

The Application of Structurally Dynamic Models in Ecology and Ecotoxicology

Sven E. Jørgensen

Abstract Structurally dynamic models (SDMs) are models that account for the changes in the model parameters due to the adaptation or the shift in species composition resulting from current changes in the forcing functions. The parameter changes are found by introduction of eco-exergy as goal function in the model. The set of parameters that give the highest eco-exergy by the prevailing conditions are currently selected. The theory behind the use of eco-exergy as goal function in ecological models is presented as a translation of Darwin's theory to thermodynamics. Two examples of SDMs are presented to illustrate the advantages and disadvantages of this model type.

Keywords Structurally dynamic models · Adaptation · Shifts in species composition · Exergy · Eco-exergy · Darwin finches · Copper

1 Introduction

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 modeling is, therefore, how can we construct models that are able to account for this enormous adaptability. The model type *structurally dynamic model* (SDM) has been developed to meet this demand. The next section will present the characteristics, the advantages, and the disadvantages of this model type and where it is most recommendable to consider to apply SDM. The following section, Sect. 3, presents the theory behind SDM, followed by a section where an illustrative example of SDMs applied in ecology is presented. The example shows clearly the idea behind this model type and under which circumstances it is advantageous to use it. The fifth section presents an ecotoxicological example and the last section concludes on the application of SDM in ecology and particularly in ecotoxicology.

S.E. Jørgensen (✉)

Section for Environmental Chemistry, Institute A, Copenhagen University, University Park 2,
2100 Copenhagen Ø, Denmark
e-mail: msijapan@hotmail.com

This model type will most probably be used increasingly in the coming years in our endeavor 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 SDMs attempt to overcome this crucial model problem.

Ecology deals with irreducible systems with many feedback mechanisms that will regulate simultaneously all the factors and rates, and they interact and are also functions of time, too, as pointed out by Straskraba [1, 2].

Table 1 shows the hierarchy of regulation mechanisms that are operating at the same time. 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 in nature from that in a laboratory where the examined components are separated from the other ecosystem components.

Known phrases in system ecology are “everything is linked to everything” and “the whole is greater than the sum of the parts.” It implies that it may be possible to examine the parts separately, but when the parts are put together, they will form a whole that behaves differently from the sum of the parts. A model seems the only useful tool when we are dealing with irreducible systems. However, we need several models simultaneously to capture a more complete image of reality. It seems our only possibility to deal with the very complex living systems. Our brain simply cannot overview what will happen in a system where, for instance, several interacting processes are working simultaneously.

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

Table 1 The hierarchy of regulating feedback mechanisms [3]

Level	Explanation of regulation process	Exemplified by phytoplankton growth
1	Rate by concentration in medium	Uptake of phosphorus in accordance with phosphorus concentration
2	Rate by needs	Uptake of phosphorus in accordance with intracellular concentration
3	Rate by other external factors	Chlorophyll concentration in accordance with previous solar radiation
4	Adaptation of properties	Change of optimal temperature for growth
5	Selection of other species	Shift to better-fitted species
6	Selection of other food web	Shift to better-fitted food web
7	Mutations, new sexual recombinations, and other shifts of genes	Emergence of new species or shifts of species properties

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 different 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, that is, 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 levels 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.

2 The Characteristics of SDM

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.

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 (example given) in ecological modeling; 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, that is, all external and internal factors including those originating from 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 species are best able to survive and grow under the conditions one time step further and two time steps further and so on? The necessity

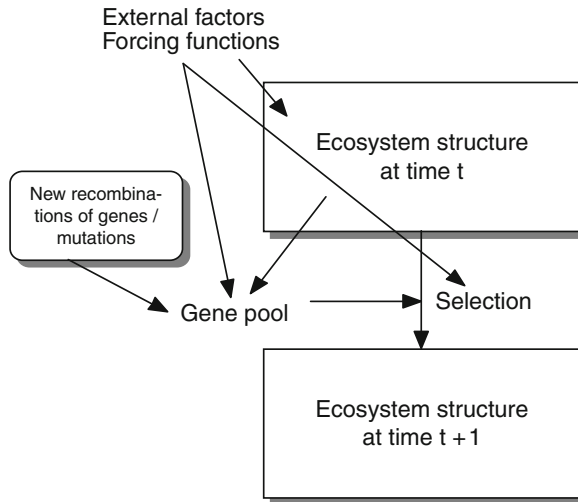


Fig. 1 Conceptualization of how the external factors steadily change the species composition. The possible shifts in species composition are determined by the gene pool, which is steadily changed due to mutations and new sexual recombinations of genes. The development is, however, more complex. This is indicated (1) by *arrows* 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 and (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

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 recombinations (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 the 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 change 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 relation 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 [4]). 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 aforementioned three assumptions cannot be conceived as a tautology, 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 have also the highest probability of survival and growth.

UNEP has developed two SDMs of lakes, which are directly accessible. Pamolare launched by UNEP can be downloaded from the homepage: <http://www.unep.or.jp/ietc/pamolare>. Pamolare 1 contains the following lake models: a one-layer model, a two-layer model, a SDM, and a drainage area model. Pamolare 2 contains a structurally dynamic shallow-lake model.

The use of SDM has particular interest in ecotoxicology, because the competing organisms have most often very different susceptibility to various toxic substances. Therefore, a clear selection of the fittest species in an ecotoxicological case study is, therefore, frequently observed.

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 expert 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 between x and y , then the growth rate of phytoplankton will be changing gradually from z to v . Examples of this type of SDMs are given in Patten [5]. 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, but only very few models that account for change in species composition or for the ability of the species to change their properties within some limits have been developed. Eco-exergy has been the most frequently applied goal function in SDM. It has successfully been used to develop SDMs in 19 cases; see Jørgensen and coworkers [6, 7]. As eco-exergy is not generally known it is necessary to introduce this thermodynamic variable in the next section.

3 Eco-Exergy as Goal Function in SDM

Exergy is defined as the work capacity the system can perform when brought into thermodynamic equilibrium with the environment.

We will name this form of exergy here as 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 relatively 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 as eco-exergy to distinguish from the technological exergy, as coming entirely from the chemical energy:

$$\sum_c (\mu_c - \mu_{co}) N_i.$$

This represents the nonflow 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 to 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 to 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:

$$\text{Ex} = RT \sum_{i=0}^{i=n} C_i \ln C_i / C_{i,0}, \quad (1)$$

where R is the gas constant ($8.317 \text{ J/K/moles} = 0.082071 \text{ atm/K/moles}$), T is the temperature of the environment, while C_i is the concentration of the i th component expressed in a suitable unit, $C_{i,0}$ is the concentration of the i th component at thermodynamic equilibrium, and n is the number of components. $C_{i,0}$ 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. $C_{i,0}$ 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 (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 is the total concentration of all components in the system.

With the introduction of this new variable, we get

$$\text{Ex} = ART \sum_{i=1}^n p_i \ln p_i/p_{i0} + A \ln A/A. \quad (2)$$

As $A \approx A_0$, eco-exergy becomes a product of the total concentration A (multiplied by RT) and Kullback measure:

$$K = \sum_{i=1}^n p_i \ln(p_i/p_{i0}),$$

where p_i and p_{i0} are probability distributions, a posteriori and a priori 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 and that eco-exergy = $ARTK$. For different organisms that contribute to the eco-exergy of the ecosystem, the eco-exergy density contribution becomes $c_i RT \ln(p_i/p_{i0})$, where c_i is the concentration of the considered organism. $RT \ln(p_i/p_{i0})$, 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. [8] and Jørgensen and Svirezhev [6], and Jørgensen and Fath [9]. In the latter reference the latest information about the calculations of RTK that denoted β values for various organisms is presented; see Table 1. The β value for detritus is in this table = 1.00, which means that the eco-exergy density is found by multiplication of the concentration c_i by β as g detritus equivalents per unit of volume or area. As detritus has about 18.7 kJ/g, eco-exergy can be found as kJ by multiplication by 18.7. For human, the β value is 2,173, when the eco-exergy is expressed in detritus equivalent or 18.7 times as much or 40,635 kJ/unit of volume or area. The β value has not surprisingly increased as a result of the evolution. To mention a few values from Table 2: bacteria 8.5, protozoa 39, flatworms 120, ants 167, crustaceans 232, mollusks 310, fish 499, reptiles 833, birds 980, and mammals 2,127.

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 value of 2.0 means that the eco-exergy embodied in the organic matter and the information is equal. As the values are much bigger than 2.0 (except for virus, where the 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 as the ecological law of thermodynamics (ELT) [6–12]: If a system receives an input of exergy, then it will utilize this exergy to perform work.

Table 2 β Values = exergy content relatively to the exergy of detritus [6]

Early organisms	Plants	Animals
Detritus		1.00
Virus		1.01
Minimal cell		5.8
Bacteria		8.5
Archaea		13.8
Protists	Algae	20
Yeast		17.8
		33 Mesozoa, Placozoa
		39 Protozoa, amoeba
		43 Phasmida (stick insects)
Fungi, moulds		61
		76 Nemertina
		91 Cnidaria (corals, sea anemones, jelly fish)
	Rhodophyta	92
		97 Gastrotricha
Prolifera, sponges		98
		109 Brachiopoda
		120 Platyhelminthes (flatworms)
		133 Nematoda (round worms)
		133 Annelida (leeches)
		143 Gnathostomulida
	Mustard weed	143
		165 Kinorhyncha
	Seedless vascular plants	158
		163 Rotifera (wheel animals)
		164 Entoprocta
	Moss	174
		167 Insecta (beetles, fruit flies, bees, wasps, bugs, ants)
		191 Coleodidea (sea squirt)
		221 Lepidoptera (butterflies)
		232 Crustaceans, Mollusca, bivalvia, gastropoda
		246 Chordata
	Rice	275
	Gynosperms (including pinus)	314
		322 Mosquito
	Flowering plants	393
		499 Fish
		688 Amphibia
		833 Reptilia
		980 Aves (birds)
		2,127 Mammalia
		2,138 Monkeys
		2,145 Anthropoid apes
		2,173 <i>Homo sapiens</i>

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 equilibrium, which is reflected in growth of gradients. If more than one pathway to depart from equilibrium is offered, 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 [3,6,7]. Survival implies maintenance of the biomass, and growth means increase of biomass and information. It costs eco-exergy to construct biomass and gain information, and therefore biomass and information possess eco-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.

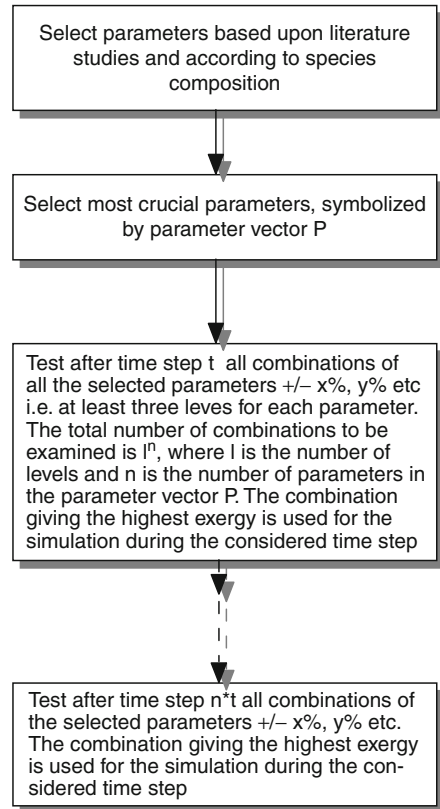
The idea of SDMs is to find continuously a new set of parameters (limited for practical reasons to the most crucial, i.e., sensitive parameters) that is better fitted for the prevailing conditions of the ecosystem. "Fitted" is defined in the Darwinian sense by the ability of the species to survive and grow, which may be measured as discussed earlier by eco-exergy. Figure 2 shows the proposed modeling procedure, which has been applied in the development of totally 19 SDMs.

For all SDMs developed with eco-exergy as the goal function, the changes obtained by the model 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 be explained by a robustness in the model calculations by the use of the β values that, of course, have uncertainties. It is noteworthy that Coffaro et al. [14], in their 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. They 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 3 illustrates the theoretical considerations behind the development of a SDM with eco-exergy as the goal function.

SDM is, of course, more cumbersome to apply than other models due to the eco-exergy optimization, which, for instance, may take place in the model every 5–30 days, but with a modern fast computer the additional computation is, of course, limited. The advantage of SDM is clearly that eventually structurally dynamic changes are considered and if that is the case, a 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 fall 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

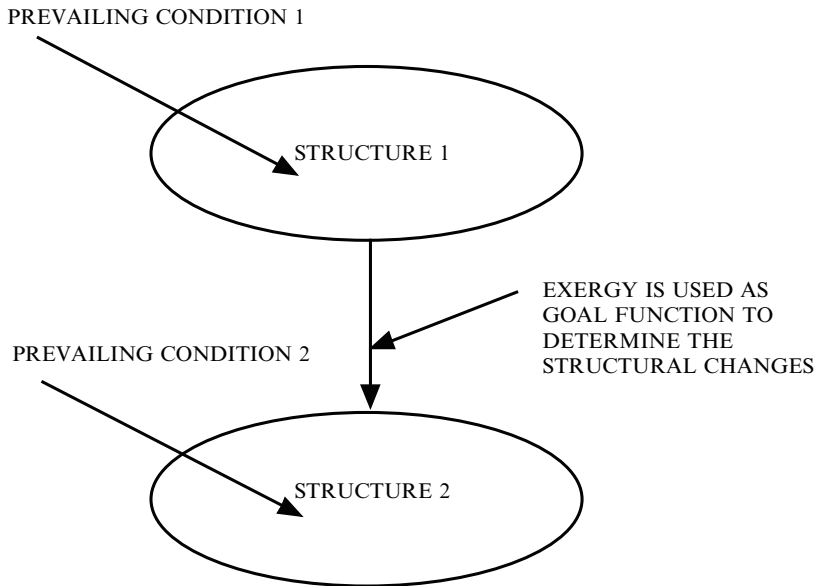
Fig. 2 The procedure used for the development of structurally dynamic models (reproduced from [13])



observations, in most cases also of some structural changes to give acceptable results. A 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.

4 An Illustrative SDM Example

The SDM of Darwin's finches by Jørgensen and Fath [7] is presented later as an illustrative example of SDM. The models reflect therefore – 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 this modeling case due to very detailed case-specific information found by Grant [15]. The model has three state variables: seed, Darwin's Finches adult, and Darwin's finches juvenile.



The structure is changed because the prevailing conditions are changed and adaptation and / or shifts in species composition can offer a better possibility for survival in the Darwinian sense. Survival is measured as biomass and information . Exergy (eco-exergy / work capacity) can therefore be used as goal function

Fig. 3 The theoretical considerations behind SDMs developed with eco-exergy as the goal function are illustrated

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 [15] + 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 [15] and the beak size = \sqrt{DH} , where D is the seed size and H is the seed hardness, which are both dependent on the precipitation, particularly in the months January to April. It is possible to determine a handling time for the finches for a given \sqrt{DH} as function of the bill depth, 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 in Grant [15] about the handling time. It influences, as mentioned earlier, the mortality of adult finches, but it has also impact on the number of eggs laid and the mortality of the juvenile finches. The growth rate and mortality of seeds is dependent on the precipitation, which is a forcing function known as a function of time. A function called shortage of food is calculated from the food required for the finches, which is

known, and from the food available (the seed state variable). How the food shortage influences the mortality of juvenile finches and adult finches can be found in [15]. The seed biomass and the number of *G. fortis* as a function of time from 1975 to 1982 are known [15]. These numbers from 1975 to 1976 have been used to calibrate the following parameters: the coefficients determining the following:

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. 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 $275 \times$ the concentration of seed + $980 \times$ the concentration of Darwin's finches (see Table 2). Every 15 days it is found if a feasible change in the beak size, taking 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 modeled changes in the beak size were confirmed by the observations. The model results of the number of Darwin's

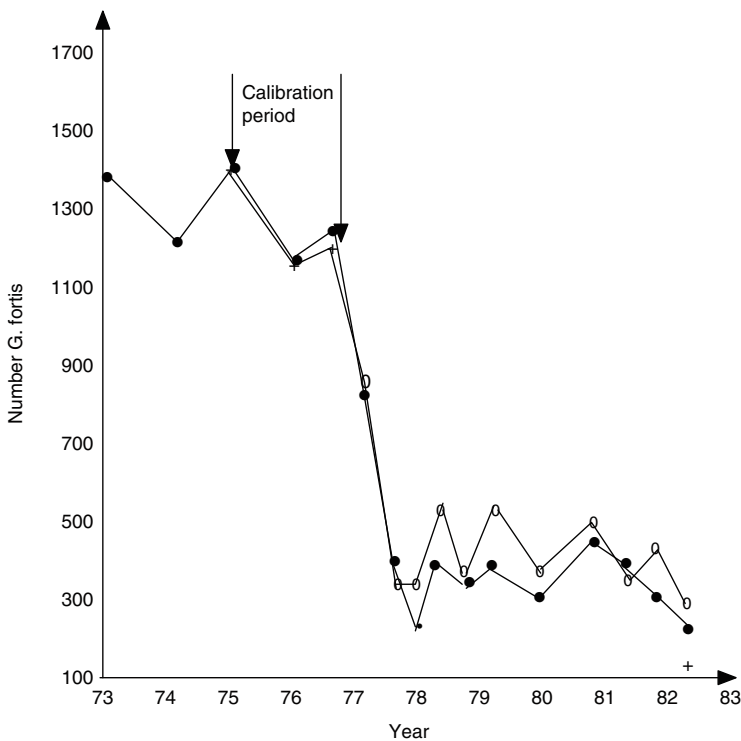


Fig. 4 The observed number of finches (*filled circles*) from 1973 to 1983, compared with the simulated result (*open circles*). 1975 and 1976 were used for calibration and 1977/1978 for the validation

finches are compared with the observations [15] in Fig. 4. The standard deviation between modeled and observed values was 11.6%, and the correlation coefficient, r^2 , for modeled versus observed values is 0.977. The results of a nonstructural dynamic model would not be able to predict the changes in the beak size and would, therefore, give much 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 Ecotoxicological SDM Example

The conceptual diagram of the ecotoxicological model that is used to illustrate SDM is shown in Fig. 5, using the modeling software STELLA. Copper is an algacide causing an increase in the mortality of phytoplankton [16] and a decrease in the phosphorus uptake and photosynthesis [17]. Copper is also reducing the carbon assimilation of bacteria [18]. The literature gives the change of the following three parameters in the model: growth rate of phytoplankton, mortality of phytoplankton,

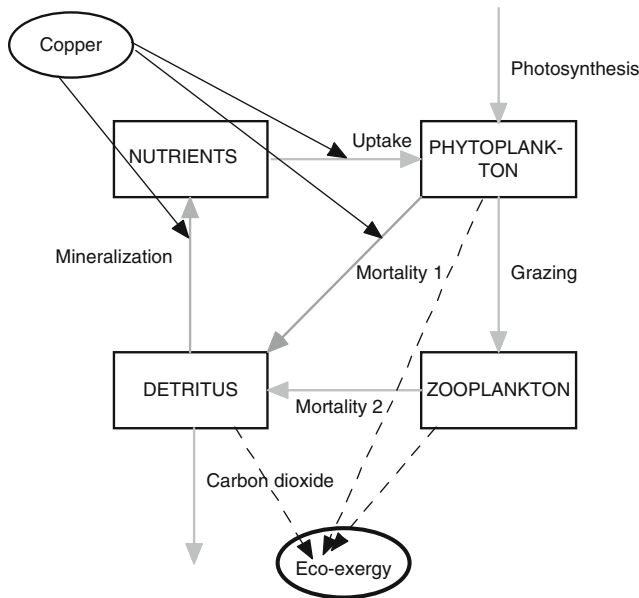


Fig. 5 Conceptual diagram of an ecotoxicological model focusing on the influence of copper on the photosynthetic rate, phytoplankton mortality rate, and the mineralization rate. The boxes are the state variables; the *thick gray arrows* symbolize processes and the *thin black arrows* indicate the influence of copper on the processes and the calculation of eco-exergy from the state variables. Because of the change in these three rates, it is an advantage for the zooplankton and the entire ecosystem to decrease their size. The model is, therefore, made structurally dynamic by allowing zooplankton to change its size and thereby the specific grazing rate and the specific mortality rate according to the allometric principles. The size yielding the highest eco-exergy is currently found

and mineralization rate of detritus with increased copper concentration [16–19]. As a result the zooplankton is reduced in size [19], which according to the allometric principles means an increased specific grazing rate and specific mortality rate [19]. It has been observed that the size of zooplankton in a closed system (a pond for instance) is reduced to less than half the size at a copper concentration of 140 mg/m^3 compared with a copper concentration of less than 10 mg/m^3 [19]. In accordance with the allometric principles [20], it would result in more than doubling of the grazing rate and the mortality rate.

The model shown in Fig. 5 was made structurally dynamic by varying the size of zooplankton and using an allometric equation to determine the corresponding specific grazing rate and specific mortality rate. The equation expresses that the two specific rates are inversely proportional to the linear size [20]. In the range of different copper concentrations from 10 to 140 mg/m^3 are found by the model which zooplankton size yields the highest eco-exergy. In accordance with the presented SDM approach it is expected that the size yielding the highest eco-exergy would be selected. The results of the model runs are shown in Figs. 6–8. The specific grazing rate, the size yielding the highest eco-exergy, and the eco-exergy are plotted versus the copper concentration in these three figures.

As expected is the eco-exergy even at the zooplankton size yielding the highest eco-exergy decreasing with increase in copper concentration due to the toxic effect on phytoplankton and bacteria.

The selected size, see Fig. 7, at 140 mg/m^3 as also indicated in the literature is less than half, namely, about 40% of the size at 10 mg/m^3 . The eco-exergy is decreasing from 198 kJ/l at 10 mg/m^3 to 8 kJ/l at 140 mg/m^3 . The toxic effect of the

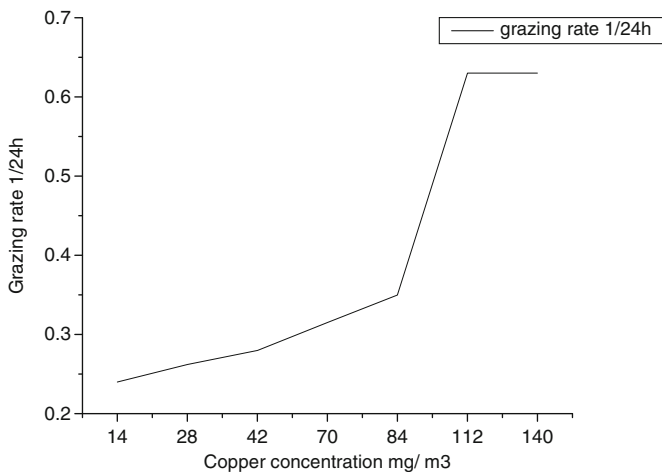


Fig. 6 The grazing rate that yields the highest eco-exergy is shown at different copper concentrations. The grazing rate is increasing more and more rapidly as the copper concentration is increasing but at a certain level, it is not possible to increase the eco-exergy further by changing the zooplankton parameters, because the amount of phytoplankton is becoming the limiting factor for zooplankton growth

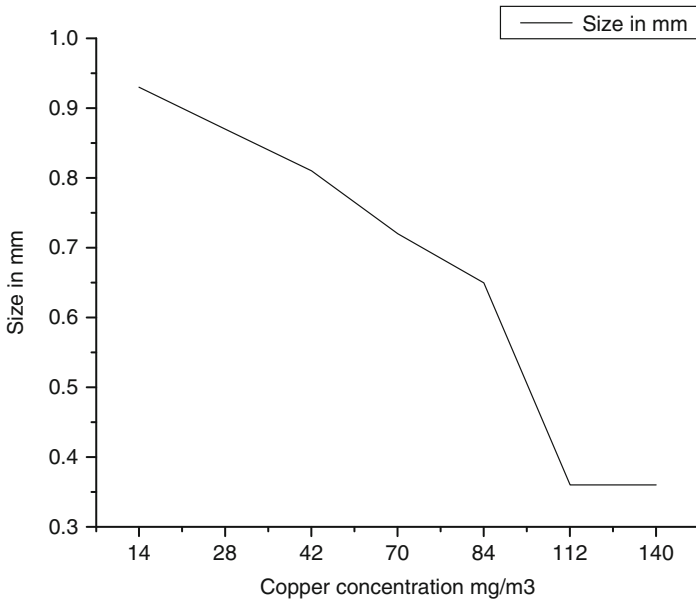


Fig. 7 The zooplankton size that yields the highest eco-exergy is plotted versus the copper concentration. The size is decreasing more and more rapidly as the copper concentration is increasing but at a certain level, it is not possible to increase the eco-exergy further by changing the zooplankton size, because the amount of phytoplankton is becoming the limiting factor for zooplankton growth

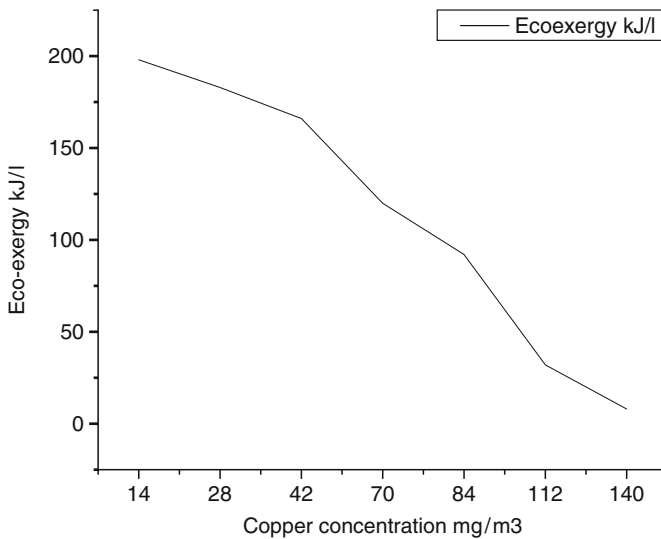


Fig. 8 The highest eco-exergy obtained when varying the zooplankton size is plotted versus the copper concentration. The eco-exergy is decreasing almost linearly with increasing copper concentration. The discrepancy from approximately a linear plot may be due to model uncertainty and discontinuous change of the copper concentration and the zooplankton size

copper is, in other words, resulting in an eco-exergy reduction to about 4% of the original eco-exergy level, which is a very significant toxic effect. If the zooplankton was not adaptable to the toxic effect by changing its size and thereby the parameters, the reduction in eco-exergy would have been even more pronounced already at a lower copper concentration. It is, therefore, important for the model results that the model is made structurally dynamic and thereby accounts for the change of parameters when the copper concentration is changed.

6 Conclusion

All organisms are able to change their properties to offer the best possibility for survival under the prevailing conditions. The generally applied bio-geo-chemical models do not consider this adaptation and they will, therefore, inevitably result in wrong prognoses. SDMs offer to solve this problem by changing currently the parameters to the values that yield the highest eco-exergy. The two presented illustrative examples have demonstrated how a SDM is working and how it is able to account for the adaptation. In the first example, the Darwin's finches are currently changing their beak size and in the ecotoxicological case study zooplankton is changing its size. In both cases the changes are approximately in accordance with the observations. It is, of course, an advantage that SDMs can predict approximately the changes of the species' properties, but it is an even more important advantage that the state variables are predicted closer to the observations by the SDMs than by bio-geo-chemical models. In accordance with the bio-geo-chemical model approach the Darwin finches would have died in the first presented example and also in the second example if the toxic effect of copper had been more pronounced, while the use of SDM in both cases gives reasonably approximate results.

References

1. Straskraba M (1979) Natural control mechanisms in models of aquatic ecosystems. *Ecol Model* 6: 305–322
2. Straskraba M (1980) The effects of physical variables on freshwater production: Analyses based on models. In: Le Cren ED, McConnell RH (eds) *The Functioning of freshwater ecosystems* (International Biological Programme 22), Cambridge University Press, Cambridge
3. Jørgensen SE (2002) *Integration of ecosystem theories: A pattern*, 3rd edition. Kluwer Academic, Dordrecht, The Netherlands
4. Stenseth NC (1986) Darwinian evolution in ecosystems: A survey of some ideas and difficulties together with some possible solutions. In: Casti JL, Karlquist A (eds) *Complexity, language and life: Mathematical approaches*, Springer Verlag, Berlin
5. Patten BC (1997) Synthesis of chaos and sustainability in a nonstationary linear dynamic model of the American black bear (*Ursus americanus* Pallas) in the Adirondack Mountains of New York. *Ecol Model* 100: 11–42
6. Jørgensen SE, Svirezhev YM (2005) *Towards a thermodynamic theory for ecological systems*, Elsevier, Amsterdam

7. Jørgensen SE, Fath B (2007) *A new ecology: A systems approach*, Elsevier, Amsterdam
8. Jørgensen SE, Patten BC, Straskraba M (2000) Ecosystems emerging. IV. Growth. *Ecol Model* 126: 249–284
9. Jørgensen SE, Fath BD (2004) Application of thermodynamic principles in ecology. *Ecol Complexity* 1: 267–280
10. Fath B, Jørgensen SE, Patten BC, Straskraba M (2004) Ecosystem growth and development. *Biol Syst* 77: 213–228
11. Jørgensen SE, Meyer HF (1977) Ecological buffer capacity. *Ecol Model* 3: 39–61
12. Jørgensen SE, Mejer HF (1979) A holistic approach to ecological modelling. *Ecol Model* 7: 169–189
13. Jørgensen SE (1992) Development of models able to account for changes in species composition. *Ecol Model* 62: 195–208
14. Coffaro G, Bocci M, Bendoricchio G (1997) Structural dynamic application to space variability of primary producers in shallow marine water. *Ecol Model* 102: 97–114
15. Grant PR (1986) *Ecology and evolution of Darwin's finches*. Reprinted in 1999. Princeton University Press, New Jersey
16. Kallqvist T, Meadows BS (1978) The toxic effects of copper on algae and rotifers from a soda lake. *Water Res* 12: 771–775
17. Hedtke SF (1984) Structure and function of copper-stressed aquatic microcosms. *Aquat Toxicol* 5: 227–244
18. Havens KE (1994) Structural and functional responses of a freshwater community to acute copper stress. *Environ Pollut* 86: 259–266
19. Fu-Liu X, Jørgensen SE, Tao S (1999) Ecological indicators for assessing the freshwater ecosystem health. *Ecol Model* 116: 77–106
20. Peters RH (1983) *The ecological implications of body size*, Cambridge University Press, Cambridge