CHAPTER

6

Application of Structurally Dynamic Models (SDMs)

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OUTLINE

6.1 INTRODUCTION

Ecological models 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 of modeling ecosystems is: How can we construct models that are able to reflect these extremely dynamic characteristics? They are of particular importance when we want to develop ecological models that considered the ecological changes due to the impacts of radical changes in

the forcing functions (impacts). Some recent development in ecological modeling has attempted to meet this challenge by the use of a new model type denoted structurally dynamic models (SDMs). Section 6.2 describes i.e., the properties of ecosystems that make it compulsory at least in some situations to use SDMs. Section 6.3 will focus on how to develop this model type and how it can be applied to consider the ecological changes that are a result of impact changes on ecosystems. It means that the changes of the state variables due to the changes of the forcing functions are considered.

SDMs can be developed by two methods: either by the use of expert knowledge or by the use of a goal function. Expert knowledge can be used to change the parameter of crucial species according to what is known about which species are characteristic for the focal ecosystem at various impacts or forcing functions or expressed differently by the prevailing conditions. The use of a goal function implies that changes of state variables due to changing forcing functions can be described by a function that is able to capture the regulating feedbacks of the ecosystem caused by changes. The most applied goal function for development of SDMs is the thermodynamic variable eco-exergy [it is exergy or work energy capacity (abbreviated as WE) defined for ecosystems; the definition and presentation is given in Section 6.3].

Section 6.4 gives an overview of SDMs developed by use of WE as goal function and Section 6.5 presents one SDM example to illustrate the model type. As it is expected that this model type will be used more generally in the future to assess the consequences of global warming, which is a very massive impact change, Section 6.6 is devoted to population dynamic examples of how the WE will change when temperature changes are realized. It means that this section will illustrate the applicability of SDMs to describe the consequences of global climate changes.

6.2 ECOSYSTEM PROPERTIES

Many researchers have advocated for a holistic approach to ecosystem science (e.g., Odum, 1953; Ulanowicz, 1986, 1995). Holism is taken to mean a description of the system level properties of an ensemble, rather than simply an exhaustive detailed description of all the components. It is thought that by adopting a holistic viewpoint, certain properties become apparent and other behaviors are made visible that otherwise would be undetected. It is, however, clear 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 average behavior and the important reactions of the system, particularly to specified impacts. It means that we can only try to reveal the basic properties behind the complexity. We have therefore 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. A brief overview of the most important system properties of ecosystems are given below.

The number of feedbacks and regulations is extremely high and makes it possible for the living organisms and populations to survive and reproduce despite changes in external conditions. 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 will take over. The change by adaptation within the same species is limited. When this limitation has been reached, other species will take over. 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. All these regulation mechanisms are rooted in the enormous amount of information that ecosystems possess.

Ecosystems show a high degree of heterogeneity in space and in time.

An ecosystem is a very dynamic system. All its components and particularly the biological ones are steadily changing 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 biodiversity is so high 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. Ecotones, the transition zones between two ecosystems, offer a particular variability in life conditions, which often results in a particular richness of species diversity. Studies of ecotones have recently drawn much attention from ecologists because ecotones have pronounced gradients in the external and internal variables, which give a clearer picture of the relation between external and internal variables.

Margalef (1991) 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 toward increasing the differences. These variations in time and space make it particularly difficult to model ecosystems and to capture the essential features of ecosystems. However, the hierarchy theory applies these variations to develop a natural hierarchy as framework for ecosystem descriptions and theory. The strength of the hierarchy theory is that it facilitates the studies and modeling of ecosystems.

Ecosystems and their biological components, the species, evolve steadily and over the long time toward higher complexity. Darwin's theory describes the competition among species and states that those species 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 modeling; see, however the next section.

All species in an ecosystem are confronted with the question: 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 coevolution, as any change in the properties of one species will influence the evolution of the other species. The environmental stage on which the selection plays out is comprised of all the interacting species, each influencing another.
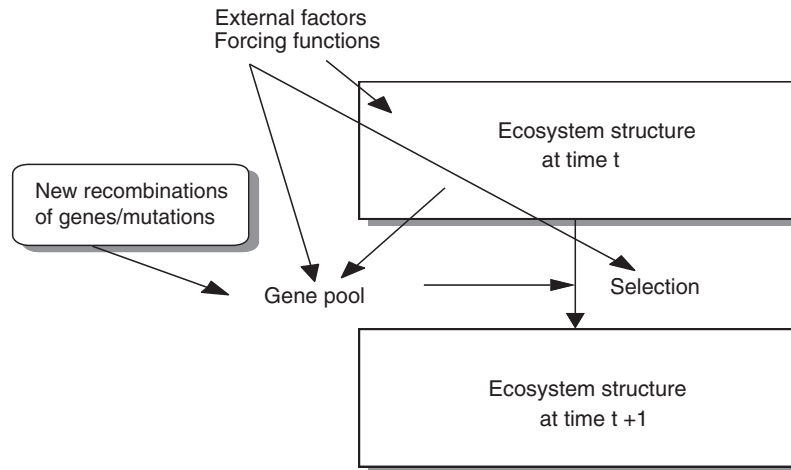
FIGURE 6.1   Conceptualization of how the external factors steadily change the species composition. The possible shifts in species composition are determined by the gene pool, which is steadily changed due to mutations and new sexual recombinations of genes. The development is, however, more complex. This is indicated by (1) arrows from "structure" to "external factors" and "selection" to account for the possibility that the species can modify their own environment (see text) 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.

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 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. 6.1. The external factors are steadily changed and some even relatively fast—partly at random, such as the meteorological or climatic factors. The species within the system are selected among the species available and represented by the genetic pool, which again is slowly, but surely changed at random or by "chance." The selection in Fig. 6.1 includes a selection of the organisms that possess the properties best fitted to the prevailing conditions.

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, 1986). But the property of fitness must be heritable 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 but may be interpreted as follows: species offer different solutions to survive under the 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.

If we follow the modeling procedure (see for instance Jørgensen and Fath, 2011), 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 response to changes in the existing conditions, determined by the forcing functions and the interrelations between the state variables—see Fig. 6.1. Our present models have rigid structures and a fixed set of parameters meaning 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 (Jørgensen et al., 2000) and described by Odum (1971). The model type that can 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 existing conditions imposed on the species, is sometimes called SDM, to indicate that they are able to capture structural changes.

It could of course be argued that the ability of ecosystems to replace present species with other, better fitted species, can be considered by constructing models that encompass all actual species for the entire period that the model attempts to cover. This approach has, however, two essential disadvantages. This will introduce a high uncertainty to the model and will render the application of the model very case specific (Nielsen, 1992a,b). In addition, the model will still be rigid and not allow the model to have continuously changing parameters even without changing the species composition (Fontaine, 1981). Straskraba (1979) 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 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 [work energy capacity (WE) including the work energy of information] has been used widely as a goal function in ecological models, and a few of the available case studies will be presented and discussed below in this section. Eco-exergy or WE has two pronounced advantages as goal function. It is defined far from thermodynamic equilibrium and it is related to the state variables, which are easily determined or measured, opposite for instance maximum power that is related to the flows. As exergy is not a generally used thermodynamic function, we need, however, first to present this concept properly. Let us translate Darwin's theory into thermodynamics, applying eco-exergy (WE) as the basic

concept. Survival implies biomass maintenance, and growth means biomass increase. It costs WE to construct biomass and biomass therefore possesses WE, which is transferable to support other work-energy requiring processes. Survival and growth can therefore be measured by use of the thermodynamic concept eco-exergy (WE). Darwin's theory may therefore be reformulated in thermodynamic terms as follows: *The prevailing conditions of an ecosystem steadily change and the system will continuously select the species and thereby the processes that can contribute most to the maintenance or even growth of the work energy of the system. This hypothesis is often denoted ELT—the Ecological Law of Thermodynamics.*

The hypothesis describes how ecosystems react when the forcing functions (impacts) are changed. These properties of ecosystems are theoretically very important for the development of SDMs.

Notice that the thermodynamic translation of Darwin's theory requires that populations have the properties of reproduction, inheritance, and variation. The selection of the species that contributes most to the WE of the system under the existing conditions requires that there are enough individuals with different properties so that a selection can take place—it means that the reproduction and the variation must be high and that once a change has taken place due to better fitness, it can be conveyed to the next generation.

6.3 DEVELOPMENT OF STRUCTURALLY DYNAMIC MODELS

Notice also the change in WE (eco-exergy) of ecosystems according to ELT is not necessarily ≥ 0; it depends on the changes of the resources of the ecosystem. The proposition claims, however, that the ecosystem attempts to reach the highest possible WE level under the given circumstances or prevailing conditions and with the available genetic pool ready for this attempt (Jørgensen and Mejer, 1977, 1979); see Fig. 6.2. Jørgensen and Mejer (1979) have shown by the use of thermodynamics that the following equation is valid for the components of an ecosystem:

$$Ex = RT \sum_{i=1}^{i=n} \left(C_i \times \ln(C_i / C_{eq,i}) - (C_i - C_{eq,i}) \right), \tag{6.1}$$

where R is the gas constant, T the temperature of the environment (Kelvin), while C_i represents the ith component expressed in a suitable unit, e.g., for phytoplankton in a lake C_i could be milligrams of a focal nutrient in the phytoplankton per liter of lake water, $C_{eq,i}$ is the concentration of the ith component at thermodynamic equilibrium. The quantity $c_{eq,i}$ represents a very small, but nonzero, concentration (except for $i = 0$, which is considered to cover the inorganic compounds), corresponding to the very low probability of forming complex organic compounds spontaneously in an inorganic soup at thermodynamic equilibrium.

The idea of the new type of models presented here 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 by the use of exergy (see Jørgensen, 1986, 1988, 1990, 1992; Jørgensen and Mejer, 1977, 1979).
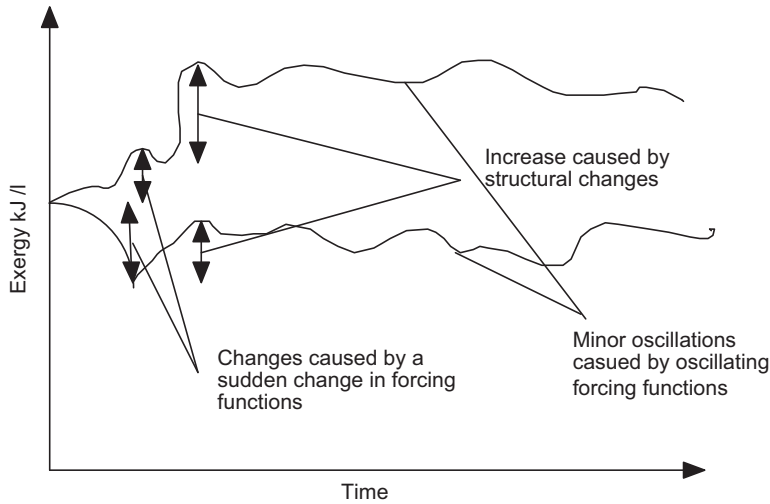
FIGURE 6.2 Exergy (eco-exergy, WE) response to increased and decreased nutrient concentration. The level of work energy can thereby increase or decrease, but when these changes have been introduced, the system will attempt to gain as much work energy as possible under the prevailing conditions.

Fig. 6.3 shows the proposed modeling procedure, which has been applied for all the cases studies listed in Section 6.4.

Eco-exergy or work energy capacity (WE) is defined as the work the system can perform when it is brought into equilibrium with the environment or another well-defined reference state. If we presume a reference environment for a system at thermodynamic equilibrium, meaning that all the components are (1) inorganic, (2) at the highest possible oxidation state signifying that all free energy has been utilized to do work, and (3) homogeneously distributed in the system, meaning no gradients, then the situation illustrated in Fig. 6.4 is valid.

It is possible to distinguish in Eq. (5.1) between the contribution to the eco-exergy from the information and from the biomass. We define p_i as c_i/A, where

$$A = \sum_{i=1}^{n} c_i \tag{6.2}$$

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

$$Ex = ART \sum_{i=1}^{n} p_i \, lnp_i/p_{io} + A \, lnA/A_o \tag{6.3}$$

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

$$K = \sum_{i=1}^{n} p_i \, ln(p_i/p_{io}) \tag{6.4}$$

Select parameters based upon ltierature studies and according to species composition

Select most crucial parameters, symbolized by parameter vector P

Test after time step t all combinations of all the selected parameters +/- x%, y% etc i.e. at least three leves for each parameter. The total number of combinations to be examined is l^n, where l is the number of levels and n is the number of parameters in the parameter vector P. The combination giving the highest exergy is used for the simulation during the considered time step

Test after time step n*t all combinations of the selected parameters +/- x%, y% etc. The combination giving the highest exergy is used for the simulation duringe the considered time step
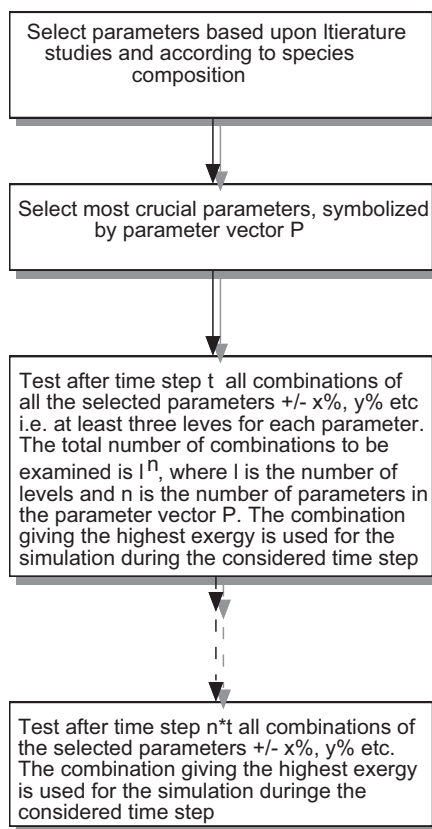
FIGURE 6.3   The procedure used for the development of structurally dynamic models.

where p_i and p_{io} 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. 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 β, is found by calculating 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 and Svirezhev (2005). In the latter reference, the latest information about the β values for various organisms is presented; see Table 5.1. For human, the β value is 2173, when the eco-exergy is expressed in detritus equivalent or 18.7 times as much or 40,635 kJ/g if the eco-exergy should be expressed as kJ and the concentration unit g per unit of volume or area. One hypothesis, apparently confirmed by observation is that the β values increase as a result of evolution. To mention a few β values from Table 8.2: bacteria 8.5, protozoa 39, flatworms 120, ants 167, crustaceans 232, mollusks 310, fish 499, reptiles 833,
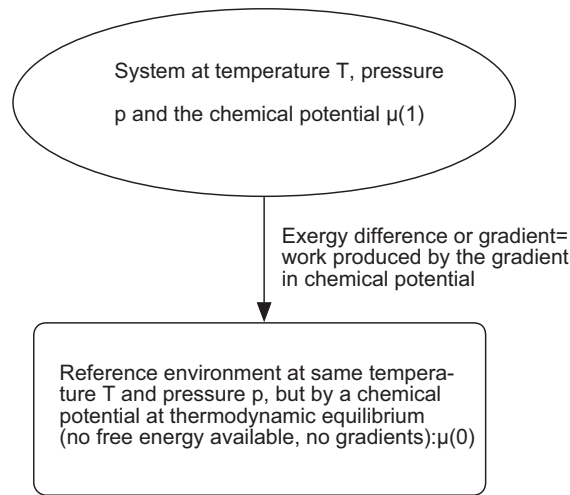
FIGURE 6.4   Illustration of the eco-exergy, work energy capacity, concept used to compute the exergy index for an ecological model. Temperature and pressure are the same for both the system and the reference state which implies that only the difference in chemical potential can contribute to the exergy.

birds 980, and mammals 2127. Evolution 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 β value of 2.0 means that the eco-exergy embodied in the organic matter and the information are equal. As the β values, see above, are much bigger than 2.0 (except for virus, where the β value is 1.01—slightly more than 1.0), the information eco-exergy is the most significant part of the eco-exergy of organisms.

In accordance with the above-presented interpretation of Eqs. (6.3) and (6.4), it is now possible to find the eco-exergy density for a model as:

$$\text{Eco-exergy density} = \sum_{i=1}^{i=n} \beta_i c_i \tag{6.5}$$

The eco-exergy due to the "fuel" value of organic matter (chemical energy) is about 18.7 kJ/g (compare with coal: about 30 kJ/g and crude oil: 42 kJ/g). It can be transferred to other energy forms for instance mechanical work directly and be measured by bomb calorimetry, which requires destruction of the sample (organism), however. The information eco-exergy = $(\beta - 1) \times$ biomass or density of information eco-exergy = $(\beta - 1) \times$ concentration. The information eco-exergy controls the function of the many biochemical processes. The ability of a living system to do work is contingent upon its functioning as a living dissipative system. Without the information eco-exergy, the organic matter could only be used as fuel similar to fossil fuel. But due to the information eco-exergy, organisms are able to make a network of the sophisticated biochemical processes that characterize life. The eco-exergy (of which the major part is embodied in the information) is a measure of the organization (Jørgensen and Svirezhev, 2005). This is the intimate relationship between energy and organization that Schrödinger (1944) was struggling to find.

The eco-exergy is a result of the evolution and of copying again and again in a long chain of copies where only minor changes are introduced for each new copy. The energy required for the copying process is very small, but it required a lot of energy to come to the "mother" copy through evolution from prokaryotes to human cells. To cite Margalef (1991) in this context: the evolution provides for cheap—unfortunately often "erroneous," i.e., not exact—copies of messages or pieces of information. The information concerns the degree of uniqueness of entities that exhibit one characteristic complexion that may be described.

Eco-exergy has successfully been used to develop SDMs in 25 case studies so far. The eco-exergy goal function is found using Eq. (6.5), while the β values are found using Table 6.1.

The application is based on what may be considered thermodynamic translation of survival of the fittest. 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 thermodynamics (ELT) (Jørgensen et al., 2007): 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 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 is supported by several ecological observations and case studies (Jørgensen and Svirezhev, 2005; Jørgensen et al., 2007; Jørgensen, 2008a,b, 2012). 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 exergy. Survival and growth can therefore be measured using the thermodynamic concept eco-exergy, which may be understood as the work capacity the ecosystem possesses.

6.4 OVERVIEW OF STRUCTURALLY DYNAMIC MODELS USING WORK ENERGY AS GOAL FUNCTION

WE, the work energy of biomass and the information that the organisms carry, also called eco-exergy, has been applied to develop SDMs in 25 cases; several of these 25 cases are presented by Zhang et al. (2010) and in the textbook Fundamentals of Ecological Modelling by Jørgensen and Fath (2011). The last four cases are published in the following papers: Cho et al. (2011), Marchi et al. (2011), Kong et al. (2013), and Jørgensen and Nielsen (2015). The 25 case studies are:

1–8. Eight eutrophication models of six different lakes,
9. A model to explain the success and failure of biomanipulation based on removal of planktivorous fish,
10. A model to explain under which circumstances submerged vegetation and phytoplankton are dominant in shallow lakes,

TABLE 6.1   β Values = Eco-exergy Content Relative to the Eco-exergy of Detritus
(Jørgensen et al., 2005)

Early organisms	Plants		Animals
Detritus		1.00	
Viroids		1.0004	
Virus		1.01	
Minimal cell		5	
Bacteria		8.5	
Archaea		13.8	
Protists	Algae	20	
	Yeast	17.8	
		33	Mesozoa, Placozoa
		39	Protozoa, amoeba
		43	Phasmida (stick insects)
	Fungi, molds	61	
		76	Nemertina
		91	Cnidaria (corals, sea anemones, jellyfish)
	Rhodophyta	92	
		97	Gastrotricha
		98	Porifera
		109	Brachiopoda
		120	Platyhelminthes
		133	Nematoda
		133	Hirudinea
		143	Gnathostomulida
	Mustard weed	143	
		165	Kinorhyncha
	Seedless angiosperms	158	
		163	Rotifera
		164	Entoprocta
	Moss	174	
		167	Insecta
		191	Coleodiea (sea squirt)

TABLE 6.1   β Values = Eco-exergy Content Relative to the Eco-exergy of Detritus (Jørgensen et al., 2005)—cont'd

Early organisms	Plants		Animals
		221	Lepidoptera
		232	Crustacea
		246	Chordata
	Rice	275	
	Gymnosperms	314	
		310	Mollusca
		322	Mosquito
	Angiosperms	393	
		499	Fish
		688	Amphibia
		833	Reptilia
		980	Aves
		2127	Mammalia
		2138	Monkeys
		2145	Anthropoid apes
		2173	*Homo sapiens*

11. A model of Lake Balaton which was used to support the intermediate disturbance hypothesis,

12–15. For small population dynamic models, a eutrophication model of

16. The Lagoon of Venice and

17. The Mondego Estuary and

18. An ecotoxicological model focusing on the influence of copper on zooplankton growth rates.

19. A model of Darwin's finches,

20. A model of the interaction between parasites and birds and

21. The SDM included in Pamolare 1 applied on Lake Fure in Denmark,

22. The role of conjugation in the gene–individual population relationship,

23. SDM of Lake Chozas,

24. Prediction the restoration effects by a structural dynamic approach in Lake Chaoku,

25. Landscape modeling.

It is not yet possible to present case studies where the structural changes have been successfully modeled in the case of climatic changes, but Section 6.5 will illustrate some first model approaches of ecosystem changes due to climatic changes. It is shown that the use

of WE as goal function seems in principle to work also in the case of climatic changes. In the last section, it will be attempted to make some first-hand conclusions to the extent that it is possible at this stage.

6.5 DEVELOPMENT OF STRUCTURALLY DYNAMIC MODEL FOR DARWIN'S FINCHES

The development of an SDM for Darwin's finches (see Jørgensen and Fath, 2011) illustrates the advantages of SDMs very clearly; see further details in Jørgensen and Fath (2004). This illustration of SDM has therefore been chosen as an example to demonstrate the applicability of SDM. 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 modeling case due to very detailed case specific information found in Grant (1986). 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 plus 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. Due to a particular low precipitation in 1977−79, the population of the Medium ground finches declined significantly and the beak size increased at the same time about 6%. An SDM was developed to be able to describe this adaptation of the beak size due to bigger and harder seeds as a result of the low precipitation.

The beak depth can vary between 3.5 and 10.3 cm according to Grant. The beak size is furthermore equal to square root of D×H, where D is the diameter and H the hardness of the seeds. Both D and H are dependent on the precipitation, particularly from January to April. The coordination or fitness of the beak size with D and H is a survival factor for the finches. The fitness function is based on the seed handling time and it influences the mortality as mentioned above, but has also an impact on the number of eggs laid and the mortality of the juveniles. The growth rate and mortality rate of the seeds is dependent on the precipitation and the temperature, which are forcing functions known as f(time). The food shortage is calculated from the food required by the finches which is known according to Grant and the actual available food according to the state function seed. How the food shortage influences the mortality of the adults and juveniles can be found in Grant (1986). The seed biomass and the number of finches are known as a function of time for the period 1975−82; see Grant (1986). The observations of the state variables from 1975 to 1977 were applied for calibration of the model, focusing on 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 (Grant, 1986). The influence is therefore calibrated within a narrow range of values,
3. the influence of precipitation on the seed biomass (growth and mortality).
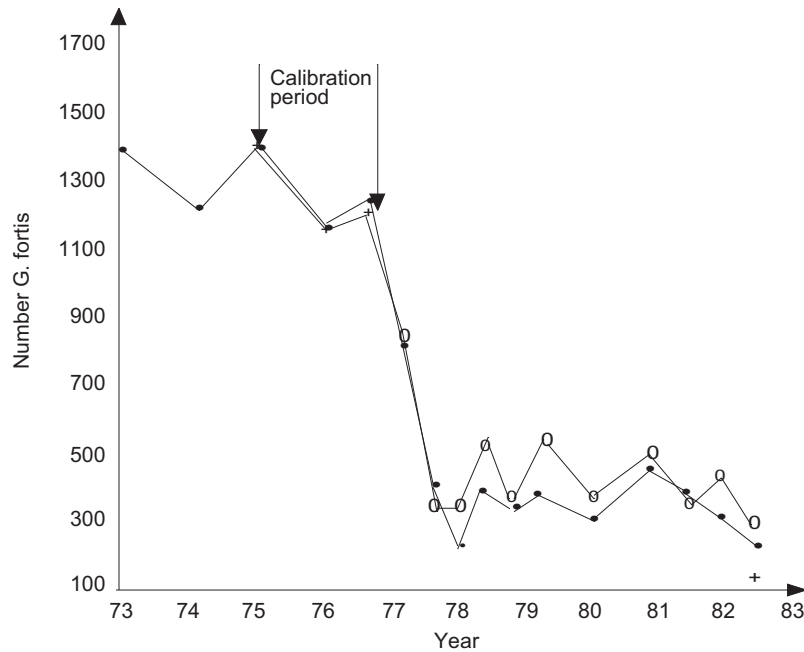
FIGURE 6.5   The observed number of finches (·) from 1973 to 1983, compared with the simulated result (0). 75 and 76 were used for calibration and 77/78 for the validation.

All other parameters are known from the literature (see Grant, 1986).

The eco-exergy density is calculated (estimated) as $275 \times$ the concentration of seed $+ 980 \times$ the concentration of finches (see Table 6.1). 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 modeled 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. 6.5. The standard deviation between modeled and observed values was 11.6%. For the validation and the correlation coefficient, r^2, for modeled versus observed values is 0.977. The results of a non-SDM 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. The calibrated model not using the eco-exergy optimization for the SDMs in the validation period 1977—82 resulted in complete extinction of the finches. A non-SDM—a normal biogeochemical model—could not describe the impact of the low precipitation, while the SDM gave an approximately correct number of finches and could describe the increase of the beak at the same time.

6.6 APPLICATION OF STRUCTURALLY DYNAMIC MODEL FOR THE ASSESSMENT OF ECOLOGICAL CHANGES DUE TO CLIMATE CHANGES

There is a scientific accordance that major climate changes can be expected in the coming decades due to the increasing emission of greenhouse gases. It is therefore very understandable that we ask the question: which ecological changes can we expect as a consequence of the foreseen global warming? How will the different types of ecosystems react to the impact of the climatic changes? Obviously, SDM is a model type that should be able to give the answer to these crucial questions. No SDMs focusing on climatic changes has, however, been developed so far, because it is of course necessary to have some observations of the influence of climate changes on the ecosystems and the ecological processes, before a model can be published and applied more generally. The calibration and validation of an SDM will inevitably require that the foreseen adaptation and/or shifts in species composition by the model are observed with a reasonable and acceptable standard deviation. Although a global temperature increase of 0.8°C has been observed, it would therefore be beneficial to provide observations over a longer period, for instance the coming decade, and furthermore preferably after a slightly higher temperature increase.

It is, however, possible to examine whether an increased temperature will give a decrease in the WE (eco-exergy = WE of biomass and information) and whether adaptation to the increased temperature afterward will yield an increase of the WE and thereby compensate for the previous drop in WE. Such an examination would with a positive result maybe not ensure that SDMs could be used to answer all the relevant questions associated with ecological changes due to climatic changes, but it would indicate that there is a high probability that SDMs could be good tools to model the ecological consequences of climate changes, applying WE (eco-exergy) as goal function.

The examination has been carried out by two population dynamic models, presented in detail in the reference Jørgensen (2015). The models applied in these two examples are shown in Figs. 6.6 and 6.7. The first model has only one state variable—a population, while the second model covers a food chain: plants, herbivores, and carnivores populations. In both models, the relatively simple Arrhenius expression for the influence of the temperature on the ecological processes has been applied: rate as f(temp) = k^|temperature − optimum temperature|. An optimum temperature of 20°C was applied, except when an adaptation was presumed. The absolute/numeric values were applied to account for the influence of the temperature difference from the optimum temperature of 20°C. A characteristic temperature pattern as f(time) for a temperate latitude was applied as a table or graph function. k was for all growth rates 1.05 and for the other processes 1.1. The result of the first model—see Fig. 6.6—is shown in Table 6.2. The biomass is indicated and as there is only one state variable, the focal population, the WE is proportional to the biomass, as the work energy is equal to biomass × the β value for the considered population × 18.7 kJ (if the biomass is in grams).

It can be seen from the results in Table 6.2, that the maximum biomass value and the final biomass value at the end of the year (the model is running 12 months) decrease when the
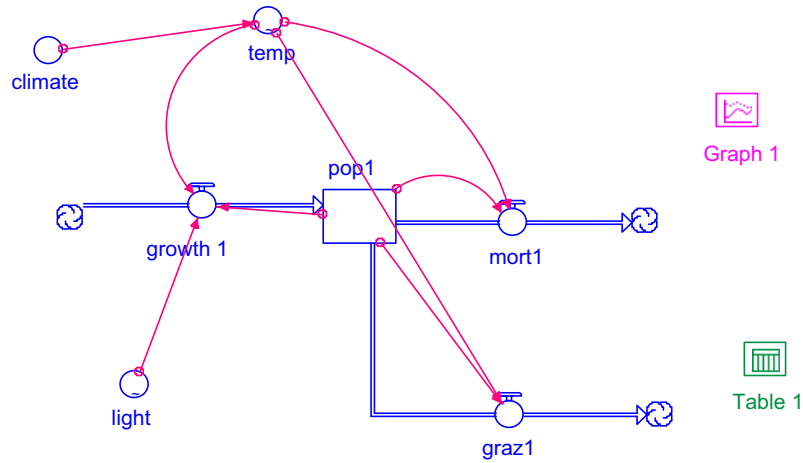
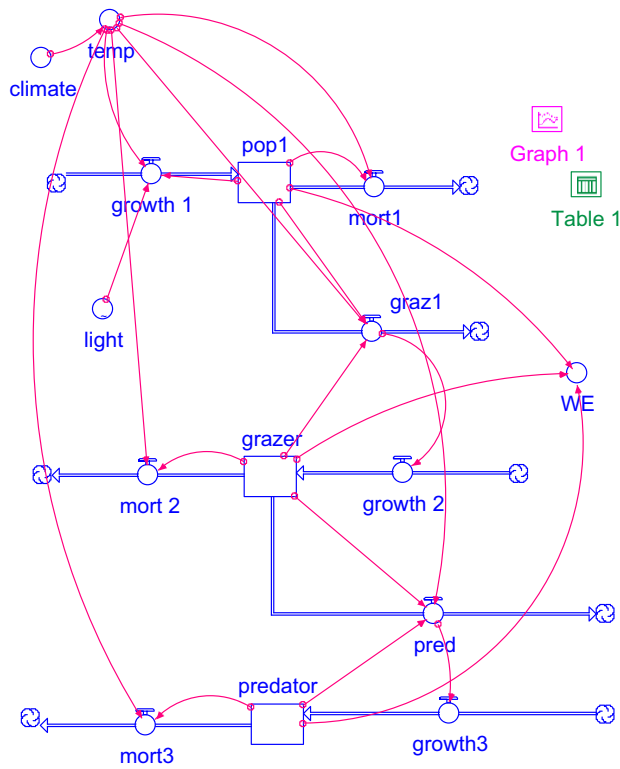FIGURE 6.6   Population dynamic model applied for the examination.

FIGURE 6.7   Food chain model applied for the examinations.

TABLE 6.2 Biomass (g per Unit of Area) for the Population in Fig. 6.6 as f(Increase of Temperature, °C) and Optimum Temperature, °C

Optimum Temperature	Increase of Temperature	Maximum Biomass	Final Biomass
20	0	1018	999
20	1	1015	1000
20	2	1011	999
20	3	1004	992
20	4	993	992
20	5	984	973
23	3	1018	1000
25	5	1018	1000

temperature increases, while a change in the optimum temperature by adaptation is able to eliminate completely the drop in biomass or WE.

The results obtained by the food chain model, Fig. 6.7 are shown in Figs. 6.8 and 6.9. Fig. 6.8 shows the results of biomass for the three populations by an optimum temperature of 20°C and with no change in the temperature, while Fig. 6.9 shows the results obtained with the same optimum temperature but with 3°C increase of the temperature as f(time). Fig. 6.10
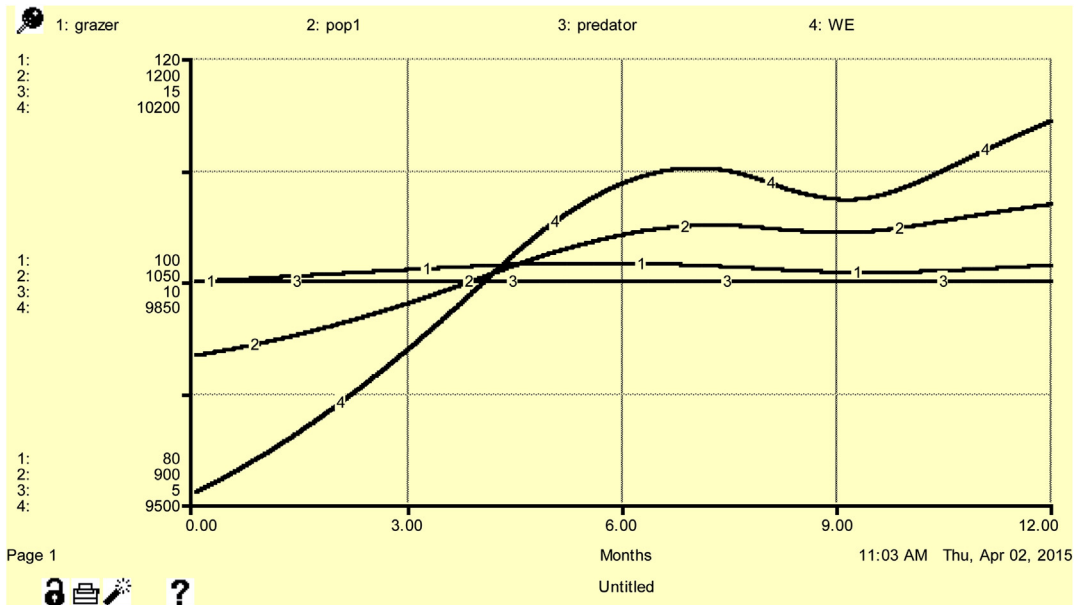

FIGURE 6.8 Biomass and work energy as f(time) for 20°C as optimum temperature and present temperature pattern.
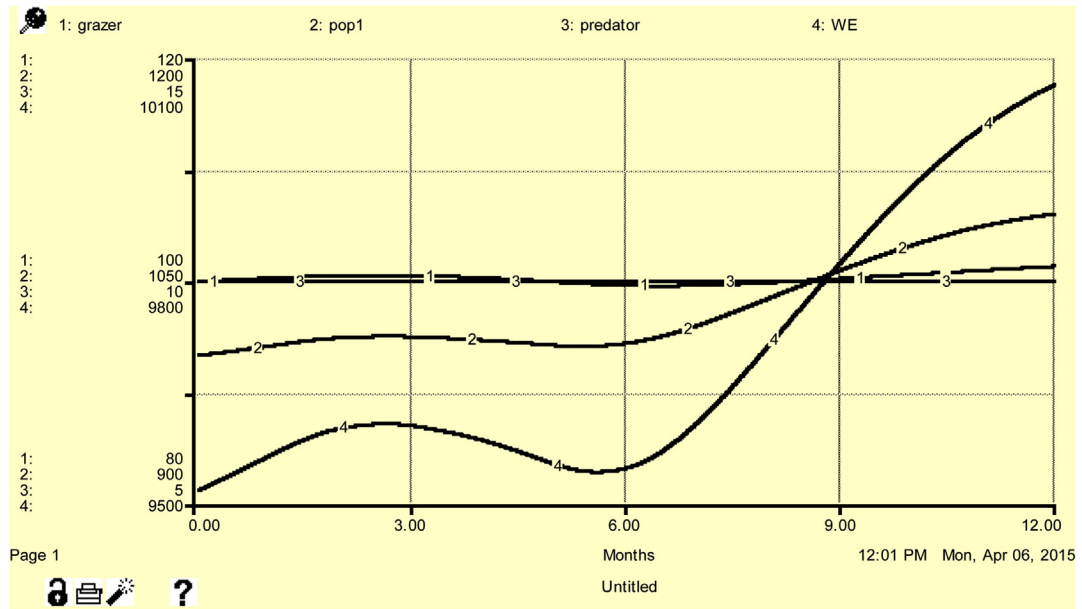
FIGURE 6.9 Biomass and work energy as f(time) for 20°C as optimum temperature and present temperature pattern +3°C. Compare with Fig. 5.7. The work energy has decreased due to the higher temperature.
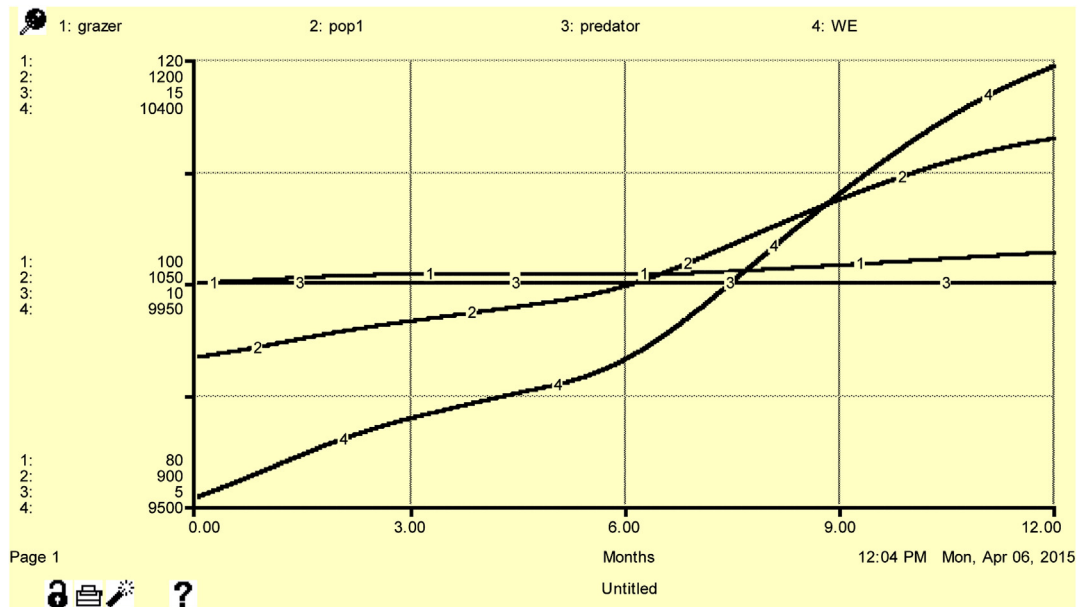

FIGURE 6.10 Biomass and work energy as f(time) for 23°C as optimum temperature and present temperature pattern +3°C. Compare with Figs. 5.7 and 5.8. The work energy has increased compared with no adaptation of the optimum temperature (Fig. 5.8) and is even slightly higher than the work energy in Fig. 5.7. The grazers have clearly benefitted by the higher temperature, but adaptation of the optimum temperature has also to take place.

shows the results achieved by an optimum temperature of 23°C and the general temperature pattern—temperature as f(time). The WE is calculated by the assumption that the food chain is grass, deer, and wolves with β values, respectively, 285, 2027, and 2027. A comparison of the results in Figs. 6.8—6.10 illustrates that the 3°C increased temperature gives a decrease in the WE, but if the optimum temperature is increased correspondingly by adaptation, the WE is regained.

6.7 CONCLUSIONS

SDM seems to be a suitable model tool to describe the expected changes of ecosystems due to impact changes, including the changes expected from global warming. It is therefore recommendable to attempt to use SDMs in our effort in the coming years to develop ecological models that are able to describe the ecological consequences of the climate changes.

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