Chapter 2
The Approach to Construct and Test the Theory of Forest Ecology

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Contents

Abstract This chapter gives the main lines of biological and methodological thinking applied in the whole book. The vision that mass and energy fluxes convey the interactions between forest ecosystem and its surroundings at different levels is the starting point of the theory formation. We formulate a common framework, called cover theory, to deal with different phenomena in the ecosystem. We analyse the fluxes generated by metabolism, and we use conservation of mass and energy for derivation of differential equations to describe each phenomenon under study. We test the dynamic models with field data to obtain feedback from nature. Finally, we combine the theories to form the physical and physiological theory of forest ecology.

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2.1 Outline

Forests are complex ecosystems including very different groups of organisms ranging from trees to soil microbes. Thus simultaneous, comprehensive and coherent treatment of the versatile phenomena in ecosystems is needed, and it can be obtained with a hierarchy of theories: *The cover theory* outlines the great lines of research, and *specific theories* deal with different phenomena within the cover theory. From the coherent framework of theories, it follows that the methods, i.e. modelling and measurements, share a common basis, and the tests of specific theories with field measurements are based on the same approach. The construction of specific theories under the guidance of the cover theory and common methodology allows proper flow of knowledge in all research concerning these versatile and complex forest ecosystems and the formation of the general theory of forest ecology.

The construction of the cover theory begins with the formulation of the vision that outlines roughly the most essential features in the interactions between forest ecosystems and their environment. It introduces in general terms the framework for the theory. Theories of physics, physiology, chemistry, anatomy and evolution provide essential background knowledge. The definition of *basic concepts* introduces tools for clarifying the vision. Basic concepts allow the formulation of the *basic ideas* to express the most essential relationships in a more exact form.

The cover theory is too general for research into all the different phenomena in trees, in ground vegetation and in soil. Therefore, specific theories are needed to be formulated and specified under the guidance of the general ideas presented in the cover theory. The specific basic concepts and ideas outline the thinking in the studies of each phenomenon, and they are intended to capture the most essential features of the study object. The construction of theoretical models is based on the analysis of material and energy fluxes and conservation of mass and energy resulting in differential or difference equations that can be tested with field measurements. The relationship between specific theories and the cover theory is visualised in Fig. 2.1.

The formation of specific theories proceeds via basic concepts and ideas to the formation of theoretical models. We need feedback from forests to evaluate and develop the theory formation. The severe testing of theoretical models puts strict requirements for the data to be used. The arrangement of measurements is a highly technical but necessary sidetrack in the theory formation. Tests of theoretical model with high-quality data are the last phase in clarifying the theory. The feedback from test to the previous phases in the theory formation is essential. The different steps in the theory formation are visualised in Fig. 2.2. The feedback from the test will result in improvements of the theory. Our methodological approach follows the ideas presented by Tuomivaara et al. (1994), Bunge (1996) and Hari (2008).

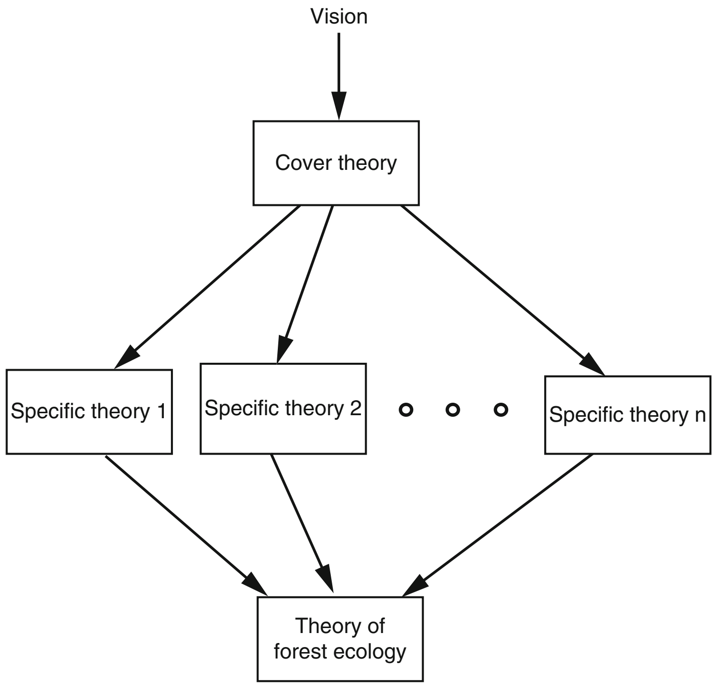

Fig. 2.1 The relationship between the cover theory and specific theories. We construct specific theories in the common framework provided by the cover theory. In this way, we can combine a coherent set of specific theories that enable knowledge flow between specific theories and construction of the theory of forest ecology. *Boxes* describe theories and *arrows* the flow of knowledge

2.2 Cover Theory of Forest Ecosystems

2.2.1 Vision

Solar radiation is the source of energy in forests. Vegetation has specialised structures that are able to convert energy in light quanta into a chemical form that is stored as carbohydrates such as sugars and starch. The chemical energy in sugars is further utilised in the synthesis of large carbon-, hydrogen- and oxygen-rich molecules. In addition, small amounts of nitrogen, phosphorus, potassium and other elements are needed for biosynthesis and the formation of special structures in vegetation. The metabolism of vegetation and microbes consumes O_2 and produces CO_2, H_2O, NH_4 and other simple compounds or ions generating material fluxes between forests and their environment. Already over 50 years ago, H. T. Odum stressed the important role of material and energy fluxes between ecosystem and their environment.

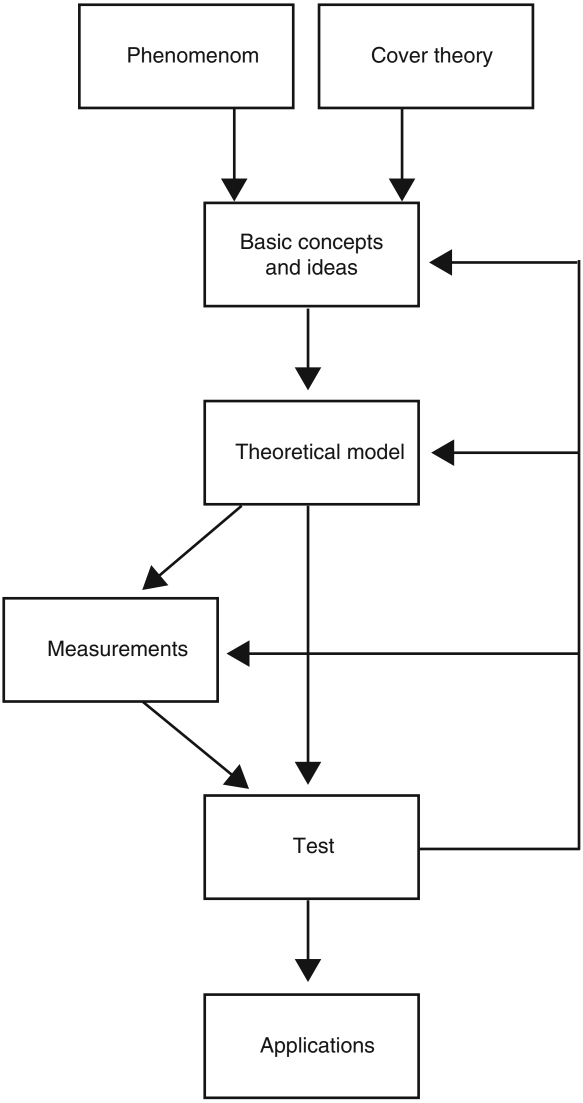

Fig. 2.2 The phases of formation of the specific theories utilising the cover theory as backbone. The feedback from the test to theory development and measurements is essential for the progress of the research. *Boxes* describe phases in the research and *arrows* the flow of knowledge

The physical distance for transport between sites of material intake and usage is in tall trees often over 20 m. Trees have effective transport structures connecting the roots and leaves with each other.

The strong annual cycle caused by the orbiting of the globe in a tilted position around the Sun is a stable characteristic for the Earth's environment. Forests have to tolerate the regular alternation of favourable and critical conditions during each year, and living organisms have means to cope with the cyclic behaviour in the environment.

Vegetation and microbes in soil have developed by evolution since the beginning of life on the Earth. The slow development during milliards of years has generated strong regularities in the structure and metabolism of living organisms. Evolution provides important insights into the present metabolism and structure of forests.

Conservation of energy and material, the cornerstone of Newtonian physics, is also a valid principle in the metabolism of vegetation and microbes in forests. Metabolism and physical phenomena convert material and energy in other forms, but the atoms and energy do not disappear. Both the environment and the state of the vegetation have effect on the conversion of material and energy, and by that they provide the causal explanations for the phenomena in forests.

The variation in the involved temporal and spatial scales is huge: from picoseconds in photosynthetic light reactions to century in the growth of a forest stand and from micrometres in the cell to hundreds of kilometres in a vegetation zone. Individuals are the basic units of the forests; they have complicated fine structure for metabolic tasks.

The vision outlines the basic features in forest ecosystems in very general form. These general ideas guide the formation of the theory of physical and physiological forest ecology. We proceed stepwise in the theory formation from background information, via definition of concepts, basic ideas and formulation of dynamic models, to their testing to give more concrete form to the vision.

2.2.2 Background

The physical and physiological theory of forest ecology utilises knowledge from very different disciplines as background. However, physics and physiology play dominating role in the argumentation.

Living organisms in forests have special structures to convert energy from light to chemical form and to utilise that chemical form in their metabolism. The intake and release of material and transport within trees take place as well via specialised structures. The discipline of anatomy provides an important insight into these rather complicated features of living organisms.

Several steps are involved in the conversion of solar energy into chemical energy as sugar. Vegetation synthesises a large number of macromolecules from sugars and ions. Each step in photosynthesis and in the synthesis of macromolecules is based on specialised enzymes, membrane pumps or pigments. The chains of steps are well balanced in such way that the sequence runs smoothly from the first step to the final product.

The enzymes, membrane pumps and pigments needed for the synthesis of new compounds are unstable proteins. They are unstable in the sense that they are fugitive over time. Their amounts and activation states fluctuate; thus new ones must be synthesised to replace the damaged ones and maintain the proper amount or activation state. This is a very demanding task for the metabolism of cells.

The annual cycle in light, temperature and other properties in the environment is an additional challenge for the metabolism of vegetation and microbes. Living processes and life in general must utilise effectively the favourable periods and tolerate the hard conditions during winter or drought. This is an additional complication in the control of the concentrations and activities of enzymes, membrane pumps and pigments. Physiology is the discipline that provides insight into the metabolism of vegetation and microbes.

Metabolism and physical phenomena generate concentration, temperature and pressure differences that cause diffusion or convection flows of mass and energy within individuals and between forest ecosystems and the environment.

The fundamental principle, conservation of mass and energy, allows the combination of metabolic and physical phenomena in a chain of conversion of energy or material. In this way, the causal relationships are introduced into the theory of forest ecology.

Effective structures, metabolism and control of enzymes, membrane pumps and pigments have developed in evolution.

Instrumentation has developed very rapidly during the last decades, and several phenomena can rather easily be measured in forests. Thus we can obtain important feedbacks from material and energy fluxes to theoretical thinking. This novel instrumentation is based on the discipline of electronics. Physical knowledge is essential for the proper understanding of fluxes, causality and electronics.

2.2.3 Basic Concepts

The construction of the cover theory begins with the definition of basic concepts. They are needed to cover the most important aspects in the interactions between forests and their environment. We should be able to introduce such concepts that characterise the most important ecological phenomena and that enable effective utilisation of the background knowledge.

The definition of basic concepts begins with the introduction of process. Large carbon molecules are characteristic for trees and other living organisms in forests. They are formed in the metabolism in long chains of biochemical reactions. The concept process is defined to characterise the conversion of material and energy in the metabolism and physical phenomena. Thus a *process*, by definition, converts material and/or energy into a new form or moves material through a membrane. For example, sugars are formed in photosynthesis from carbon dioxide and water using solar energy. Thus photosynthesis is a process according to the definition in the cover theory. Similarly, formation of new tissues and nitrogen uptake by roots are processes. They are characterised by the amounts of material converted to new forms or penetrated through a biological membrane. Processes are quantified by the fluxes of material or energy generated by the process under consideration.

The processes respond to the environment and also to the state of the living organisms. Thus concepts are needed to characterise the environment and the state of the living individual. *Environmental factors*, by definition, are those features in the environment that have effect on the processes. For example, light intensity, temperature and carbon dioxide concentration have substantial effects on photosynthesis. Thus at least these three are environmental factors.

Stable carbon compounds form the *structure* of living organisms. Cells are basic structural units of living organisms. Similar cells form tissues: They build up organs and finally organisms to form ecosystems. The structure involves several levels that have their characteristic phenomena. Geometrical features, chemical composition and mass characterise the structure.

Metabolic processes are non-spontaneous and special biological structures make them possible. *Functional substances* enable the metabolic processes in living organisms. Most of the structure of plant cells is formed by cell walls and lipid bilayers, which are passive skeletons for the metabolism. All biochemical processes have specific catalysing enzymes, membrane pumps actively transport material through membranes, and pigments capture light quanta. Thus enzymes, membrane pumps and pigments form the functional substances, and they play a key role in the utilisation of physiological knowledge in the formation of our forest ecological theory.

Functional substances are often non-stable large molecules; thus their lifetime is shorter than that of cell walls. In addition, the functional substances have often active and passive forms. Thus synthesis, decomposition, activation and deactivation of functional substances must take place in all living cells. Several processes and subprocesses are interrelated, and the functional substances of different processes and subprocesses have to match with each other to produce balanced metabolism, and the functional substances form large chains and webs to fulfil the metabolic needs. Living organisms have proteins, under the control of genetic system, that synthesise, decompose, activate and deactivate the functional substances. We call, by definition, these proteins and their genetic background as a *biochemical regulation system* and their action as *regulation*.

The metabolism of living organisms and physical phenomena convert material and energy to other forms. Thus metabolism and physical phenomena require new material or energy often from distant places. *Transport* moves material or energy in space. The long distances to be traversed by materials within trees have intrigued scientists for a long time, and transport phenomena are still being actively researched. *Fluxes* are material or energy flows per a unit of area during a unit time. Transport plays an important role when physical knowledge is utilised as background knowledge in ecology.

Forest ecosystems are very versatile and size differences between acting individuals are huge, ranging from microbes to large trees. In addition, the timescale runs from picoseconds to 100 years. Thus we need means to handle all these different space and timescales. An ordered structure is called a *hierarchy*. Proper knowledge flow between the different hierarchical levels of our analysis allows utilisation of knowledge gained on detailed level in the analysis at more aggregated one.

Forest ecosystems are complex hierarchical systems, and several simultaneous phenomena occur in the hierarchy. The interactions at lower levels generate new phenomena and properties at higher levels. These novelties are *emergent properties* in the system. There are several definitions of the emergence, and our definition is often called as weak emergence. The characteristic emergent properties at each level in the hierarchy should be identified and introduced into the treatment of phenomena.

The globe has orbited the Sun during the whole period of development of life on the Earth. This is why biochemical regulation systems have developed in evolution to cope with the very regular and strong annual cycle of light and temperature that is a characteristic feature of the environmental factors. The *annual cycle of metabolism* covers the changes in the biochemical regulation systems, in functional substances and in structures matching vegetation with the annual cycle of environment. The processes in living organisms have their own annual cycle since biochemical regulations system changes the concentrations and activities of the functional substances.

Besides the annual cycle, there are slow (i.e. during the lifetime of individuals) and irregular changes in the environment such as extreme weather events. *Acclimations of processes* are changes in functional substances and in the biochemical regulation system matching processes in vegetation with the slow and irregular changes in environment. *Acclimations of structure* are slow changes in structure matching it with irregular changes in the environment such as changes in light environment after collapse of a neighbour tree. In contrast to adaptations, which occur over evolutionary timescales, acclimations occur over days, months and years, and they do not involve alterations in the genetic composition.

Vegetation synthesises annually large amounts of energy-rich macromolecules, especially into cell walls. The senescent tissues are the source of energy and raw material for life in the soil. In *decomposition* microbes transform the large organic molecules into smaller molecules that are utilised in the microbial metabolism. The nutrients in the senescent tissues are released into the soil, and they are available for reuse by the vegetation.

Individuals are the fundamental functional units in a forest ecosystem, they are first born, and they metabolise and finally die. The ecosystem is not only the sum of the individuals but novel features emerge. The effects between individuals in an ecosystem are called *interactions*. The behaviour of the individuals determines the interactions, but they are characteristic for the ecosystem. The reduction of photosynthesis in the canopy caused by shading is the dominating interaction in forest ecosystems.

The regularities in phenomena in forests can now be analysed with the basic concepts: process, transport, environmental factors, hierarchy, regulation, annual cycle, interaction, emergence, acclimation and decomposition. The basic concepts are used to characterise the essential features of the study object. Visual symbols for most of the basic concepts are introduced (Fig. 2.3) to clarify the ideas dealing with the behaviour of the object. Material/energy flows, process, biochemical regulation system, transport, structure and functional substances have their own symbols in the visual language; thus flows can be visualised utilising physiological, physical and anatomical knowledge as background in each phenomenon under study.

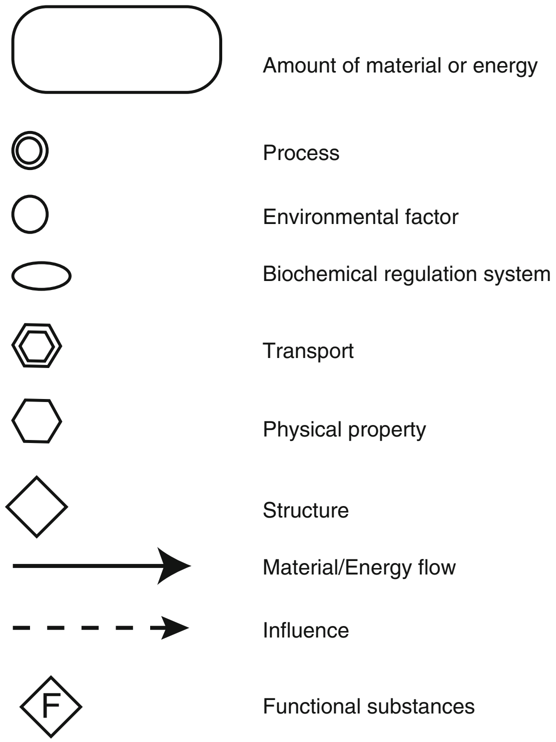

Fig. 2.3 Symbols describing the basic concepts to be used in the visualisation of theoretical ideas

2.2.4 Basic Ideas

The basic ideas link the basic concepts with each other and they enable the clarification of the vision. The basic ideas in the cover theory are:

1. The environmental factors vary greatly both in time and space. The orbiting of the globe around the Sun generates strong annual cycle, whereas the spinning of the globe creates strong daily cycle in environmental factors such as light and temperature. Spatial processes give rise to spatial and temporal variation in environmental factors. For example, photosynthesis decreases and respiration increases the surrounding CO_2 concentration near leaf surface.
2. The determination of environmental factors is problematic due to their great variability in time and space. Environmental factors can be well defined only in sufficiently small space and time elements. The scales of the environmental factors determine the most detailed level in the hierarchy. The great variability is characteristic for light, but also, e.g. concentrations and temperatures vary strongly in space and time.
3. The properties of the environment and of living organisms are reflected in the metabolism of living organisms. Environmental factors and the functional substances determine the conversion of material and energy in processes.

The relationships between processes and environmental factors can be determined properly only at the level of space and time elements due to the great variability of environment. The space and time element has to be so small that the variation in environmental factors is negligible within the element.

4. Cells (space element), individuals and ecosystems are natural spatial units. The metabolism responds very rapidly to environmental factors, i.e. during a short time element. The other evident timescales are year and rotation period. Thus the spatial levels of hierarchy are space elements of tissue, individual and ecosystem. The temporal levels of hierarchy are time element, year and rotation period. The flow of knowledge between the hierarchical levels, especially from detailed to more aggregated ones, is important in the analysis of the interactions between ecosystems and their environment.
5. The short lifetime of functional substances calls for a need to maintain the concentrations of the enzymes, membrane pumps and pigments in a long chain of steps generating the metabolic process. The biochemical regulation system synthesises, decomposes, activates and deactivates the functional substances. The actions of biochemical regulation systems keep the concentrations of the functional substances stable or change them, and the resulting regularities in the involved functional substances are emergent properties. The changes in the concentration or activity of functional substances are reflected in the effects of environmental factors on processes.
6. Material and energy fluxes mediate the interactions between ecosystems and their environment. In addition, the material fluxes within individuals are important due to the long distances between the locations of production and consumption. This is why transport plays a key role in forest ecology. Physical properties such as pressure, temperature or concentration difference generate material and energy fluxes, and in this way, physical knowledge is necessary in forest ecology.
7. Living organisms are the consequence of evolution over milliards of years. The emergence of novel features and their test against the existing ones result in effective metabolic, structural and regulation solutions. Thus efficient processes, transport structures and biochemical regulation systems have developed during evolution. Efficient solutions can, at least in some cases, be found as mathematical solutions of optimisation problems.
8. The strong and regular annual cycle in environmental factors has been a characteristic feature in the environment during the entire period of evolution, and a clear annual cycle in metabolism has developed to utilise the regular sequence of favourable and critical periods. In addition, the annual cycle of metabolism has been well tested during evolution, and it enables individuals to utilise the very regular alternation of warm and freezing or rain and dry periods in the climate of forests.
9. Acclimations are common in forests and they benefit the individuals since most of them have been tested in evolution. The acclimations of processes, structures and biochemical regulations have been tested during evolution only if the environmental factors generating the acclimation have varied during

the lifetime of individuals. Responses to increasing shading and drought are examples of well-tested acclimations. The atmospheric CO_2 concentration has varied considerably during the last million years, but during the lifetime of individuals, the concentration has been stable due to slow concentration changes. The present increase, about 100 ppm/100 years, is outside the range tested during evolution. Thus acclimation to CO_2 can benefit or harm the individual, and the predictions of the acclimations of forests to increasing CO_2 are problematic.

10. Important metabolic processes and transport phenomena have their own specialised structures. Actions of the biochemical regulation systems, together with the genetic code, determine the properties of the structure. The resulting regularities in the tree structure are emergent properties. The genetic code determines the great features, and regulation tunes it to the prevailing situation resulting in acclimations of the structure.
11. The interactions between individuals in a forest ecosystem are numerous and versatile. However, some interactions are more important and dominate the development of the forest ecosystem. Environmental factors convey the interactions in a plant community. Extinction of light and reduced photosynthesis in lower parts of a canopy is the most important interaction. The spatial variation in other environmental factors, especially between individuals, is small, and the different plants experience about the same environment. Thus spatially homogeneous environment is unable to convey interactions between individuals.
12. Conservation principles are cornerstones of Newtonian physics, and huge evidence has piled to support this theoretical idea. The living objects cannot violate the fundamental physical laws. The form of chemical compounds and energy may change, but the overall number of atoms and the total amount of energy do not change during processes or in transport.
13. The flow of information from the space and time element to the ecosystem level plays an important role in the analysis of the fluxes between forest ecosystems and their environment. However, it is very problematic to utilise detailed knowledge at the aggregated level, because the analyses become heavy and the small details easily hinder the researcher's view of important aspects. There are emergent properties at the various levels in ecosystems, and these new features allow the utilisation of the detailed knowledge at lower level in the hierarchy in condensed forms. The emergent features should be carefully analysed at each level, and the possibilities to utilise knowledge on more detailed level as emergent properties should be carefully analysed.
14. The carbon flow through ecosystem and circulation of nitrogen within the ecosystem, via photosynthesis, synthesis of macromolecules and finally decomposition of macromolecules in soil by soil invertebrates and microbes, are characteristic features for forests. In the soil, microbes decompose the macromolecules through the action of extracellular enzymes and utilise the resulting small energy-rich molecules in their metabolism. Without microbial activity, the organic matter would accumulate in the soil and nutrient cycling would be impossible.

A general description of vegetation and soil structures is also included in the cover theory to give the necessary background for theories of specific phenomena.

The cover theory outlines the research dealing with different phenomena in forest ecosystems. However, it is too general to be applied, and it must be developed to meet the properties of each single phenomenon under study within specific theories.

2.3 Constructing a Specific Theory

2.3.1 Phenomenon

There are several processes in forest ecosystems that contribute to the interactions between the ecosystem and its environment. In addition, the emergent properties, generated by the action of the biochemical regulation systems in the functional substances, in the tree structure and in the interactions between individuals, play an important role in the interactions. These phenomena serve closer attention and formation of specific theories within the cover theory, i.e. the rather general concepts and ideas in the cover theory are specified to meet the properties of each phenomenon under study.

The construction of the specific theory begins with the general description of the phenomenon under study, especially the connections with the material and energy fluxes in the ecosystems. The history of the research and the literature in the field is shortly described.

2.3.2 Structural, Metabolic and Physical Background

Metabolic processes in the different structures in ecosystems consume, convert and produce material and energy, whereas material and energy fluxes are physical phenomena. This structural, metabolic and physical background of the phenomenon is analysed.

There are highly specialised structures for each important phenomenon in forest ecosystems at each hierarchical level: The cells and the functional substances at tissue level, transporting structures at tree level and the organisms form the structural background at ecosystem level. Anatomy can provide useful knowledge for description of the structures involved.

The consumed/produced amounts of material and energy are in the focus of the treatment of metabolism. The action of the regulation systems changes the functional substances. The relationship between environment factors and metabolism respond to the change in the enzymes, membrane pumps and pigments. Physiological knowledge provides necessary understanding of the regularities in the metabolism.

The metabolism generates concentration, pressure and temperature differences, which give rise to material and energy fluxes at cellular, individual and ecosystem level. Physical knowledge contributes to the understanding of the fluxes and their connection to the metabolism.

The analysis of the structures, metabolism and transport phenomena is needed as background for proper understanding of the fluxes generating the phenomenon under study.

2.3.3 Specification of Basic Concepts and Ideas

The basic concepts in the cover theory deal with all phenomena in the ecosystem, and most of them can be omitted when dealing with some single phenomenon in the ecosystem. The necessary concepts are identified and clarified to correspond with the special features of the phenomenon under study in the framework of the general basic concepts in the cover theory.

The detailed analysis of the structures, metabolism and transport and specific concepts enables rather precise formulation of the basic ideas dealing with the phenomenon under study. These obtained specifications of the basic ideas in the cover theory are utilised in the formation of the theoretical model.

2.3.4 Theoretical Model

The basic ideas outline the fluxes and the factors affecting on the fluxes in a forest ecosystem. They must be clarified to be able to predict phenomena, especially fluxes. Then quantitative measures are introduced, and the phenomenon is studied in quantitative terms, because it allows more exact formulation of the ideas, it is more effective, and it enables utilisation of measurements.

The phenomenon under study includes often a space element having inflow, i, and outflow, o, of material or energy (Fig. 2.4). Metabolic processes and transport phenomena generate usually the inflows and outflows; thus physics and physiology provide causal explanations for the flows. Let X denote the amount of material or energy in the space element. Let Δt be such a short time interval that the inflow and outflows remain constant during Δt. Then the content of the space element at moment $t + \Delta t$, $X(t + \Delta t)$, can be obtained with the content at t, $X(t)$, and the in- and outflows utilising conservation of mass (Basic idea 10):

$$X(t + \Delta t) = X(t) + (i - o)\Delta t. \tag{2.1}$$

When we move $X(t)$ to the left-hand side of the equation and divide it with Δt, we get

$$\frac{X\,(t + \Delta t) - X(t)}{\Delta t} = i - o. \tag{2.2}$$

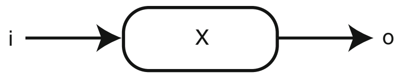

Fig. 2.4 Inflow and outflow in a container

When Δt approaches zero, the Eq. (2.2) results in differential equation

$$\frac{dX}{dt} = i - o. \tag{2.3}$$

Metabolic and physical processes and transport determine the in- and outflows. Thus physiological and physical knowledge can provide causal explanations for the material and energy fluxes between living organisms and their environment. In addition, physiological and physical knowledge determines the model structures linking the in- and outflows with environmental factors and functional substances (basic idea 3) and with concentration, pressure and temperature differences (basic idea 6). In this way, we can derive causal theoretical models, based on physical and physiological knowledge, to describe the fluxes between living organisms and their environment. The derivation of the models for in- and outflows requires additional simplifying assumptions and idealisations that can introduce shortcomings into model structures.

We meet quite often the situation where one single volume element is not sufficient, but a chain of interconnected volume elements are needed. The difference models, analogous to the model (Eq. 2.3), can often be constructed utilising physiological and physical knowledge. This approach leads to partial differential equations when the volume of the volume elements approaches zero. The chains of difference equations or partial differential equations result in the dependences of concentration or of temperature on space coordinates.

Often the fluxes between living organisms and their environment and the spatial patterns of concentration or temperature can be measured in the field. This provides the means to test the theoretical models, and in this way, we can get feedback from nature to the theory development.

2.3.5 Measurements

The aim of the measurements is to produce data to test specific theories and to provide descriptions of ecosystems. The theories deal with the fluxes between living organisms and their environment, and therefore, they should be measured in the field in addition to the environmental factors that influence them. After we have measured values of the response and its explaining factors, we can compare the model predictions with measured values enabling tests of the theory underlying the model.

Measurements of the response and explaining factors introduce an additional complication since measurements always include systematic and random errors. Let ε be the random, s the systematic measuring error of a theoretical quantity X and x the measured values of X. If we assume that the errors are additive with the signal to be measured, then

$$x = X + s + \varepsilon. \tag{2.4}$$

The noise and the systematic error in measurements reduce the quality of data, and they should be carefully analysed and reduced with technical arrangements.

We can never avoid systematic measuring errors, and their treatment is highly problematic. If we know the systematic error, it is easy to remove and correct the measurements, but in most cases, the systematic error is unknown and we have no means to correct it. However, we can often get an estimate of the magnitude of the systematic measuring error, and in this way, we can evaluate the possible bias in the results.

We can determine the statistical properties of the measuring noise with proper additional measurements. In addition, we can convert measuring noise in explaining factors with simulations utilising artificial data to random disturbance in the model behaviour. If the measuring noise of response or the random component in the model behaviour generated by noise in explaining factors is large when compared with the signal to be detected in the model behaviour, then the measuring noise smears the value of the data as test material.

2.3.6 Test with Field Measurements

We cannot prove a theory as a truthful description of the reality; we can only test the theory. Severe testing can detect shortcoming in the theory, it may provide explaining power of the theory, and it enables comparison with other theories in the field.

Determination of the values of the parameters. The test of the theory with field measurements begins with the determination of the values of unknown parameters in the theoretical model. The model fitting results in biased agreement between the modelled and measured values in the used data set. This is why we divide the data into two sets, estimation and testing data. We use the estimation data in the estimation of the parameter values, and we test the theory, whenever it is possible, with data that are not utilised in the model fitting to avoid the bias in conclusions caused by estimation.

The estimation is performed with normal statistical methods, e.g. minimising the residual sum of squares. This method is non-problematic if the explaining factors are independent from each other and if the parameters in the model do not compensate each other. In ecology, the explaining factors are often strongly interconnected and the parameters are interrelated. These features often make the estimation of the parameter values problematic, and the model structures must be simplified by reducing the number of parameters to be estimated; otherwise, the solution of the minimisation problem is not stable.

Prediction of characteristic features. Each phenomenon under study has its characteristic features that can be seen in the measurements. For example, the observed responses may have clear daily and annual patterns or rapid variation generated by changes in environmental factors. The first step in the test of the theory and the theoretical model is to answer the question: Is the theoretical model able to predict the characteristic features in the phenomenon under study in the test data set?

The focused study on characteristic features in the measurements enables qualitative evaluation of the explaining ability of the theory during informative episodes of the measurements. The analysis of the characteristic features focuses the test to critical part of the data, and in this way, shortcomings in the theory can be effectively seen.

Adequacy of model structure. The qualitative study of the prediction and explaining ability of the characteristic features in the behaviour of the study object is able to utilise only short episodes in the measured responses. Quantitative study of the agreement between observed and predicted behaviour of the research object enables treatment of large data sets, and it may detect rather small discrepancies between the theory and measurements, and it provides a measure of the agreement between prediction and observations.

Models are never truthful descriptions of the reality, and they always include shortcomings generated by the theory itself or the simplifying assumptions or idealisations in the derivation of the models for the fluxes involved. Measured field data enable the evaluation of the role of the shortcomings in the model structures within the accuracy and precision of the measurements. Special attention should be paid to the simplifying assumptions and to the idealisations done in the derivation of the models for the in- and outflows. The systematic measuring errors may confound the evaluation of the model behaviour.

The residuals, i.e. the differences between observed and modelled responses, are the basis of a tool to study the adequacy of the model structure. If there is some systematic behaviour in the residuals as a function of an explaining factor of the theoretical model or of any other factor, this is an indication of a shortcoming in the model structure or a sign of a systematic measuring error. The magnitudes of the systematic features in the residuals and their role in the reduction of the explaining power of the theory should be analysed. The reason of the systematic behaviour of the residuals should be carefully studied.

Explaining power. The theoretical explanation is the most important virtue of theories. The physical and physiological theory of forest ecology explains the observed behaviour of the system with the properties of the functional substances, with the action of the regulation system and with regularities in structures using evolution theory, physics, physiology, anatomy and chemistry as background knowledge. The crucial question is whether these concepts and background knowledge are sufficient to explain the observed behaviour in forest ecosystems.

Proportion of explained variance (PEV) is the quantitative measure of the power of the theoretical model to explain the observed variation in the behaviour of the research object. The remaining residual variation is caused by the shortcomings of the theoretical model, systematic measuring errors and random variation in the measurements. The PEV is calculated as one minus the ratio of variances of the residuals and of the measured responses. If measuring noises of response and explaining variables are small when compared with the residual variation, then small shortcomings in the theoretical model can be detected. Thus reduction of the measuring noises makes the test of the theoretical model more effective. The understanding of the reasons of the residual variation is important; thus we should analyse the roles of measuring noises, parameter estimation and shortcomings in the applied model structure in the observed residual variation.

Comparison with other theories. The last step in the theory testing is the comparison with other theories in the field. Then the basic concepts, ideas and theoretical models are compared. The field data are used to evaluate the relevance of the differences in field conditions. The performance of the models is based on their explaining and prediction power in the test data set. The differences in measurements, especially in measuring noise, and different environments are additional complications in the comparison.

Conclusion

The testing of the theory includes four aspects, i.e. (1) ability to predict and explain the characteristic features in the behaviour of the study object, (2) evaluation of the adequacy of the model structures, (3) determination of the explaining power and (4) comparison with competing theories. If the theory fails in some of the above four aspects, then it should be improved or rejected. If the theory is successful in all four aspects, then it gains corroboration and it is the best knowledge in its domain until a better theory is developed and tested. Development, testing and improvement of the forest ecological theories (Fig. 2.2) result in slow development and accumulation of knowledge dealing with the interactions between forests and their environment.

The four steps to test theories will play a major role in the Chaps. 4, 5, 6, 7, 9.

2.4 Formation of the Theory of Forest Ecology

Forest ecosystems are versatile and complex systems, and therefore, also the theoretical treatment of forest ecology is a demanding task. Knowledge can be gained about several phenomena at different levels in the hierarchy of space and time. Any forest

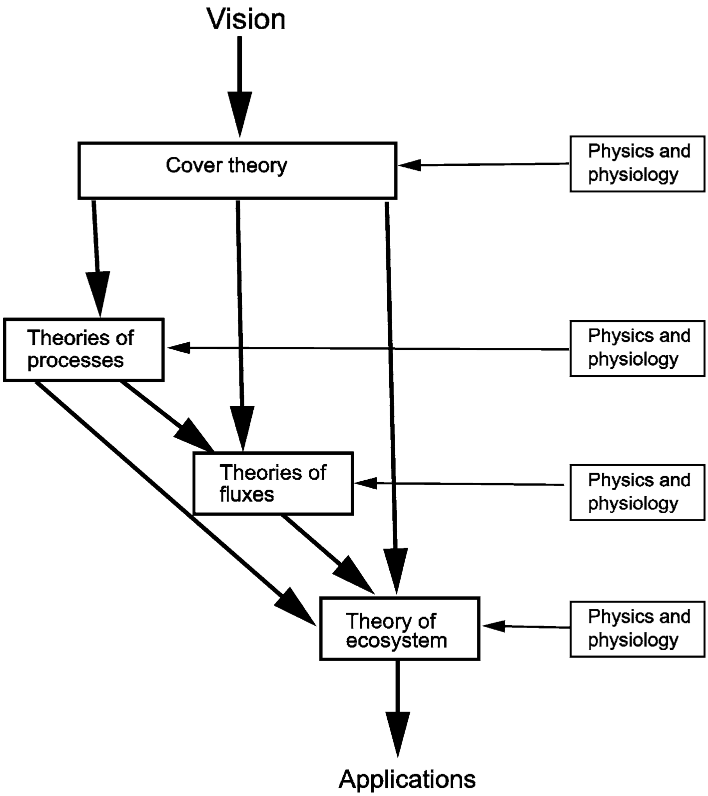

Fig. 2.5 Flow of knowledge in the formation of the physical and physiological theory of forest ecology. *Boxes* describe theory and *arrows* flow of knowledge

ecological theory should be able to combine the knowledge to a coherent system in which the understanding of different aspects is utilised at the ecosystem level.

Our solution to the problem of complexity is a web of specific theories under the guidance of the cover theory. The vision determines the main approach. Moreover, it outlines the objects, their characteristic properties and also the background knowledge. The definition of basic concepts allows the expression of the ideas in a more concrete form. The vision together with the basic concepts and ideas forms the cover theory, and they are applied as backbone in the formation of specific theories to deal with studied phenomena in forest ecosystems.

However, each phenomenon in the forest ecosystem requires its own specific theory including the specification of the basic concepts and ideas to meet the properties of the phenomenon. We can often derive a theoretical model using physiological and physical knowledge and the conservation of mass and energy. The theoretical model is interpreted as causal when it describes responses generated by metabolic and physical phenomenon. Field measurements allow testing of the theoretical model. If it predicts the flows well enough, then the model gains corroboration, and if it fails, then the approach should be improved.

The last step in the formation of the physical and physiological theory of forest ecology is to combine the specific theories to a coherent set of theories to cover the material and energy flows within an ecosystem and between the ecosystem and its surroundings (Fig. 2.5). This is possible since the specific theories 'speak the same language' due to the cover theory.

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