next time step and so on.

Eco-exergy has successfully been used to develop SDM in 17 cases (see Jørgensen [29–33]) and as a holistic ecological indicator (see Jørgensen [29–33]). As eco-exergy is not generally known, it is necessary here to introduce this thermodynamic variable. Exergy is defined as the work capacity the system can perform when brought into thermodynamic equilibrium with the environment.

This form of exergy we will name here technological exergy. Technological exergy is not practical to use in the ecosystem context, because it presumes that the environment is the reference state, which means for an ecosystem the next ecosystem. As the energy embodied in the organic components and the biological structure and information contributes far most to the exergy content of an ecosystem, there seems to be no reason to assume a (minor) temperature and pressure difference between the ecosystem and the reference environment. Eco-exergy is defined as the work the ecosystem can perform relative to the same ecosystem at the same temperature and pressure, but at thermodynamic equilibrium, where there are no gradients and all components are inorganic at the highest possible oxidation state. Under these circumstances, we can calculate the exergy, which has been denoted eco-exergy to distinguish from the technological exergy, as coming entirely from the chemical energy:

\[
\sum_c (\mu_c - \mu_{co}) N_c. \tag{1}
\]

This represents the non-flow biochemical exergy. We can measure the concentrations in the ecosystem, but the concentrations in the reference state (thermodynamic equilibrium) could be based on the usual use of chemical equilibrium constants. Eco-exergy is a concept close to Gibb’s free energy, but opposite Gibb’s free energy, eco-exergy has a different reference state from case to case (from ecosystem to ecosystem) and it can furthermore be used far from thermodynamic equilibrium, while Gibb’s free energy, in accordance with its exact thermodynamic definition, is a state function close to thermodynamic equilibrium. In addition, eco-exergy of organisms is mainly embodied in the information content and should therefore not be considered the same as the chemical energy of fossil fuel.

As \((\mu_c - \mu_{co})\) can be found from the definition of the chemical potential replacing activities with approximations by concentrations, we get the following expressions for the exergy:

\[
Ex = RT \sum_{i=0}^{n} C_i \ln C_i / C_{i,o}, \tag{2}
\]

where \(R\) is the gas constant \((8.317 \, J/K \, mol = 0.08207 \, l \, atm/K \, mol)\), \(T\) is the temperature of the environment, while \(C_i\) is the concentration of the \(i\)th component expressed in a suitable unit. \(C_{i,o}\) is the concentration of the \(i\)th component at thermodynamic equilibrium and \(n\) is the number of components. \(C_{i,o}\) is, of course, a very small concentration (except for \(i = 0\), which is considered to cover the inorganic compounds), corresponding to a very low probability of forming complex organic compounds spontaneously in an inorganic soup at thermodynamic equilibrium. \(C_{i,o}\) is even lower for the various organisms, because the probability of forming the organisms is very low with their embodied information, which implies that the genetic code should be correct.

By using this particular exergy based on the same system at thermodynamic equilibrium as reference, the eco-exergy becomes dependent only on the chemical potential of the numerous biochemical components.
It is possible to distinguish in eqn (1) between the contribution to the eco-exergy from the information and from the biomass. We define $p_i$ as $c_i/A$, where

$$A = \sum_{i=1}^{n} c_i$$

is the total amount of matter density in the system. With introduction of this new variable, we get:

$$Ex = ART \sum_{i=0}^{n} \ln p_i / p_{io} + A \ln A/A_o.$$  \hspace{1cm} (3)

As $A = A_o$, eco-exergy becomes a product of the total biomass $A$ (multiplied by $RT$) and Kullback measure:

$$K = \sum_{i=0}^{n} p_i \ln p_i / p_{io}.$$  \hspace{1cm} (4)

where $p_i$ and $p_{io}$ are probability distributions $a$ posteriori and $a$ priori, respectively, to an observation of the molecular detail of the system. It means that $K$ expresses the amount of information that is gained as a result of the observations. For different organisms that contribute to the eco-exergy of the ecosystem, the eco-exergy density becomes $cRT \ln(p_i/p_{io})$, where $c$ is the concentration of the considered organism. $RT \ln(p_i/p_{io})$, denoted $\beta$, is found by calculation of the probability to form the considered organism at thermodynamic equilibrium, which would require that organic matter is formed and that the proteins (enzymes) controlling the life processes in the considered organism have the right amino acid sequence. These calculations can be seen in Jørgensen et al. [29] and Jørgensen and Svirezhev [30] and Jørgensen and Fath [31]. In the [31], the latest information about the $\beta$-values for various organisms is presented; see Table 3. The $\beta$-value for detritus is in this table = 1.00, which means that the eco-exergy is found as g detritus equivalents. As detritus has about 18.7 kJ/g, eco-xergy can be found as kJ by multiplication by 18.7. For human, the $\beta$-value is 2173, when the eco-exergy is expressed in detritus equivalent or 18.7 times as much or 40635 kJ/g if the eco-exergy should be expressed as kJ and the concentration unit g/unit of volume or area. The $\beta$-value has not surprisingly increased as a result of the evolution. To mention a few $\beta$-values from Table 3: bacteria 8.5, protozoa 39, flatworms 120, ants 167, crustaceans 232, molluscs 310, fish 499, reptiles 833, birds 980 and mammals 2127.

The evolution has, in other words, resulted in a more and more effective transfer of what we could call the classical work capacity to the work capacity of the information. A $\beta$-value of 2.0 means that the eco-exergy embodied in the organic matter and the information are equal. As the $\beta$-values; see above are much bigger than 2.0 (except for virus, where the $\beta$-value is 1.01 – slightly more than 1.0) the information eco-exergy is the most significant part of the eco-exergy of organisms.

Biological systems have many possibilities for moving away from thermodynamic equilibrium, and it is important to know along which pathways among the possible ones a system will develop. This leads to the following hypothesis sometimes denoted the ecological law of thermodynamic (see Jørgensen and Mejer [32, 33], Jørgensen [8, 9],] Jørgensen and Fath [31, 34] and Fath et al. [35]): If a system receives an input of exergy, then it will utilize this exergy to perform work. The work performed is first applied to maintain the system (far) away from thermodynamic equilibrium whereby exergy is lost by transformation into heat at the temperature of the environment. If more exergy is available, then the system is moved further away from thermodynamic
Table 3: The b-values.

<table>
<thead>
<tr>
<th>Early organisms</th>
<th>Plants</th>
<th>Animals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Detritus</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>Virus</td>
<td>1.01</td>
<td></td>
</tr>
<tr>
<td>Minimal cell</td>
<td>5.8</td>
<td></td>
</tr>
<tr>
<td>bacteria</td>
<td>8.5</td>
<td></td>
</tr>
<tr>
<td>Archaea</td>
<td>13.8</td>
<td></td>
</tr>
<tr>
<td>Protists</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td>Yeast</td>
<td>17.8</td>
<td></td>
</tr>
<tr>
<td>Detritus</td>
<td>33</td>
<td>Mesozoa, Placozoa</td>
</tr>
<tr>
<td>Virus</td>
<td>39</td>
<td>Protozoa, amoeba</td>
</tr>
<tr>
<td>Minimal cell</td>
<td>43</td>
<td>Phasmida (stick insects)</td>
</tr>
<tr>
<td>bacteria</td>
<td>61</td>
<td></td>
</tr>
<tr>
<td>Archaea</td>
<td>76</td>
<td></td>
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<tr>
<td>Protists</td>
<td>91</td>
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<td>Algae</td>
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<td>Yeast</td>
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<tr>
<td>Fungi, moulds</td>
<td>109</td>
<td>Brachiopoda</td>
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<td></td>
<td>120</td>
<td>Platyhelminthes (flatworms)</td>
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<td></td>
<td>133</td>
<td>Nematoda (round worms)</td>
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<td>133</td>
<td>Annelida (leeches)</td>
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<td></td>
<td>143</td>
<td>Gnaostomulida</td>
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<td>Rhodophyta</td>
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<tr>
<td>Prolifera, sponges</td>
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<td>Kinorhyncha</td>
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<td>Mustard weed</td>
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<tr>
<td>Seedless vascular plants (incl. ferns)</td>
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<td></td>
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<td></td>
<td>163</td>
<td>Rotifera (wheel animals)</td>
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<td></td>
<td>164</td>
<td>Entoprocta</td>
</tr>
<tr>
<td>Moss</td>
<td>174</td>
<td></td>
</tr>
<tr>
<td>Rice</td>
<td>175</td>
<td></td>
</tr>
<tr>
<td>Gynosperms (incl. pinus)</td>
<td>314</td>
<td></td>
</tr>
<tr>
<td></td>
<td>310</td>
<td>Mollusca, bivalvia, gastropodea</td>
</tr>
<tr>
<td></td>
<td>322</td>
<td>Mosquito</td>
</tr>
<tr>
<td>Flowering plants</td>
<td>393</td>
<td></td>
</tr>
<tr>
<td></td>
<td>499</td>
<td>Fish</td>
</tr>
<tr>
<td></td>
<td>688</td>
<td>Amphibia</td>
</tr>
<tr>
<td></td>
<td>833</td>
<td>Reptilia</td>
</tr>
<tr>
<td></td>
<td>980</td>
<td>Aves (Birds)</td>
</tr>
<tr>
<td></td>
<td>2127</td>
<td>Mammalia</td>
</tr>
<tr>
<td></td>
<td>2138</td>
<td>Monkeys</td>
</tr>
<tr>
<td></td>
<td>2145</td>
<td>Anthropoid apes</td>
</tr>
<tr>
<td></td>
<td>2173</td>
<td>Homo Sapiens</td>
</tr>
</tbody>
</table>

equilibrium, reflected in growth of gradients. If there is offered more than one pathway to depart from equilibrium, then the one yielding the highest eco-exergy storage (denoted Ex) will tend to be selected. Or expressed differently: Among the many ways for ecosystems to move away from thermodynamic equilibrium, the one maximizing dEx/dt under the prevailing conditions will have a propensity to be selected.

This hypothesis can be considered a translation of Darwin’s theory into thermodynamics. It is supported by several ecological observations and case studies (see Jørgensen and Svirezhev [30] and Jørgensen and Fath [34]). Survival implies maintenance of the biomass and growth means increase of biomass and information. It costs exergy to construct biomass and gain information and biomass and information possess therefore exergy. Survival and growth can therefore be measured by use of the thermodynamic concept eco-exergy, which may be understood as the work capacity the ecosystem possesses.

The idea of SDMs is to find continuously a new set of parameters (limited for practical reasons to the most crucial, i.e. sensitive parameters) that is better fitted for the prevailing conditions of...
the ecosystem. ‘Fitted’ is defined in the Darwinian sense by the ability of the species to survive and grow, which may be measured as discussed above by eco-exergy. Figure 2 shows the proposed modelling procedure, which has been applied in the development of totally 17 SDMs.

For all SDMs developed with eco-exergy as the goal function, the changes obtained were in accordance with actual observations. At least in models, the applicability of the eco-exergy calculations has shown their more practical use, which can possibly be explained by a robustness in the model calculations. It is noteworthy that Coffaro et al. [36], in his structural-dynamic model of the Lagoon of Venice, did not calibrate the model describing the spatial pattern of various macrophyte species such as Ulva and Zostera, but used exergy-index optimization to estimate parameters determining the spatial distribution of these species. He found good accordance between observations and model, as was able by this method without calibration, to explain more than 90% of the observed spatial distribution of various species of Zostera and Ulva.

Figure 2: The procedure used for the development of structurally dynamic models, reproduced from [1].
Figure 3 illustrates the theoretical considerations behind the development of a SDM with eco-exergy as the goal function.

Application of SDM is, of course, more cumbersome than other models due to the eco-exergy optimization that takes place every 5–30 days, but with a modern fast computer, the additional computation is limited. The advantage of SDM is clearly that eventually structurally dynamic changes are considered and if that is the case, an SDM will inevitably give a more accurate result. It may also be needed to use SDM for the calibration, because changes in, for instance, phytoplankton composition from spring to summer to autumn may imply that different parameters should be applied in the different seasons. The conclusion is therefore that it is recommended to use SDM whenever it is known or even suspected that structurally changes will take place. SDM requires, however, good observations, in most cases also of some structural changes to give acceptable results. An SDM will not necessarily be more expensive to develop than other models, but the need for good observations and a good data set will often make the entire project more expensive.

As mentioned above, eco-exergy has been applied to develop SDM in 17 cases; see Jørgensen [7–9]. The 17 case studies are nine eutrophication models of six different lakes, a model to explain the success and failure of biomanipulation based on removal of planktivorous fish, a model to explain under which circumstances submerged vegetation and phytoplankton are dominant in shallow lakes, three small population dynamic models, a eutrophication model of The Lagoon of Venice and the Mondego Estuary. The last two case studies are presented below as illustrations of structurally dynamic modelling.
4 Development of SDM for Darwin’s finches

The development of a structurally dynamic model for Darwin’s finches was published in Jørgensen and Fath [31]. The model reflects – as all models – the available knowledge, which, in this case, is comprehensive and sufficient to validate even the ability of the model to describe the changes in the beak size as a result of climatic changes, causing changes in the amount, availability and quality of the seeds that make up the main food item for the finches. The medium ground finches, Geospiza fortis, on the island Daphne Major were selected for these modelling case due to very detailed case specific information found in Grant [37]. The model has three state variables: seed, Darwin’s Finches adult and Darwin’s finches juvenile. The juvenile finches are promoted to adult finches 120 days after birth. The mortality of the adult finches is expressed as a normal mortality rate + an additional mortality rate due to food shortage and an additional mortality rate caused by a disagreement between bill depth and the size and hardness of seeds.

The beak depth can vary between 3.5 and 10.3 cm as pointed out by Grant [37]. The beak size = $\sqrt{DH}$, where $D$ is the seed size and $H$ the seed hardness which are both dependent on the precipitation, particularly in the months of January–April [37]. It is possible to determine a handling time for the finches for a given $\sqrt{DH}$ as function of the bill depth [37], which explains that the accordance between $\sqrt{DH}$ and the beak depth becomes an important survival factor. The relationship is used in the model to find a function called ‘diet’, which is compared with $\sqrt{DH}$ to find how well the bill depth fits to the $\sqrt{DH}$ of the seed. This fitness function is based on information given by Grant [37] about the handling time. It influences, as mentioned above, the mortality of adult finches, but has also impact on the number of eggs laid and the mortality of the juvenile finches. The growth rate and mortality of seeds are dependent on the precipitation, which is a forcing function known as function of time. A function called shortage of food is calculated from the food required for the finches, which is known [37], and from the food available (the seed state variable). The food shortage influences the mortality of juvenile finches and adult finches can be found in Grant [37]. The seed biomass and the number of G. fortis as function of time from 1975 to 1982 are known according to Grant [37]. These numbers from 1975 to 1976 have been used to calibrate the following parameters:

1. The influence of the fitness function on (a) the mortality of adult finches, (b) the mortality of juvenile finches and (c) the number of eggs laid.
2. The influence of food shortage on the mortality of adult and juvenile finches is known [37]. The influence is therefore calibrated within a narrow range of values.
3. The influence of precipitation on the seed biomass (growth and mortality).

All other parameters are known from the literature.

The exergy density is calculated (estimated) as $275 \times \text{the concentration of seed} + 980 \times \text{the concentration of Darwin’s finches}$ (see Table 3). Every 15 days, it is found if a feasible change in the beak size taken the generation time and the variations in the beak size into consideration will give a higher exergy. If it is the case, then the beak size is changed accordingly. The modelled changes in the beak size were confirmed by the observations. The model results of the number of Darwin’s finches are compared with the observations in Fig. 4. The standard deviation between modelled and observed values was 11.6% and the correlation coefficient $r^2$ for modelled versus observed values is 0.977. The results of a non-structural dynamic model would not be able to predict the changes in the beak size and would therefore give too low values for the number of Darwin’s finches because their beak would not adapt to the lower precipitation yielding harder and bigger seeds.
5 Model of the ectoparasite–bird interactions

Ectoparasites use in their interactions with birds, a relatively high initial, but thereafter decreasing mortality; see Tripet and Richner [38]. The results are also consistent with what is found by other parasite observations by Tripet and Richner [38]. Why do ectoparasites use this strategy? It can be shown by an SDM that the strategy is consistent with an optimization of eco-exergy for the parasites.

The model has three state variables: number of birds (hosts), number of parasites and weight of parasites.

The differential equations of the state variables are:

\[
d_{\text{bird}}/dt = -\text{mortality} \\
d_{\text{parasites}}/dt = -\text{mortality of parasites} \\
d_{\text{weight}}/dt = \text{growth rate}
\]

The model follows over one season, let us say 120 days, the survival of a number of birds that have been infected by ectoparasites. Therefore, the number of birds and ectoparasites are decreasing steadily, while the ectoparasites are growing – the weight is increasing for the

Figure 4: The observed number of finches (●) from 1973 to 1983, compared with the simulated result (○). The numbers from 1975 and 1976 were used for calibration and from 1977/1978 for the validation.
individual ectoparasites over time. The ectoparasites use a strategy whereby they obtain the
highest survival, which is also or at least close to the highest survival of the host, because the
survival of the ectoparasites is dependent on the survival of the host. On the other side, the host
will inevitably reduce the probability of survival due to the presence of the ectoparasites. The
ectoparasites find a balance, which can be shown to correspond to a relatively high initial, but
thereafter decreasing mortality of the parasites. By using a structurally dynamic model with eco-
exergy of the parasites as model goal function, it should be possible to find the optimum strategy
of the growth rate and the mortality rate of the ectoparasites.

The eco-exergy is calculated as contribution of eco-exergy from the birds and contribution of
eco-exergy from the parasites. The contribution of eco-exergy from the birds is

\[
\text{Eco-exergy of birds} = \text{birds} \times 20 \times 980,
\]

corresponding to the weight (20 g) and the information content factor 980 (see Table 3) and the
contribution of eco-exergy from the parasites is

\[
\text{Eco-exergy of the parasites} = \text{number of parasites} \times \text{weight of parasites} \times 167,
\]

where 167 is the information content factor for the parasites (see again Table 3).

Total eco-exergy = eco-exergy of the birds + eco-exergy of the parasites.

Figure 5 gives that conceptual diagram using the symbols of the STELLA software.

From the differential equations, it can be seen that there are three processes. They are formulated by using the following equations:

\[
\text{Mortality (birds)} = \text{bird mortality coefficient} \times \text{number of parasites} \\
\times \text{weight of parasites} \times \text{number of birds}
\]

\[
\text{Mortality parasites} = 0.025 \times \text{mortality coefficient} \\
\times \text{number of parasites}/(\text{number of birds} + 1)^{0.3}
\]

\[
\text{Growth rate (of parasites)} = (\text{basic growth rate} + \text{growth rate increase}) \\
\times (1 – \text{weight}/\text{max. weight}).
\]

Before it is possible to run the model, it is necessary to select the initial values of the state
variables, the parameters and the initial value of the two parameters that are presumed functions
of the time.

The model has been developed in a C++ program. STELLA is not able to make a current opti-
mization of a goal function. It cannot be excluded that some parameter combinations will not
give feasible results. Therefore, it is recommendable to use the default values (ranges and default
values; see Table 4) when it is the intention to illustrate the possibilities of the structurally
dynamic modelling approach.

It is recommended to run the model simulation for a period of 60–180 days, for instance,
120 days equal to 4 months. When the structurally dynamic model approach is applied, the
model will stop every x days, where the user can select x between 5 and 20 days. Two parameters
namely mortality coefficient of the parasites and the growth rate increase of parasites
are functions of the time. When the model is stopped every x days, all combinations of the
present mortality coefficient + and −0.02 and the present growth rate increase + and −0.001,
totally nine combinations, are tested for the next x days and the combination giving the high-
est total eco-exergy after the x days is selected and so on. The variation in the two variable
parameters will be shown by the developed model software as a result of this structural
dynamic calibration.
Table 4: Parameters and initial values of the state variables.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Possible range</th>
<th>Default value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial number of birds</td>
<td>50–10000</td>
<td>100</td>
</tr>
<tr>
<td>Initial number of parasites</td>
<td>100–1000</td>
<td>240</td>
</tr>
<tr>
<td>Initial values of weight (g)</td>
<td>0.001–0.2</td>
<td>0.02</td>
</tr>
<tr>
<td>Bird mortality coefficient</td>
<td>0.000001–0.001</td>
<td>0.00001</td>
</tr>
<tr>
<td>Initial value of mortality coefficient</td>
<td>0.005–1.0</td>
<td>0.5</td>
</tr>
<tr>
<td>Basic growth rate</td>
<td>0.0001–0.1</td>
<td>0.005</td>
</tr>
<tr>
<td>Growth rate increase, initial value</td>
<td>–0.01 to +0.05</td>
<td>0.001</td>
</tr>
<tr>
<td>Max weight</td>
<td>0.05–0.3</td>
<td>0.12</td>
</tr>
</tbody>
</table>

Figure 5: The conceptual diagram of the model, using the symbols of the STELLA software. The model has been developed in C++ because STELLA is not able to optimize a goal function – in this case, exergy. The C++ model is available on the enclosed CD.
The model results are the three state variables and the eco-exergy of the birds, the eco-exergy of parasites, which are applied for the optimization and the total eco-exergy. All variables are indicated by the software available on the CD as function of time, using both graphs and tables.

Run the model for instance with an initial mortality of 0.5 \(1/24\) h and the structurally dynamic model will show a stepwise decrease in the mortality and a stepwise increase in the growth rate. Let us say that the optimization was carried out every 10 days, it means totally 12 times. The mortality will then decrease from the initial value, 0.5 \(1/24\) h, to 0.26 \(1/24\) h, on average, 0.38 \(1/24\) h. Compare the final eco-exergy of the birds, of the parasites and the total eco-exergy with the non-structurally dynamic case, where an average mortality (in our example 0.38 \(1/24\) h) and average growth rate are used. The comparison will show that the structurally dynamic case is resulting in higher eco-exergy values. The strategy to start at a higher but decreasing mortality and a lower but increasing growth rate is beneficial for the parasites.

It is, of course, possible to apply different mortality and growth rates and they will all give higher total eco-exergy for the structurally dynamic approach compared with the constant parameter case. Figure 6 illustrates the results of several model runs, using different initial values for the mortality rate.

References


Jørgensen, S.E., Use of models as experimental tools to show that structural changes are accompanied by increased exergy. *Ecological Modelling*, 41, pp. 117–126, 1988.


