

UNITY IN ECOLOGY?

**AN INVESTIGATION OF PATTERNS, PROBLEMS, AND
UNIFYING CONCEPTS OF POPULATION ECOLOGY,
SYSTEMS ECOLOGY AND EVOLUTIONARY ECOLOGY**

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1 Introduction

The problem of the unity of science has always been an important topic among philosophers and scientists. Philosophers wanted to arrive at a unity of science by means of reduction of all complex theories to the fundamental theories and laws of physics. The unity of science was then provided by basic physical theories which were intended to be able to explain everything happening in nature. This aim proved to be impossible and today this form of unity seems to be no longer interesting for philosophers. Contemporary philosophers of science are interested in details of scientific practice and stress the heterogeneity of scientific disciplines. However, this does not mean that the topic of unity is uninteresting or that other forms of unity are impossible. Today philosophers look at ways of unification in small scientific fields or even in particular research programs.

Ecology is considered a heterogeneous discipline with many different methods and theories which sometimes even contradict. However, ecology is regarded as one scientific discipline. That is why it is interesting to investigate the discipline of ecology in order to see whether there might be some reasons for supposing a unified discipline. The ultimate challenge of ecology is the integration and synthesis of all ecological information available. This is impossible by summarizing everything; we have to find other ways which make it possible to understand the diversity and complexity of ecological objects and processes. We have to develop such forms of unifying explanations not only in order to cope with the diversity but also in order to *understand* the diversity by basic ecological principles.

With my dissertation, I want to contribute to the solution of the problems regarding the unity of science. I will deal with an old question in the philosophy of science using a new case study, ecology, which, up to now, has not been taken into account by philosophers. Since ecology has generally not been in the focus of philosophers this task is especially interesting. It will become obvious that in ecology we have to deal with the topic of unity in a different way than in physics. For this reason, this introduction starts dealing with concepts of the unity of science which have been developed by means of physics. Then, I will continue by looking at unifying concepts in biology before dealing with unifying concepts in ecology. In this last part of the

introduction, I will outline the guidelines for the remainder of the book.

1.1 Concepts of Unification in Science

Questions about the unity of science have always been a much-discussed topic among philosophers of science. For Logical Positivism, *Einheitswissenschaft* indicates a methodological unity of science being characterized by the unity of language. Statements from all disciplines should be translated into one language to impose a unified system (cf. Heggemann 1992, 12). However, there have been too many problems of translatability and the program failed. The successors of Logical Positivism developed an even stronger notion of unity. By means of *reduction*, they wanted to show that theories of complex processes (e.g. the movement of a group of bowls) could be explained by a more fundamental theory and thus be unified. They accepted different “languages“ in different scientific disciplines but required these “languages” to be translatable into each other. In addition, they demanded the deduction of the theorem of the reduced theory. Accordingly, a reduction of a complex theory of complex entities to a more fundamental one is successful if the complex theory can be deduced from the fundamental one. The unity of science is reached when fundamental theories can explain all natural phenomena by means of fundamental laws and a fixed vocabulary.

In 1948, a seminal paper on scientific explanation was published (Hempel & Oppenheim 1948). The authors assumed that explanations are deductive arguments and answers to why-questions. For them, the statement to be explained (the explanandum) is scientifically explained, iff it can be derived from statements of antecedent conditions and general laws, the explanans (Hempel & Oppenheim 1948, 12). The gist of this theory of explanation is the idea that universal laws cover all natural phenomena. Accordingly, every natural phenomenon can be subsumed under at least one of those laws. This theory of explanation (the covering law model) has had a big impact on all following accounts of explanation in philosophy of science until now.

Philosophers, using the covering law model, have considered scientific explanations to be unifying arguments that explain natural phenomena by means of fundamental universally valid laws. Oppenheim and Putnam (1958) combined the covering law model with the notion of the “unity of science” and developed the classic program of a unifying reductionist explanation. They proposed that nature had a hierarchical structure and that higher levels were composed of parts of lower levels. Thus, a

discipline on a higher level (B2) investigating whole objects being only composed of parts investigated by a more fundamental discipline (B1) can be reduced to this fundamental discipline. This form of reduction is called *micro-reduction*. The existence of complex entities and their behavior is explained by the composition of elementary components and their properties. This program finally aims at a theory of nature, which explains the existence of levels of nature and their complexity by fundamental laws and some initial conditions. Thus, there will be one or a few basic theories that organize the behavior of the fundamental elements (Oppenheim & Putnam 1958). Since the scientific theories are constructed according to a nested hierarchy, every special science like biology or sociology can be reduced to physics in case the translatability of the different scientific languages is given. Thus, for a scientific explanation, only fundamental physics is sufficient, at least in principle, and special sciences are only of pragmatic value.

Different forms of reduction have always been considered a tool with which to reach the unity of science. In general, reduction is a process that reduces entities, terms, laws or theories to other, more fundamental entities, terms, laws or theories. In philosophy of science, reduction is traditionally regarded as reduction of theories being articulated in its canonical form by Ernest Nagel (1949, 1961). A successful reduction of theories is reached iff it is possible to deduce the laws or theories of one discipline from the laws or theories of a more fundamental discipline (condition of derivability). Often, the terms of the reducing theory are not the ones used in the theory to be reduced. In this case, a deduction and vice versa a reduction is impossible because you cannot draw a conclusion that contains terms which are not included in the premises. In such cases, terms in the reducing theory and in the theory to be reduced have to be connected by additional bridge principles (condition of connectability, Nagel 1961, 354).

Most of the philosophical investigations on reduction and on the unity of science have been performed by examples from physics. Since the main goal of a science has been considered to establish general laws for systematic explanation and prediction (Nagel 1961, 450), physics has been regarded as the paradigmatic scientific discipline because it provided universal laws. Theoretical structures of physics have been considered the standard ones for every other science as well. Within physics, one can find some examples of successful reductions, although the used concept of reduction will be broader than the one developed by Nagel. The first step to make before trying

to reduce theories is a rational reconstruction of the theories involved (Scheibe 1997, 35f.). This demonstrates that even physical theories are in most cases not articulated in the logical form that is needed for a reduction of theories.

The unity of science, at least of scientific disciplines like physics, chemistry, and biology has always been an important aim of scientific research. Nevertheless, in contemporary science and especially in complex disciplines like economy and ecology, pluralist explanations seem to be much more acknowledged by philosophers of science. This may be because the notions of the unity of science were very ambitious and that the demanded (methodological) unities of science could not have been achieved. Often, philosophers of science do no longer accept classical concepts of unity and they question the possibility of reduction of complex theories to fundamental laws of basic theories. They stress the existence of special sciences. Not all empirical patterns about which counterfactual supporting generalizations can be made are from or correspond to physical sciences (e.g. Fodor 1974).

The possibility of a unifying explanation by means of reduction is controversially discussed, even for physics. There seem to be only a few textbook examples of successful reductions, but, in many fields of physics, successful reductions could not be performed. Other objections against reductions are that the reconstructed theories used for reduction are too idealized and that a reduction is too far away from the empirical science to say much about nature. Many antireductionists do even claim that the aim of a unity of science is wrong and impossible to reach (e.g. Cartwright 1983, Dupré 1993, 7).

Cartwright (1983) argues that a good scientific explanation is not covered by true universal laws but at best by *ceteris paribus* generalizations. These generalizations only hold under ideal conditions and they will no longer be valid if these conditions are not met. Cartwright assumes that nature is not totally governed by universal laws like the positivist philosophers and their followers have done. Possibly, natural objects are constrained by some specific laws and general principles, but in detail, they are perhaps not even statistically determined. In case this be true, most of the accepted laws (as descriptive statements) are false. A unification of science is not possible with these laws; we should be lucky to be able to organize natural phenomena at all (Cartwright 1983, 53).

Most contemporary philosophers of science are interested in the investigation of scientific practice. They focus on the examination of striking particularities and

detailed scientific methods and they are not interested in general unifying explanations (cf. Stump 1996, 443). The heterogeneity of the different disciplines is considered an important characteristic of science.

However, there are several arguments for the existence of laws and the unity of science. Many scientific explanations of different disciplines complement each other and there are no contradictory laws, at least not on the fundamental level. Thus, fundamental laws form a coherent system of constraints for all natural phenomena. Sometimes, they are overlapping (e.g. gravitational and electrostatic forces) but no case for contradiction is known. The known facts and our limited epistemological capability do not allow us to decide which of the metaphysical assumptions on the existence of laws and unity are correct. However, I do not see any reason why we should not look for unifying explanations but for pluralistic ones. There are even some good reasons why the search for unity is important for scientists and philosophers. Undoubtedly, a plurality of methods and even explanations (as working hypotheses) is necessary for good science but we cannot end with them. The goal of science should be to find comprehensive explanations that unify nature and help us better to understand it. I claim that most scientists who are not interested in scientific applications and technology but in basic research assume that there is only one world and they are interested in unifying theories (e.g. Wilson 1998). For me, it is much more plausible to assume that nature is a unity that we are able to conceive some aspects of it than that nature is pluralistic, and that the various scientific disciplines are not connected. The big unifying theories like Newton's theory of gravitation, Einstein's theory of relativity or Darwin's theory of natural selection have been very successful and are considered to be big advancements in science by nearly every scientist, philosopher and historian of science. In addition, probably the most important reason for those theories being so successful is their unifying power which enables us to better understand nature and its complexity (cf. Friedman 1974, Kitcher 1981, 1989).

As already outlined, one can distinguish between a methodological unity and an ontological or metaphysical unity of science. A methodological unity does not seem to be a very promising way to come to a unified science (and indeed the program of the Logical Empiricism has not led to success). Such a unity in terms of a unified language, a unified scientific method or a unified level of explanation (e.g. atoms) surely takes away a lot of scientific creativity and attraction of the different scientific disciplines. But one has to distinguish whether one should explain everything on the level of atoms as

a methodological prescription (that would be boring indeed because one would always have to deal with the same processes and it would not be possible to understand specific biological properties of e.g. a bumble bee) or whether one *can* explain a complex natural phenomenon from basic units and their properties only (in this case a unity provided by basic units and fundamental laws would be an attractive program). One could talk of a unity from an ontological point of view, which means that one will reach a unity which is provided by nature. In my view, the search for an “ontological unity” of science and unifying explanations of nature is what makes science interesting and meaningful. Unifying theories are necessary for scientific explaining and understanding and it is not possible to understand nature without understanding the connections and dependencies of different phenomena. Thus, I consider the aspect of unification to be fundamental to the conception of explanation. This conception is especially useful for biology and ecology because it deals with an immense variety and complexity of phenomena that can only be understood by means of unification.

Above, I mentioned the ideas of Cartwright (1983) and I think she has good reasons to doubt that a universal law covers every natural phenomenon. She has been able to show that at least until now scientists have not been able to demonstrate laws as universally applicable. However, she cannot show the non-existence of universal laws. The assumption of the covering law model that universal laws determine all natural phenomena is as possibly true as the idea that there are no universal laws and that natural phenomena behave like people in a society without being determined in detail (cf. Cartwright 1983, 49). But if Cartwright is right (and I think she is for many “laws” but probably not for all), then the idea to reach a unity of science by means of reduction to fundamental laws will not work because we are not able to exactly determine these laws. Most laws are only applicable by including *ceteris paribus* clauses.

Accepting this, we have two possibilities, either a reduction is impossible because there are no fundamental laws or we can perform a reduction with laws that are too idealized. In both cases, a unified theory as an adequate description of nature seems to be impossible. Nevertheless, this conclusion only follows if the conception of unity is strictly connected with the existence of fundamental laws. There is, however, no reason why this should be so. Perhaps it is possible to establish an “ontological unity” of science without the existence of fundamental laws. At least in biology and in ecology this form of unity is possible which will be demonstrated in the remainder of the book.

Besides reductionism, there are other ways of how to arrive at a unity of science. An important conception is to be found in the systems theory developed by Bertalanffy (1949, 1968). Bertalanffy believed that a unified conception of the world could much better be reached by means of isomorphism and analogies of mathematical structures describing different natural systems than by reduction to basic laws. Scientists should not try to reduce every level of reality to the laws and basic units of physics but they should look for structural uniformities of the different levels that are manifested by isomorphic traces of order. Many complex systems function in a similar way and show analogue processes. These analogies hint at an “organizational” unity of the world that can be described by *structural laws*¹. This conception may be called *perspectivism* in contrast to reductionism. The unifying principle is that one can find similar organizations at every level described by specific structural laws (Bertalanffy 1968, 48f.).

This form of unity should be reached by means of a general systems theory.² This approach works to a considerable degree with mathematical methods, aiming at the formulation and derivation of general principles, which hold for any system, without bothering too much about the elements of the investigated system. At last, general systems theory would have an axiomatic character (Bertalanffy 1949). Similar conceptions are provided by synergetics describing isomorphic traits in the behavior of complex systems (Haken & Knyazeva 2000, 31). This way of explaining via analogies and isomorphic traces of order has become very important both in biology and especially in systems ecology.

In the following section, I want to give an account of the most important ways of explanation and unification in biology. It will be shown that biology has to be dealt with differently than physics by philosophers of science. First, I will have a look at the special status of biology before looking at the philosophical approach that is mostly used for biology. In the last part of the next section, I will deal with unification in biology.

¹ The distinction between fundamental and structural laws is important and leads to quite different notions of unity. As will be demonstrated, this distinction will help to clarify the debate on laws in biology and ecology (cf. section 2.4.2.2).

² This conception of unity is quite different from the one provided by reductionism. As we will see, one can distinguish two opposing approaches in ecology, one accepting the reductionism (population ecology), the other one accepting the perspectivism (systems ecology).

1.2 Concepts of Unification in Biology

1.2.1 Scientific Particularities of Biology

Proponents of the Logical Positivism interested in the *Einheitswissenschaft* tried to deal with biology by applying the same methods they used for physics. They did not pay attention to specific biological patterns and considered physics the fundamental scientific discipline providing the paradigmatic theoretical structures of science. Until the late sixties, philosophy of biology had just been a secondary sub-discipline of the philosophy of science and biology had been considered an immature science (cf. Wolters 1999).

The situation began to change in the sixties. Philosophy of biology became an accepted sub-discipline of philosophy of science. Philosophers of biology asked other questions than philosophers of physics and considered biology to be an autonomous science being distinctly distinguished from physics. In 1961, Ernst Mayr wrote a seminal paper on causes in biology. He distinguished two forms of biological explanation, one that he called *functional* whereas the other was termed *evolutionary*. This distinction is a characteristic of biology and cannot be met in physics or other scientific disciplines. Functional or *proximate* explanations are used to explain *how* biological processes work whereas evolutionary or *ultimate* explanations shall explain *why* biological processes work the way they do. The functional biologist is interested in actual processes, e.g. in the hormonal changes that induce bird migration whereas, the evolutionary biologist is interested in the genesis and history of the hormonal change and in the rules that control these changes from generation to generation. In biology, both proximate and ultimate forms of cause are used in explanations and it is nearly impossible to explain either by proximate or by ultimate causes alone. To come to a complete understanding of biological phenomena, it is necessary to consider both forms of cause (Mayr 1961).

Evolutionary explanations are typical for biology and characterize its autonomy from physics. Normally, physicists are not interested in ultimate causes. Physicists can mostly apply the covering law model which corresponds to a form of proximate explanation and one does not need ultimate and historical explanations to understand the phenomena. However, in biology the evolutionary explanation is nearly always necessary to understand biological processes. Although there are some physical disciplines like cosmology that use evolutionary explanations, physics in general, is an

ahistoric science. Physical disciplines using historical accounts correspond much more to biological disciplines than the classical physical disciplines like mechanics or electrodynamics.

In biology, there are nearly no cases where the covering law model of explanation can be applied. Since every biological pattern that can be described by a “law” is a product of evolution, there are no universally valid generalizations (cf. Beatty 1995).³ Accordingly, in biology we cannot explain by fundamental laws as we do in physics. Although biologists can reconstruct the evolutionary process and explain specific properties by means of evolutionary and genetic theories, they are not able to predict future events accurately (cf. Scriven 1959). Nevertheless, this problem is also provided by physical disciplines like cosmology and meteorology.

In biology, one can find traits that are highly complex and demonstrate an extreme perfection, e.g. the mammalian eye. Although they are considered adaptations, they can hardly be explained in detail by natural selection. However, it is possible to provide an account of how they could evolve. This typical biological form of explaining is called a *how-possible explanation* (Brandon 1990, 178). Although one cannot know whether the used explanation is true it increases our understanding of a trait.⁴ One can find as well *how-actually explanations* in biology which explain how an adaptation has actually evolved but they are only rarely met (Brandon 1990, 183).

Physicists and biologists pose different questions thereby characterizing a methodological distinction between physics and biology. A typical biological question is *what for* specific functions and traits in nature are developed. This question expresses a difference between the way historical physical disciplines like cosmology deal with genesis and evolution and the way biology does. Physicist will never ask such a question. Although biologists do not consider evolution to be a teleological process, they often use a teleological language in their descriptions (for this sometimes the term *teleonomy* is used, meaning the apparent purposefulness of organisms and characteristics, cf. Mayr 1961). The specific scientific status of biology is then provided by the use of a teleological language (cf. Kochanski 1979, 87). Biologists describe the behavior of organisms as if the organisms had specific goals, but this does not mean

³ I will elaborate a discussion on this problem and its significance for ecology in the second chapter (2.4.2.1), thus the demonstration at this place is very rough.

⁴ It may be possible to find several how-possible explanations for the same trait that are in coherence with the known facts of evolution of the investigated object. Consequently, biologists are not seeking for the *one* correct mechanism; rather they are interested in the relative significance of different accounts for specific explanations (cf. Beatty 1997).

that evolution is a teleological process. It shows that biologists use a different method to describe natural phenomena than physicists, but this does not tell us whether the ontological status of physical objects is different from the one of biological objects.

There are, however, many factors in which biological and physical objects differ. The advantage of physics is that physicists are able to isolate physical systems and investigate them without losing too much of empirical accuracy while this is impossible in biology. Biological entities are unique (due to their historical origin) and very complex and every organic or ecological system is so interwoven and influenced by constraints of most different factors that it is hardly possible to isolate them without changing their behavior. Biological and ecological systems underlie so many feedbacks, homeostatic devices and potential multiple pathways that a complete description is quite impossible. Furthermore, the analysis of such a system by means of isolation of its parts would require its destruction. That is why it would be futile to explain the system as a biological one. One can explain it by means of its abiotic parts (atoms, molecules, etc) but the specific biological aspect will be lost. Biological things are complex and diverse, while physical things are complex and uniform. This means that theoretical models in physics can be general and accurate whereas biological ones are either accurate and specific or general and strongly idealized. A model for a population of atoms will be applicable to other populations of atoms as well, other things being equal, but this is not the case for models of populations of organisms (Horan 1988, 273). This is one of the major differences between biological and physical disciplines.

Due to the demonstrated differences, philosophers and biologists often do not talk of theories and laws in biology but rather of *models*. Most of the philosophers of biology are proponents of the semantic view of theories that focus on models. For this reason, in the following part I will give a short description of the semantic view of theories. I will oppose it to the classical view of theories, which is still predominant in physics, and thereby I will demonstrate the theoretical differences between physics and biology.

1.2.2 Philosophical Approach to Biology

The classical or *received view* of theories considers theories to be sets of statements. Philosophy of science was regarded as the logical analysis of scientific concepts and theories (cf. Giere 2000). Theories were considered linguistic entities, which are characterized by their syntactic properties. The scientific language can be divided into three forms of terms, the logical, the observational and the theoretical ones. The

observational terms were fully interpreted but theoretical terms were only partially interpreted by means of correspondence rules in a mixed language (Suppe 2000). According to the classical view, a theory is a set of uninterpreted axioms in a specified formal language and a set of correspondence rules providing a partial empirical interpretation in terms of observable entities and processes. A theory will be true iff all interpreted axioms are true (cf. Giere 2000).

The *received view* was attacked on various reasons. The theory - observation distinction proved untenable because observations are always theory-laden. Thus, theories have been considered more than just linguistic entities. That is why they cannot be articulated in axiomatic systems, and symbolic logic is an inappropriate formalism (cf. Suppe 2000). In contrast to the *received view* of theories, philosophers developed another conception, which wanted to avoid the obvious difficulties. This conception was called *semantic view*. The term *semantic* refers to the fact that there is a model providing a realization in which the theory is satisfied. The focus of interest has shifted from the axioms as linguistic entities to models, which are considered non-linguistic entities. A theory is considered to be (1) a theoretical definition plus (2) a number of theoretical hypotheses. Theoretical hypotheses claim that certain things satisfying the definition may be true or false. A theory can be true if all its associated theoretical hypotheses are true (Giere 2000).

Most proponents of the *received view* of scientific explanation stress the importance of universally valid laws. However, in many cases these "laws" prove to be no more than *ceteris paribus* generalizations. This is especially true for biology. Although biologists have to work with *ceteris paribus* clauses to come to generalizations these clauses (all else being equal), do not match the biological world as well as the physical. Thus, the notion of universally valid laws in biology is not very useful and most philosophers of biology will follow the conception of explanation and law of the semantic view. According to the semantic conception, a scientific theory is defined by specifying the behavior of a physical system in a mathematical language. A physical system is a highly abstract and idealized replica of a real phenomenon, showing how the phenomenon would behave in case the idealized conditions were met (Thompson 1988). Laws are not used to describe real phenomena which have been observed. They are rather descriptions of an idealized model. These laws are always applicable but this does not tell us anything about their general truth. One problem of this conception is the question which degree of idealization is allowed. Proponents of the

semantic view defend different opinions about these questions and there have been long discussions about whether this conception of theories is instrumentalist or realistic (cf. Horan 1988, Lloyd 1988, Thompson 1988). Since there are both realists and instrumentalists among the proponents of the semantic view, it seems to be combinable with both views.

In spite of the open realist/instrumentalist discussion, the semantic view has some advantages compared to the received view. That is why most philosophers of biology prefer it. Advantages of the semantic conception are seen in the fact that it is closer to the practice of scientists and their reasoning and that it does not require the existence of *laws of nature* (the "laws" used in semantic conceptions are no more than descriptions of models and do not have any metaphysical implications like laws of nature). Two different axiomatic systems that are semantically equivalent, this means that they share the same models, constitute one theory, not two, as it would be the case in the *received view* (Lloyd 1988). Thus, the semantic conception gives a much better account of explanation and theory structure in biology than the *received view* (Thompson 1988, 293).

Since the notion of laws and theories is different in biology from the one used in classical physics, one can well imagine that there are consequences for the conceptions of unity in biology. I will deal with these conceptions in the next section.

1.2.3 Unity and Reductionism in Biology

From the previous illustration, it seems to be obvious that the unifying concepts used for physics cannot be used for biology. Biology has to do with singular phenomena that cannot be unified by means of general biological laws. Explanations following the covering law model and predictions from fundamental laws are not usual for biology. Instead, biologists work with descriptions, comparisons and generalizations which are in most cases not very far-reaching and cannot be reduced to elementary units. Nevertheless, these "biological explanations" have the same scientific value as deductive explanations in physics and thus stress the autonomy of biology (Mayr 1985). For Mayr, there is no unitary form of explanation in biology and there can be no unitary philosophy of science. The need for ultimate explanations in biology prevents a reduction of biology to chemistry and physics. Thus, the need for ultimate explanations ensures the autonomy of biology and the autonomy of the philosophy of biology as well (cf. Beatty 1994, 352).

Philosophers of biology conceived of reduction in a different way as philosophers of physics. Commonly, they make a distinction between three different forms of reduction, the *ontological*, the *methodological* and *epistemological* form (Ayala 1974, viii, cf. Kochanski 1979, 78f. Hoyningen-Huene 1985; Morchio 1991). *Ontological reductionism* for biology means that physical parts compose biological entities and that no special vital force is needed to produce life. This view implies that the laws of physics and chemistry can be fully applied to all biological processes. The *methodological reductionism* is concerned with strategies of research and the level of explanation. It assumes that every scientific research as well as every explanation should be performed on the most fundamental level. The epistemological reductionism corresponds to the classical concept of theory reduction assuming that biological theories are formally reducible to physical ones. This form of reductionism should rather be termed *meta-theoretical* reductionism because the term *epistemological* seems to distract from the main aspect of this field of reduction (cf. Kochanski 1979, 80).

In physics, one normally does not distinguish between meta-theoretical and ontological forms of reduction. This is probably due to the different ways of looking at theories by philosophers of physics and of biology. In the *received view*, theories and observation are connected by correspondence rules. Thus, theoretical terms can be truly interpreted and they provide an exact explanation on what is going on in nature. In this case, a difference between the ontological and the meta-theoretical form of reduction is not necessary. The claims of the ontological reductionism will be demonstrated by a formal reduction of the corresponding theories. This is different in the case of the semantic view, where the distinction between ontological and meta-theoretical reduction is justified. Since biologists do not assume to be able to describe all biological processes with their theories there is another reason why the meta-theoretical field of reduction should be separated from the ontological one. Most biologists will be in favor of an ontological reductionism but they will argue against the possibility of a meta-theoretical reduction (cf. Ayala 1974, xi) or they are not interested in it.

Although most biologists and philosophers of biology are proponents of an in-principle (ontological) reduction from biology to physics, they will not deal with a reduction of theories in a formal manner. They often argue that a theory reduction from biology to physics is not possible, because the understanding of physical and chemical

structures is not sufficient to explain biological processes. Yet in most cases, biologists will not doubt that physical parts and principles in general can explain biological processes only, although this cannot be demonstrated in detail (cf. Morchio 1991). Biologists often reject forms of methodological reductionism for the same reason as physicists. It would take too much time to explain on the most fundamental level always (e.g. explaining the courtship behavior of a loon in terms of atoms) and it would take away the specific biological aspect of investigation and explanation. Thus, biologists and other scientists dealing with complex systems will reject the methodological form of reduction.

As already demonstrated in the previous parts, there are other notions of unity as by means of reduction. I already mentioned the systems conception of Bertalanffy, which had a much stronger impact on biological thinking than on physical thinking. However, one can find different forms of unity. Thus, there are connections and interdependencies between theories which do not allow one theory being replaced by another, but will hint at a unity of science. At least in the case of molecular biology, interconnections like supervenience, heuristic dependence and confirmationally dependence do not support reducibility but show that there is a unity between chemistry and biology (Kincaid 1990, 589ff.).

Other forms of unification in biology are provided by analogies, e.g. Darwin's natural selection and artificial selection, interfield theories and postulation of a new level of organization. Thus, one can consider the chromosome theory of Mendelian heredity to be an interfield theory that made predictions for Mendelian genetics and for cell theory based on related information from the other. The cell theory served to unify botany and zoology by finding a new level of organization that had similar features in animals and plants (Darden 1986, 102).

A very good example of a form of unifying explanation which cannot be reduced to the fundamental laws of physics is Darwin's theory of evolution. Biologists normally assume a unified biological nature being composed up of molecular particles by means of the (biological) mechanisms *mutation* and *selection*. With the help of these causal mechanisms, it is possible to explain the complexity and heterogeneity of biological nature without reference to physical laws. However, evolutionary theory does not just unify biological phenomena but also helps to unify the science of biology. Without evolutionary theory, biology would be split into many different disciplines that are not connected with each other. If there were no evolutionary theory, cell biology, zoo

physiology, botany, zoology, ecology etc would be autonomous disciplines and it would be hardly possible to integrate them to form the science of biology. This demonstrates that a unification of scientific objects by means of an evolutionary unifying explanation (one can explain every biological entity by initial circumstances and basic mechanisms) can result in a unification of science. This form of unity is only possible within biology. Thus, the way of explaining and unifying by evolutionary theory is the best argument for the autonomy of biology.

This form of biological explanation is not interested in explaining every detail of the world. It rather aims at a better general understanding. Many biological phenomena can only be explained very roughly and not in detail by the mechanisms of mutation and selection. However, these mechanisms help us to come to a unified understanding of the entire biological world. In many specific cases, an exact explanation will not be possible because the mechanisms are not known exactly and cannot be applied to the concrete case. However, rough estimations and how-possibly explanations will increase our understanding of biological nature.

Ecology provides these general features of biology as well. Since ecology is a biological discipline dealing with complex biotic and abiotic processes, I will start investigating the concepts of unity in ecology. The next section is as well the introduction into what follows in the remainder of the book.

1.3 Unifying Concepts in Ecology

In this section, I want to introduce the field of investigation of this book – concepts of unity and unification in ecology. In the philosophy of biology, the fields investigated have been evolutionary theory and genetics⁵; largely, philosophers of science have neglected other biological disciplines. There is hardly any philosophical investigation of plant physiology, animal behavior, botany etc. Ecology has also been neglected for a long time but the interest of philosophers of biology in ecology seems to have

⁵ Philosophers of biology have dealt with the questions of unity and reductionism nearly always by means of evolutionary theory or genetics. It has been discussed among philosophers of science, whether classical genetics could be reduced to molecular genetics and whether morphological traits can be explained by molecular processes (Schaffner 1967, 1969, 1974, Hull 1974, 1982, Ruse 1984, Rosenberg 1985, Vance 1996). The claim of Schaffner (1967, 1969, 1974) that this reduction is possible with a modified model of Nagel's conception of reduction, initiated a discussion between the proponents of reductionism Schaffner (1967, 1969, 1974), Ruse (1974), and the antireductionists Hull (1974, 1982), Kitcher (1984) and Rosenberg (1985).

increased during the last few years and there has been an ever-increasing amount of philosophical investigation of ecological research.⁶

Unity in ecology is an especially attractive topic because ecology is a very heterogeneous discipline and serves as a good case study for investigations of unity and disunity of science. Most ecologists and philosophers doubt whether a unification of the discipline of ecology will be possible. In case they deal with the problem of unity, they only investigate a small part of ecological research. In contrast, I want to deal with the whole field of ecology in order to develop a general framework for the establishment of unifying explanations. The aim of this investigation is to show that it is possible to develop some forms of explanation which will arrive at a unity of ecology. This unity is specific for ecology and is very different from the conceptions of unity used in the philosophy of physics

Problems of reductionism and holism have always been discussed in ecology, - mostly by ecologists and not by philosophers. These discussions generally lack the philosophical foundation and they confound different aspects like methodological and ontological questions on reduction. As will be obvious by these debates, ecologists talk about reductionism and holism in a different way than physicists. For this reason, I do not think that a classical account on reductionism can help to arrive at a unity of ecology. A useful approach for ecology will not concentrate on laws but will rather be interested in a simplification and an integration of complexity so that we can get a better understanding of ecological processes. As for biology, the unificationist approach of Friedman (1974) and Kitcher (1981, 1989) seems rather promising for ecology. In their opinion, the main aspect of a scientific explanation is the *unifying power* leading to an *increase of our understanding* of the world.

For the investigation of the unification in ecology, I will use a modified conception of the thesis that explanatory unification increases our understanding of nature. In contrast to Kitcher, I am not so much interested in deductive argument patterns of explanation (cf. Kitcher 1981) but rather in those points of explanation helping us to arrive at an understanding of nature. We will not need fundamental laws to increase our understanding; it is enough to understand contemporary complex phenomena as developed from former and simpler phenomena by means of some general

⁶ At the meeting of the International Society for the History Philosophy and Social Studies of Biology (July 2001 in Connecticut) there were two sections on philosophy of ecology and in September 2001 there was an whole issue of *Biology & Philosophy* dedicated to the philosophy of ecology.

mechanisms. Although this is not an accurate explanation, it helps to understand nature and its great diversity as a unity.

I will start with the investigation of the scientific status of contemporary ecology (Chapter 2). I will describe the heterogeneity of ecological objects and the heterogeneous scientific approaches (2.1). Since one can distinguish between many different approaches, I will try to bundle them according to their respective ideas on explanation and unification. I will distinguish between three different approaches which use different methods of research and start from different assumptions on the ontological status of ecological objects. These three approaches are *population ecology*, *systems ecology* and *evolutionary ecology*. I will give a short historical account on them in order to understand the contemporary differences of the approaches. Evolutionary ecology developed later than the other approaches, and there is no settled opinion on what evolutionary ecology is. In most cases, it has been considered a form of population ecology but I do not think that this is correct. I will plead for the autonomy of evolutionary ecology and develop a conception of this approach which lies somewhere between holistic systems ecology and reductionistic population ecology (2.2).

After having demonstrated the three approaches, I will continue with an investigation of the methods and the theoretical structures of contemporary ecology. I will have a short look at methodical problems of ecology and thereby investigating some problems of terminology and experiments (2.3). Then, I will come to the main point of the second chapter: the examination of ecological explanations and generalizations (2.4). Ecological explanations in general do not use laws but only restricted generalizations. These forms of explanation are often denominated as “models”. That is why I will give an account on models in the philosophy of science and in ecology (2.4.3). The last section of the second chapter deals with a specific form of modeling in ecology, the computer simulation (2.4.4). Computer simulation is a form of explanation combining the typical aspects of explanation of the population-oriented view with some aspects of the systems theoretical view. Simulation is an important form of unifying explanation which helps better to understand ecological phenomena but cannot explain them in detail.

The third chapter deals with some conceptions of complex ecological entities like ecosystems and communities. *Ecosystem* is a term with many different notions and it is often used in connection with metaphysical views on nature. It plays an important role

in the discussions on nature conservation, and even basic research is influenced by it. The term *ecosystem* is used in a wider and in a more restricted sense. I will demonstrate that its specific meaning, a level of integration just above the level of community is not justified. *Ecosystem* should thus be used as a pragmatic term without a specific meaning, it can in most cases, be replaced by the more general “ecological system” (3.1). Another level of integration commonly assumed is the *community*. It will become obvious that the term *community* is as plurivalent as the term *ecosystem* and that it corresponds to various levels of integration (3.2.1). Since the concept of community has mostly been applied to plants, I will consider the way botanists investigate plant communities (3.2.1.1, 3.2.1.2). In vegetation science, a hierarchy of plant communities has been developed, which can be considered a (methodological) unification which has been established in order to cope with the diversity of plants (3.2.1.3). In the last section of this chapter I will demonstrate that one can come to better characterizations of communities and ecosystems by evolutionary explanations than by phytosociological ones (3.2.2).

The significance of evolutionary theory for ecology will be elaborated in the forth chapter. There, I will investigate the unifying strategies of population ecology (4.1), systems ecology (4.2) and evolutionary ecology (4.3). In population ecology, we can find some claims of successful reductions, as an example I will take the Lotka-Volterra equations. Within population ecology there has been a long debate on holism and reductionism by the example of the formation of a community. Although one can distinguish between a radical form of reductionistic explanation and a more temperate one, the entire approach of population ecology belongs to a reductionistic approach. Systems ecology imposes a different way to come to a unity by means of analogies and isomorphism. Most forms of contemporary systems ecology are not interested in ontological questions. Although proponents stress their holistic way of thinking, I will demonstrate that their methodology is reductionistic. Modern forms of systems ecology want to apply hierarchy theories in order to combine holism with reductionism and to arrive at a unity of ecology (4.2.2). Both forms of systems ecology do not provide any means for a unity from an ontological point of view, but they provide unifying methods. Both, population ecology and systems ecology produce proximate explanations and are thus unable to come to a unity based on fundamental material units. Only ultimate explanations can provide a material unity of ecology.

For this reason, I will investigate the relations between evolutionary theory and ecology in order to develop an *evolutionary ecology* which can provide unifying explanations based on material units (4.3). The role of historical thinking will be investigated because we do not have to deal with genetic mechanisms only but also with the historical process of evolution (4.3.1). Different ecological and evolutionary hierarchies evolved by means of the historical process of evolution (4.3.2). Obviously, there is a connection between evolutionary and ecological hierarchies. I want to investigate how evolutionary units could have become ecological units and vice versa. I want to envisage a picture on the relationship of higher ecological levels with evolutionary ones (4.3.3). The meeting points, as I will demonstrate, are co-evolutionary units (4.3.4). In the last section of this chapter (4.3.5), I will outline the significance of evolutionary ecology for the unity of ecology. Evolutionary ecology as a historical approach has not been able to explain in detail how the formation of complex co-evolutionary units evolved but it can develop guidelines increasing our understanding.

In the fifth chapter, I will discuss whether my results for ecology are also applicable to other scientific disciplines. Ecology has to deal with always changing constraints and evolutionary contingencies, this problem can also be found in some physical disciplines making use of historical explanations. Finally, I will plead for the suggestion that physics should no longer be the leading scientific discipline. This role should be handed over to ecology, because we can learn more about nature from it than from physics.

2 Patterns and Problems of Contemporary Ecology

In this chapter, I want to investigate the scientific status of contemporary ecology. First, I will look at the field of ecology and the different approaches which can be found in that discipline. Although the discipline is very heterogeneous, it is possible to distinguish three big approaches which are characterized by different ways of method, explanation, and unification. It is assumed that the reasons for this disunity can be found in the particular history of ecology that is why I want to outline some important historical features of this discipline. I will go on by looking at some methodical problems of ecology before dealing with theoretical structures. The investigation of laws, models and simulations being important elements of different ways to arrive at unifying explanations will be the main aspect of this chapter. I will begin by some introductory examples which describe the diversity of ecological research.

2.1 The Field of Investigation in Ecology: Examples and Explication

Before going into the details, I will give some examples of what ecologists do. Then I will continue by canvassing the meaning of the term *ecology* and examine the tasks and objectives of this discipline. Ecology is not just considered a scientific discipline but also a form of ideological and political approach to human beings and their environment (cf. Trepl 1987, 12). Even scientists often conceive of ecology as a normative discipline stressing the connections between scientific results of ecology and conservation management or political strategies etc.⁷ In the following, however, I will use the term *ecology* as far as possible in a restricted sense and deal with it as a biological sub-discipline only.⁸

Now one could assume that a scientific discipline has a limited field of investigation and that it is characterized in a unified way by its proponents and that it provides a number

⁷ In ecology, one can find several forms of “applied ecology”. In general, this form of ecology deals with the development of strategies for the conservation of nature (e.g. how to cope with environmental pollution).

⁸ An analysis of the history of the relationships between the scientific discipline of ecology, ecology as a political guideline and the ecological movement can be found in Trepl (1987) and Hagen (1992).

of reliable methods and theories. Apparently, this is not the case in ecology. This discipline is very heterogeneous and uses many different methods and theories to explain the behavior of a wide variety of very different research objects. Ecologists use not only biological methods and theories but chemical, physical, mathematical, systems theoretical, and cybernetic ones as well. Thus, ecology appears to be a merger of a variety of disciplines and their methodological approaches rather than a discipline on its own.

One important task of ecology is the investigation of abundance and distribution of organisms and the factors that determine them. Ecologists want to know how many species of animals, plants, fungi etc are living in one particular habitat (the area in which the investigated organisms live) and why they do not live in others. In order to answer these questions, the first task for ecologists is to take stock of the different species. Since it is impossible to record all the species of a specified area, ecologists investigate only several groups of organisms (like birds or plants). This stocktaking is an important precondition for the investigation of ecological questions and can take a lot of time and resources. Many scientists refer to it as unscientific "natural history", but it is an integral part of scientific ecology.

Most ecological questions are concerned with the interrelationships of organisms and species with others and their abiotic environment. Thus, many ecologists are interested in the interdependencies of animals and plants. They investigate whether some insect species (like ants, bees, beetles etc) are bound by specific plants to pollinate them or to disperse their seeds. In many cases, one can find specific mechanisms used by plants to attract pollinators or seed dispersers, e.g. the production of sweet liquids. These mechanisms are different for each species of plant or pollinator. This means that every system of pollination has to be investigated on its own. Nevertheless, there are also other dependencies between plants and animals to be examined. Ecologists investigate whether caterpillars use the leaves of only one plant species for food (monophagous caterpillars) whether they are bound to only certain plant species (oligophagous caterpillars), or whether they can eat leaves from nearly any plant (polyphagous caterpillars). They want to know how many leaves can be eaten by a caterpillar per day, how many caterpillars can live on an individual plant without doing harm to it etc. Similar investigations can be performed with any plant-eating animal species.

Ecologists often examine density regulation in populations. They are interested in what factors (biotic or abiotic) are necessary to increase (or reduce) the number of species in a given environment. Well-known examples are predator-prey-systems such as foxes and hares whose populations are dependent on each other. Whenever there are many hares, the number of foxes will increase because they have plenty of prey, which in turn reduces the number of hares. This causes the number of foxes to decrease since there are not enough hares to eat. The small number of foxes allows the population of hares to grow again. Both populations oscillate but remain more or less stable in their density (considered over a longer period). There are many such investigations on density in populations and communities. For example, ecologists also investigate how many individuals of a bird species (e.g. puffins) can breed together in a limited area (intraspecific competition), or they look at interspecific competition, e.g. by analyzing the amount of plant species being able to exist on meadows with a controlled amount of nitrogen.

The factors regulating population density can be both organic and inorganic. Some ecologists are mostly interested in abiotic factors and their influence on life. Those ecologists examine cycles of energy and matter like the cycle of nitrogen or sulphur. They want to know how much energy is used by a specific organism, a population or even a community. They are interested in functions of ecosystems (interrelations of organisms and their environment) by measuring the flux of energy in a system, the amount of biomass produced, and the influence of chemicals like nitrogen, biocides or even acid rain. They investigate the relations between producers of biomass (photosynthesizing plants), consumers (herbivorous and carnivorous animals) and decomposers (bacteria and fungi) that separate biomass into inorganic matter and energy.

Another type of ecologist is interested in questions like “*Why* are there so many kinds of animals?” (cf. Hutchinson 1959). These ecologists want to know *why* some caterpillars are obligatorily bound to a specific plant species. *Why* are there so many different niches in a specified area? *Why* are there some “hot spots” of species diversity while other places on earth are poor in species diversity? *Why* are there so many insects and so few mammals? *Why* do some animals develop by a complete metamorphosis while others have a direct development and *why* do some species reproduce sexually and others asexually? Ecologists answer these questions by using the results of the investigations mentioned above and by considering evolutionary

theory. Although these questions do not seem to have too much to do with ecology, one can explain many ecological processes by means of the answers and will better understand the ecological diversity.

If we do not only look at what ecologists do but also consider what they believe to be the objectives of ecology, we can find a wide variety of definitions, explications and characterizations. Generally, it is accepted that ecologists are interested in the interrelationships between organisms and their environment.⁹ According to this characterization, ecology is not a specific discipline but a very broad form of biological research and it is not possible to draw a line between ecology and other biological disciplines. In this case, every form of biological research investigating more than one organism should belong to ecology. However, this is not the case. Parasitology, for example, belongs to this category. It has never been considered a branch of ecology, although significant ecological work was based on studies with parasites (cf. McIntosh 1985, 161). Therefore, this general characterization concerning ecology is not very illuminating.

Other general characterizations of ecology emphasize more specific aspects: "Scientific ecology in the broadest sense is interested in causal and functional relations on the levels of organisms, populations¹⁰ and communities (biocoenoses):¹¹ ecology considers the interrelationships of the organisms of one level with each other and with their environment" (Czihak et al. 1984, 705).¹² In this characterization of ecology, different levels of investigation come into play. These levels correspond to levels of a hierarchical organization of ecological objects (cf. pct. 1).

⁹ "Ökologie befasst sich mit Wechselwirkungen zwischen Organismen und ihrer Umwelt – und da letztere zum großen Teil wieder aus Organismen besteht, mit den Wechselbeziehungen von Organismen untereinander." (Wehner & Gehring 1990, 502) Similar statements can be found in most of the contemporary textbooks of biology.

¹⁰ A population is a group of individuals of the same species living in the same area. Members of a population can reproduce themselves by means of sexual interaction and thus have the possibility of genetic exchange.

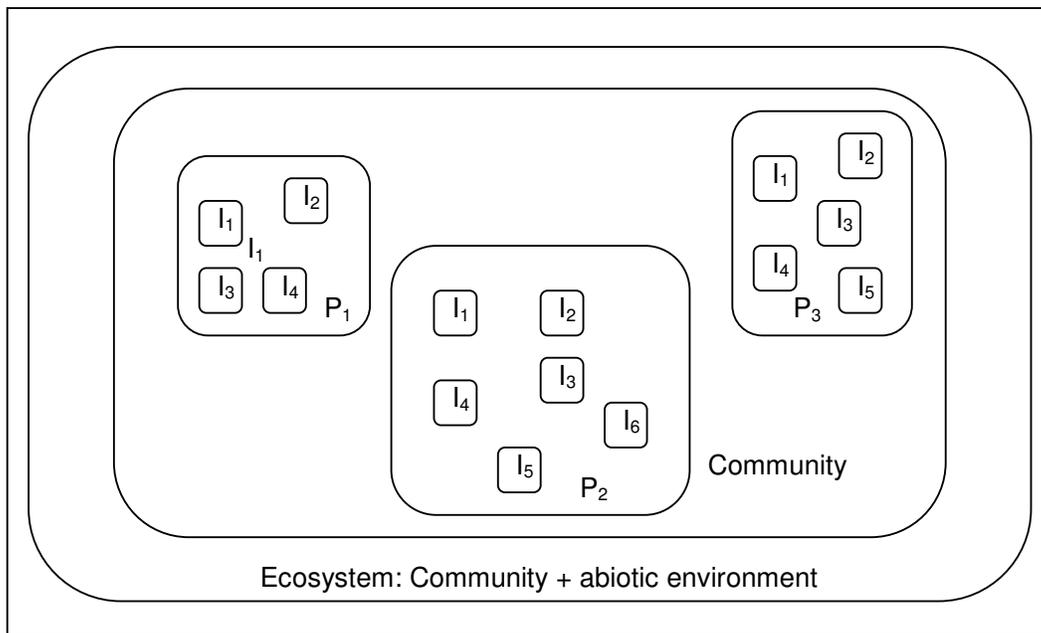
¹¹ The terms *biocoenosis* (mostly used in Continental Europe) and *community* (mostly used in the United States and England) are roughly synonymous (cf. Odum 1971, 5) and I will exclusively use the term *community*. *Community* describes the associations of different populations by means of the nature of their interaction or the place in which they live (cf. Ricklefs 1993, 539). According to the Committee on Nomenclature of the Ecological Society of America from 1933, *community* is a general term to designate organic assemblages of every degree from the simplest co-occurrence of different species like a few beetles on a special plant to the most complex interactions in a multistoried rainforest (cf. Anderson & Kikkawa 1986, 3).

¹² "Wissenschaftliche Ökologie im weitesten Sinne befasst sich mit Kausal- und Funktionszusammenhängen auf den Ebenen der Organismen, der Populationen und der Lebensgemeinschaften: die Ökologie behandelt die Wechselbeziehungen der Elemente einer Ebene untereinander und mit ihrer Umwelt."

The research on organisms and their environment is called *aut-ecology*. It examines the physiological adaptations of one species to its environment by means of the investigation of individuals. The investigation of one or various populations and their behavior is called *demecology* or *population ecology* (which is the term currently used). Synecology investigates the interactions of different populations at the level of communities. Today, one mostly talks of community ecology¹³ or systems ecology. Community ecology investigates the community by stressing biotic interactions, whereas systems ecology emphasizes abiotic factors and does not talk of communities but of ecosystems, i.e. the community plus its abiotic environment (cf. pct. 1).¹⁴ The ecological hierarchies are often extended, spanning from cells over organisms, populations, communities, ecosystems, landscapes and biomes to the biosphere which is the highest level including all other ecological entities (cf. Allen & Hoekstra 1992, 7). The levels of organism, population, community and ecosystem are the most common ones for investigation by ecologists.

¹³ As we will see, community ecology sometimes is considered to be quite opposite to systems ecology. This depends on the perspective whether one considers a community to be a composition of several populations or whether the community is considered to be a whole.

¹⁴ This understanding of ecosystem is widely distributed but corresponds more to a level of integration than to a system. In the third chapter, I will investigate the different conceptions of ecosystem and community in detail.



Picture 1: Scheme of the hierarchical ecological organization demonstrating the main levels of investigation by ecologists. The ecosystem consists of a community with its abiotic constraints. Every community is composed of populations (P), and every population is composed of individuals (I).¹⁵

However, the above characterization of ecology is still a very wide one and does not specify what ecologists do. For a better understanding of what *ecology* can mean for ecologists, I gathered several characterizations and explications of ecology from ecological textbooks. They prove to be quite different but one can divide them into various groups. The first one contains general statements¹⁶ on ecology that will probably be accepted by every ecologist.

"Ecology is the scientific study of the relationships between organisms and their environments." (McNaughton and Wolfe 1979, 1)

"Ecology is the study of the relationships between organisms and the totality of the physical and biological factors affecting them or influenced by them." (Pianka 1978, 2)

¹⁵ As we will see, this hierarchical order is not without its problems. I will discuss them in the chapters 3 and 4.

¹⁶ These statements often have the form of an explication, sometimes they are used as a definition other ecologists just want to describe the objectives of ecology. Thus, the following is a mixture of different forms of statements that are used to characterize the discipline of ecology.

"Our goal in ecology is to understand the interrelations of organisms and their environments *under natural conditions*." (Clarke 1966, 3)

"Ecology is the study of the relationship between organisms and their physical and biological environments." (Ehrlich and Roughgarden 1987, 3)

Not all statements on ecology are so general. The following statements stress one aspect of ecology, the investigation of distribution and abundance of organisms. They emphasize the investigation of natural patterns by examining specific populations or communities.

"The science of ecology is the study of distribution and abundance. In other words, we are interested in predicting where organisms occur (distribution) and the sizes of their population (abundance). Ecological studies rely on measurements of distribution and abundance in nature, so we need the tools of mathematics and statistics to summarize and interpret these measurements." (Gotelli 1998, XVII)

"Ecology as a science involves detailed and painstaking measurements of population sizes of plants and animals, birth and death rates, the supply and utilization of energy and nutrients in the environment, and related subjects. It is really a sophisticated and academic form of natural history." (Owen 1980, 4)

"The word "Ecology" is invented to convey the idea of "The study of animals and plants in relation to their habit and habitat." (Colinvaux 1973, 2)

The next group of statements stresses a different aspect of ecology. They all characterize the discipline of ecology by the description and understanding of functional processes in ecology. They are interested in the roles of biotic and abiotic processes of a larger system and they do not care about the individual components. The objects of research are ecosystems (communities and their abiotic environment).

"Usually ecology is defined as the study of the relation of organisms or groups of organisms to their environment, or the science of the interrelations between living organisms and their environment. Because ecology is concerned especially with the biology of *groups* of organisms and with *functional* processes on the land, in the oceans, and in fresh waters, it is more in keeping with the modern emphasis to define ecology as the study of the structure and function of nature, it being understood that mankind is a part of nature. One of the definitions in Webster's Unabridged Dictionary seems especially appropriate for the closing decades of the 20th century, namely, 'the totality or pattern of relations between organisms and their environment.' In the long run the best definition for a broad

subject field is probably the shortest and least technical one, as, for example, 'environmental biology'." (Odum 1971, 3)

"Ecology is the science of energetic and biogeochemical cycles of the biosphere and its subunits (e.g. ecosystems) and of the interrelations between different organisms, between organisms and abiotic factors and between single abiotic factors." (Bick 1998, 8)¹⁷

"Ecology is that part of biology dealing with the economy of nature, which means the *relationships of organisms to their environment*, it includes abiotic disciplines (chemistry, physics, social sciences). The environment of an organism – viewed by the individual, the population or the species- contains all biological and abiotic factors and elements that can be found in its environment influencing – directly or indirectly - the organism and/or being influenced by it. The manifold and complex interrelationships between environmental factors and populations constitute more or less delimited, superorganismic entities: ecosystems (in the broadest sense). Their analysis and understanding are the final aim of ecology." (Müller 1991, 15)¹⁸

"Ecosystems are the subject matter of ecology, and an understanding of their structure and function is the concern of the ecologist." (Kormondy 1984, 2)

The two groups of statements just mentioned are concerned with quite different aspects that are often difficult to combine. The first group stresses the importance of natural patterns and the investigation of concrete objects mostly by means of their biological properties, the second group contends the significance of biotic and abiotic functions without bothering too much about the concerned concrete entities. There are only few characterizations trying to combine these both views, like the following:

"Ecology is the study of the structure and function of nature. Structure includes the distribution and abundance of organisms as influenced by the biotic and abiotic elements of the environment; and function includes how populations grow and interact, including competition, predation, parasitism, mutualisms, and transfers of nutrients and energy." (Smith 1980, 3)

¹⁷ "Ökologie ist die Wissenschaft vom Stoff- und Energiehaushalt der Biosphäre und ihrer Untereinheiten (z.B. Ökosysteme) sowie von den Wechselwirkungen zwischen den verschiedenen Organismen, zwischen Organismen und den auf sie einwirkenden unbelebten Umweltfaktoren sowie zwischen den einzelnen unbelebten Umweltfaktoren." (Bick 1998, 8)

¹⁸ "Ökologie ist der Teil der Biologie, der sich mit dem Haushalt der Natur, d.h. mit den *Beziehungen der Organismen zu ihrer Umwelt* befasst und damit auch nichtbiologische Disziplinen (Chemie, Physik, Soziologie) einbezieht. Die Umwelt eines Organismus – aus der Sicht des Individuums, der Population oder der Art - enthält alle belebten (biotischen) und unbelebten (abiotischen) Faktoren und Elemente, die in seiner Umgebung vorhanden sind und – direkt oder indirekt – auf ihn wirken und/oder von ihm beeinflusst werden. Die vielfältigen und komplexen Beziehungsgefüge zwischen den Umweltfaktoren und den Organismenpopulationen bilden mehr oder weniger abgrenzbare, überorganismische Einheiten: Ökosysteme (im weitesten Sinne). Ihre Analyse, ihr Verständnis stellt das Endziel der Ökologie dar." (Müller 1991, 15)

The last group of statements is concerned with general principles that govern the processes of adaptation and aim to explain natural patterns and functional processes by means of ultimate explanations.

"Ecology is the study of the patterns of nature and how those patterns came to be, and how they change in space and time."
(Kingsland 1995, 1)

"Ecology is the scientific study of the interactions that determine the distribution and abundance of organisms." (Krebs 1972, 4)

"Ecology is the study of the principles which govern temporal and spatial patterns for assemblages of organisms." (Fenchel 1987, 12)

"Ecology is in large part the study of the adaptation of organisms to their environment." (Emlen 1973, 1)

From the given statements, we can distinguish three basic approaches in modern ecology.¹⁹ One approach is mostly interested in patterns of distribution and abundance of organisms. In general, it is interested in concrete entities (individuals, populations or small communities). This approach corresponds to *population ecology*. The other approach, interested mostly in functions and abiotic constraints of large ecological systems, corresponds to *systems ecology*. It is mostly concerned with a functional analysis of ecosystems. The third approach, called *evolutionary ecology*, wants to explain interactions between organisms and their biological and abiotic environment by means of adaptation and natural selection. It works to a considerable degree with models from population genetics and is mostly concerned with population phenomena. Thus, we have a strong relationship between evolutionary ecology and population ecology.

Now we can characterize ecology as one scientific discipline that is interested in the interrelationships between organisms and their environment but that has three quite different approaches. Ecology can be characterized as one discipline by its objects: interrelations of living beings with each other and their abiotic environment. However, this conception is very broad so that there are a many different possibilities to pose questions and to use methods. In fact, the three approaches are so different in their methods and questions they pose that it is hard to consider them as belonging to one discipline. Although all approaches correspond to the general statements on ecology listed in the first group, they stress quite different aspects of interrelationships between

¹⁹ The first group of statements is so general that I will not consider it to be a specific approach to ecology. One can also find other divisions into sub-fields or approaches. This division represents the different forms of explanation.

organisms and environment. Population ecology and systems ecology and even more systems ecology and evolutionary ecology are sometimes so at odds that scientists cannot understand each other and there is even a certain amount of hostility between the different fields. Thus, one might think they were various disciplines. Nevertheless, in my opinion, there are good reasons to consider ecology to be one discipline, and I will provide the reasons for this in the remainder of the book.

In the following investigation, I will focus on the three different aspects of ecology just sketched that can be characterized by the keywords: distribution (population ecology), function (systems ecology), and evolution (evolutionary ecology). Although there are strong controversies between systems ecologists and evolutionary ecologists, there are also attempts to combine the different approaches and one can find similar aspects, which can be connected. This leads to the problem that the approaches are not always clearly separated; sometimes it is even difficult to decide whether one theory or method belongs to the one or to the other approach. It is possible that systems ecologists will not only deal with ecosystems but also with populations or small groups of individuals.²⁰ Even within one of the three approaches, we can find pluralistic forms of research but in their explanations, they stress the functional, the distributional or the evolutionary point of view.

Each one of these three approaches shows a special way of explaining and understanding objects of ecological investigation. Thus, we can find a plurality of ecological theories and concepts. Ecologists themselves are aware of the conceptual disunity and they often describe their discipline as immature (cf. Fretwell 1981, Strong et al. 1984, Peters 1991, 273) or even as anomal (Hagen 1989). Although ecology is about as old as genetics and even older than biochemistry, it lacks the conceptual unity that characterizes these disciplines. It is assumed that one reason for this anomaly is to be found in the history of ecology. From the beginning of scientific ecology, it was divided into at least two approaches which have never been unified. By looking at specific historical aspects of ecology I will illustrate why the contemporary approaches are at odds. Obviously, there are many traditional opinions and hostilities in ecology. That is why it is difficult for contemporary ecologists to co-operate. By means of the historical origins of the different approaches, it will become obvious why they still exist

²⁰ As I will demonstrate shown in the third chapter, there are good reasons to consider populations and small groups of individual organisms' forms of ecosystems as well.

and why the differences have even increased during the last forty years. I will illustrate this in the next sections.

2.2 Approaches in Ecology – Historical Traits and Contemporary Differences

As we have seen, ecology is a very heterogeneous discipline. Many aspects of this heterogeneity are at least partly due to the history of the discipline. Thus, the history of ecology accounts for several aspects of the conceptual disunity of the ecological approaches. There are several investigations on the history of ecology, but they all consider one part of ecology only, e.g. animal ecology, plant ecology, population ecology, systems ecology etc (cf. Trepl 1987, 30). Ecology is so heterogeneous that it does not have anything like a history (Beatty 1988, 245; Trepl 1987, 29). Yet it is possible to find important and seminal concepts in the different strands of ecology influencing contemporary patterns of ecological theory. I will have a look at some concepts that still characterize the different ecological approaches. In this way, it will be obvious why population ecology and systems ecology are in disagreement, although one can find many similarities in their methods. In general, I will focus on the development of theoretical concepts in ecology, but for systems ecology I will consider roughly social and political impacts because they have been very important for the establishment and wide acceptance of this approach, at least in the United States. I will begin with a general overview on the history of ecology, then I will go on to look at the history of the different approaches and at their contemporary particularities.

2.2.1 Historical Traits of Ecology

Since the 18th century, the science of biology could be characterized by two different scientific approaches. One is the *physiological* approach, the other is the approach of *natural history*. *Physiology* is interested in explaining *processes* of living nature, e.g. the chemical reactions that lead to the flowering of a plant at a particular time. The aim of this research is to detect *how* biological processes work and to find general explanations (laws) for these processes. Physiologists have often used experiments to find these laws. The classic *natural history* on the other hand is interested in collecting and describing organisms and looks for distribution patterns of every living being that can be found in nature. It answers the questions *what, where, and when* things

happen.²¹ It is interested in concrete objects and their properties whereas physiologists want to establish general laws.

Although proponents of natural history in the 18th century considered nature to be a stable object with elements which have teleological functions, they were not interested in investigating actual processes. In contrast to the physiological approach, natural history did not work with experiments but was much more concerned with comparing and ordering natural phenomena to establish a system of the living world. The functional harmony of nature was considered a demonstration for God' s providence. Although Linné replaced the term “divine economy” by “economy of nature” (cf. Schramm 1984, 33)²², he conceived of nature as a science of God. Every individual had its role in the functional harmony of nature. Thus, the conception of nature stressed the teleological roles of organisms on the one hand but also the importance of classification of concrete individuals on the other. Moreover, both views were not connected, the functional harmony was the metaphysical background whereas the classification of individuals was the scientific program. One can understand the *oeconomia naturae* as an early form of general ecology (Trepl 1987, 71ff.).

The meaning of *natural history* changed when George Cuvier integrated new concepts at the beginning of the 19th century. He considered natural history to be a special part of physics. The laws of physics should be applied on the diversity of nature and their organisms to explain the properties of these living beings. The basis for natural history should be a system of nature containing the names of every known living being, categorized in classes and subclasses according to their morphological and anatomical traits (cf. Rieppel 2001, 144). The classical period of natural history was interested in the role and the morphology of organs and organisms. Cuvier modified this aspect and considered the physiology of individuals to be the most important object of research. Life is not just a trait of organisms in distinction to abiotic objects as assumed in classical natural history but it is rather a form of organization specified by interrelations between organism and environment (cf. Trepl 1987, 94). Successors of Cuvier have explained properties of organisms by the structure of the relationships to their environment. In this form of natural history, there is no room for teleological

²¹ This is a very rough and incomplete characterization of natural history. As we will see, there are lots of modifications and other aspects in natural history especially after the year 1800.

²² This is still the way how most ecologists try to understand the patterns and functions of nature, as an economy. So the title of a contemporary textbook in ecology is called *The Economy of Nature* (Ricklefs 1993).

explanations. The existence of this form of natural history is the precondition that enabled the development of the scientific discipline of ecology (cf. Trepl 1987, 93f.).²³

Ernst Haeckel coined the term ecology (Ökologie) in 1866. By "Ökologie" he wanted to describe the discipline interested in the economy of nature.²⁴ Haeckel, like Linné used social and economic concepts to describe natural processes. The new science of ecology should investigate the relationships of an organism to its inorganic and organic environment that means all the entangled interrelationships recognized by Darwin as the conditions of the struggle for survival. Haeckel described ecology as a part of natural history²⁵ and conceived of it in the form it was established by Cuvier and his followers. The biologists that regarded themselves as ecologists can be called outdoor physiologists (cf. Kingsland 1995, 23). They have been interested in experimental research on individuals. We can regard this as an early form of aut-ecology.

Before the beginning of the 20th century, ecology was hardly regarded as a scientific discipline at all. However, in the first 30 years of the new century the development of ecology into a self-conscious scientific discipline proceeded rapidly. In 1915 already, the *Ecological Society of America* was founded²⁶ but ecology was not a unified discipline at all. On the one hand, ecology was considered a new or scientific form of natural history (e.g. Adams 1917; Elton 1927). Natural historians at that time were interested in the distribution and abundance of organisms and in the history of nature. They wanted to understand the conditions of individual living beings of the present and of the past (Wilson 1901, 22). It was the study of individuals, how they were suited to the conditions under which they had evolved and now lived. On the other side, ecology was the investigation of how groups of organisms lived together and how the effects of many species living and interacting together produced more or less stable structures

²³ At this time in natural history we can find beginnings of systematic and theoretical science. Sometimes the term *natural history* is only justified by its naturalist tradition (Trepl 1987, 45).

²⁴ "By the term ecology we understand the science of the relationships of the organism to the external world, where we can find every condition of existence (Unter Ökologie verstehen wir die gesamte Wissenschaft von den Beziehungen des Organismus zur umgebenden Außenwelt, wohin wir im weiteren Sinne alle 'Existenzbedingungen' rechnen können." (Haeckel 1866, 286)

²⁵ "Unter Ökologie verstehen wir die Lehre von der Ökonomie, von dem Haushalt der tierischen Organismen. Diese hat die gesamten Beziehungen des Tieres sowohl zu seiner anorganischen als zu seiner organischen Umgebung zu untersuchen, vor allem die freundlichen und feindlichen Beziehungen zu denjenigen Tieren und Pflanzen, mit denen es in direkte oder indirekte Berührung kommt; oder mit einem Worte alle diejenigen verwickelten Wechselbeziehungen, welche Darwin als die Bedingungen des Kampfes ums Dasein bezeichnet. Diese Ökologie (oft auch unpassend als Biologie im engsten Sinne bezeichnet) bildete bisher den Hauptbestandteil der sogenannten "Naturgeschichte" in dem gewöhnlichen Sinne des Wortes." (Haeckel 1869, 49)

²⁶ In England, the Ecological Society was already founded in 1913 whereas the German Ecological society was not founded before 1971.

like communities, societies, associations etc (cf. Kingsland 1995, 23). Apart from these different approaches, ecology consisted of distinct and independent different “sub-disciplines” like animal ecology, plant ecology and limnology²⁷ (cf. Bick 1998, 2-4).²⁸

Early plant ecology had the most considerable impact on theoretical concepts of ecology, many of them are still used today (cf. Trepl 1987, 30). Forbes (1887), Cowles (1899) and especially Clements (1916) brought experimental methods into vegetation science and provided a holistic view of biological associations. Forbes (1887) regarded a group of organisms occurring at the same place as a unit and thus developed the concept of a biological community (cf. Hagen 1992, 7). Clements transferred the physiological approach from individuals to the community which he considered to be like an organism. A community of plants, the occurrence of typical plants in a specific place, is considered a whole and compared with an organism. The different elements (plant species) of the community are dependent on the “superorganism” and not vice versa. The community as a whole behaves according to physiological laws. It develops through a definite number of stages (succession) until it reaches its maturity, the *climax*. The process of succession is invariably fixed by the given climate and it will run according to physiological laws. Hence, the stage of climax will be reached necessarily. It will remain stable forever if the climate does not change and man does not intervene. The status of climax forms the basis for the natural classification of plant communities (Clements 1936).²⁹

At the same time, Gleason (1917, 1926) developed an individualistic concept of a plant association. He considered a plant community as a random assembly of individual species. The distribution and abundance of species in a plant association are a result of migration of species and environmental selection (Gleason 1926, 24). Seeds of different species have different abilities to migrate and they are influenced by edaphic (soil properties) and climatic factors. Thus, an association is not a whole but a coincidental environmentally influenced assembly of species sharing the same area. There is no reason why we should expect to find exactly the same assembly of plant species in two different places on earth. However, we will find many similar

²⁷ Limnology is the branch of ecology that investigates the ecology of sweet waters (lakes, rivers and creeks).

²⁸ Sometimes ecologists talk of ecological sub-disciplines, but there is no specified catalogue of them. One can find as different categories as aut-ecology, plant ecology, limnology and community ecology. Thus, we had better talk of different aspects or fields of ecology instead of sub-disciplines.

²⁹ Although these ideas stress the dynamics of communities, one should not mix it with an historical or evolutionary approach. The processes of succession will occur again given specific initial states and general laws. This is not the case in evolutionary and historical processes (cf. 2.4.2.1).

associations of plants in different places in the world because the individual particularities of migration and the environmental requirements of species will lead to very similar aggregations in areas with a similar environment (Gleason 1926, 26). Thus, the development of a community lacks the deterministic factors. The developed community then is a form of random association.

The Gleasonian approach is in the tradition of natural history in that it examines the properties of individual species and their properties in relation to the abiotic environment. In some ways, it contradicts the concept developed by Clements. Clements assumed that plant communities behave like organisms following specific physiological processes. Thus, a plant will necessarily reach a definitive climax-structure. Gleason denies both the similarity between organisms and plant communities and the deterministic character of their development. Every assembly of plants can only be understood by examining the properties of its individual species. It has to be isolated arbitrarily and is unique because it consists of individual and broadly overlapping populations (cf. Kormondy 1984, 196).³⁰ Sometimes we may find sharply delimited assemblies due to a strong climatic or edaphic change but every association is a composition of elementary parts and has to be explained by reducing it to the peculiarities of the composing species. We may find similar associations in similar climatic environments but they will never be exactly the same ones. The vegetational succession has a non-determining and historical character (cf. Trepl 1987, 157).³¹

Until the Second World War, the Gleasonian concept was widely ignored and the holistic concept of Clements could be found in most textbooks of ecology (especially in the United States).³² During and after the war, there was a general trend to make ecology more scientific by the extensive use of mathematics. The intention was that ecology should become an exact science with the possibility to predict events according to the pattern of physical theories (e.g. Haskell 1940). In 1947, Egler, Cain and Mason rediscovered the Gleasonian concept. It was renewed to attack the still predominant Clementsian paradigm. Gleason's individualistic concept was promoted as empirically based whereas the Clementsian assumption of community development

³⁰ The Clementsian view faces the problem to specify the borders of a community. This problem will be discussed in the sections on communities (cf. 3.2.1).

³¹ In historical disciplines, we have a concrete object whereas theoretical disciplines are not so much interested in concrete objects but in the law describing the behavior of the investigated objects. A historical object can hardly be integrated into an exact theory (Trepl 1987, 53f.).

³² The holistic ideas of the popular philosopher Smuts (1926) had a considerable impact on ecological concepts. The British ecologist Phillips performed his ecological work explicitly in order to support these ideas of Smuts (cf. Trepl 1987, 148).

was thought to be an empirically void explanation (cf. Simberloff 1980, 16). Thus, a new form of population ecology was established.

Nevertheless, the holistic conceptions of community were modified as well. The community was no longer considered an organism but a *system*, the organism metaphors were replaced by technological ones (cf. Trepl 1987, 177). Ecological systems or ecosystems should follow specific laws like a machine. Systems ecology wanted to explain the functional relationships in nature with the help of technological analogies and new mathematical tools. An important influence for this way of 'physiological' research³³ was Bertalanffy's *General System Theory* (cf. McIntosh 1985, 232), which had an important impact on the systems ecological conception of unity.

General systems theory wants to formulate and derive general principles that are valid for any system (cf. introduction). Systems ecology was considered a novel and scientific approach to ecology and was therefore called *New Ecology* (Odum 1964).³⁴ Systems ecology wanted to impose holism on science and technology. It dealt with the supra individual levels of organization and developed the ecosystem concept as central and unifying focus. By including all the biotic and abiotic factors into the object of investigation, the ecosystem, systems ecology wanted to unify the distinctly separated fields of plant and animal ecology. Thus, one can conceive of systems ecology as a holistic discipline (Odum 1977). Systems ecologists wanted ecology to be more scientific and methodologically unified by extensive use of mathematics and other non-biological scientific methods like systems analysis. They included elements from general systems theory, mathematics, information theory, and cybernetics into ecological theories in order to make ecology a hard science (Trepl 1987, 202).

Population ecologists sometimes designated population ecology as well as *New Ecology* (McIntosh 1985, 199f.). This has led to a separation of systems and population ecology. People like Mac Arthur, a skilled mathematician, were very interested in applying their mathematical ideas and found an ideal field in ecology. By mathematization, population ecology should become a hard science. Like systems ecology, population ecology was interested in explaining natural processes by

³³ From the beginning of systems ecology it seems to be better to talk of *functional* instead of physiological research because ecologists do not deal with organisms and their physiological constraints but with systems and their functional interrelationships. This difference also stresses the distinction between organism (physiology) and system (function).

³⁴ Odum is one of the most well-known proponents of the *New Ecology*. But there were also population ecologists like Mac Arthur who regarded themselves as belonging to a *New Ecology*. In ecology one can always find a *New Ecology* used by its proponents stressing that their form of ecological research is a revolution in ecology and helps ecology to being a real science (cf. McIntosh 1987).

extensive use of mathematics. Population ecologists in contrast to systems ecologists did not use technical analogies and they were interested in reductionist explanations. They looked for equations that could explain how the behavior of individual species or populations results in community phenomena. Although we can find many similarities between theoretical population ecology and systems ecology, we still have the basic difference of holist and reductionist research strategies. Ecologists themselves are aware of this division. Hutchinson (1964) distinguished between the holistic approaches (which he called *holological*) of Forbes, Clements, Birge, Thienemann and Allee, and the reductionistic (*merological*) approaches founded by Lotka, Volterra and renewed by Hutchinson himself and Mac Arthur (Hutchinson 1964). Population ecology is still more inclined to natural history than systems ecology because it has to consider concrete objects (individuals or populations). Population ecology tries to find laws of specific elements (species, populations, individuals) whereas systems ecology attempts to find general structural laws by abstracting from the concrete entities and by looking at functions only.

In the sixties and seventies, a new approach to population ecology resulted in a new sub-field of ecology: evolutionary ecology. The integration of population genetics with population ecology led to new forms of explanation for group phenomena. Proponents of this field considered ecological and evolutionary phenomena by means of a genetic framework, starting with Williams (1966). Especially social and altruistic behavior in animals, which was formerly explained by forms of group selection could be explained by means of individual selection and genetic mechanisms. These concepts helped to explain many observations that could not be explained by the traditional instruments of evolutionary or ecological theories (e.g., why bees and ants often form social groups).

Evolutionary ecology is mostly considered a part of the population ecology approach. Indeed, after the establishment of evolutionary ecology the gap between population ecological accounts and systems ecology seemed to be unbridgeable. Evolutionary ecology wanted to explain complex ecological phenomena by means of individual selection and genetic mechanisms whereas systems ecology has been interested in explaining complex systems by neglecting the constituting individual parts as far as possible just by considering them in terms of their role. Thus, there was a distinct division between evolutionary ecology and systems ecology in the seventies. The optimism of obtaining a unified general theory of ecology that was provided by

proponents of systems ecology and of evolutionary ecology also was gone, because these approaches could not be unified (cf. Hagen 1992, 162/3).

In contemporary ecology, the approaches of Clements and Gleason are still existent. On the one hand, ecology is a discipline which works mostly with holistic and functional explanations without considering the specific elements of a system. On the other hand ecological systems are considered under population orientated individual and reductionistic aspects. Today both approaches try to describe *how* ecological processes work either by a holistic perspective from ecosystems or by a reductionistic perspective from populations or individuals. Many aspects of ecology in the last decades must be seen as a split between these two camps, based mostly not on scientific or technical grounds but on philosophical ones - on a fundamental difference about how to do science (cf. McIntosh 1985, 200f.). The existence of these two very different perspectives is largely responsible for the intellectual immaturity of ecology (Hagen 1989, 434). The basis of contemporary ecology lies both in the holistic physiological (e.g. Clements) and in the reductionistic natural history approach (cf. Tuomivaara 1994, 219; McIntosh 1985, 4; Hagen 1989, 434f.), but several other aspects can be found in the contemporary approaches.

Finally, we can conclude that ecology has developed from a describing and comparing discipline (natural history) via a physiological and function-orientated approach (outdoor physiology, systems ecology, mathematical population ecology) to an evolutionary ecology that provides ultimate explanations of natural diversity and ecological processes. All three forms of ecology still exist in contemporary ecology, sometimes distinctly sometimes hardly separated.

I have just given a broad overview of the principal concepts in ecology that can partly explain the existing ambiguities in contemporary ecology. In the next sections, I want to go on to analyze particular features of the three approaches of contemporary ecology, because they are not as monolithic as I described them in order to stress the differences.³⁵

³⁵ There are also some other ways to categorize the different ecological approaches. Hengeveld und Walter (1999) distinguish between two ecological paradigms, the aut-ecological one and the demographical one that exclude each other. In my opinion these paradigms correspond to different forms of the population ecology approach. Communities and ecosystems seem to be neglected or they have to be integrated into the demographical paradigm. As we will see in the following, the different approaches and their forms are more complex than this suggestion assumes.

2.2.2 Population Ecology

Population ecology is concerned with the investigation of distribution and abundance of species by means of the investigation of populations. It studies the interactions of populations with their biotic and abiotic environment and investigates how those interactions give rise to the larger patterns of communities and ecosystems (cf. Kingsland 1995, 1). This approach can be regarded as a successor of Gleason's view of nature in that it is individualistic (cf. Hagen 1989). In general, population ecological research focuses on the dynamics of a single species population, or on interactions of two or three species populations but rarely on more (McIntosh 1985, 151).

Although the study of populations is an old subject in biology, the autonomy of population ecology as a distinct and important branch of ecology was secured as late as the mid fifties of the last century only (cf. Hagen 1989, 440). Many animal population records were made by amateur ornithologists, economic entomologists, or fisheries' personnel who were interested in economic questions, e.g. how to reduce the harm of migrating grasshoppers on crops or how to maximize the outcome of fish ponds. Although these people were primarily interested in economical questions, their research resulted in an increase of ecological knowledge. The investigation of populations as part of ecology began in about 1920 in the United States, largely due to economic problems caused by the importation of harmful insects like the Mediterranean fruit fly or the European corn borer (cf. (Kingsland 1995, 50f.)). Only in the 1960s, there was an overlap between population ecology and population genetics, although both fields had originated in the 1920s (Kingsland 1995, 1).

However, population ecology is no unified approach. One can find two distinct strands that differ in their way to explain the existence of communities that are composed of basic components (individuals [species], populations) investigated by population biology. One strand emphasizes the independence of individual populations and the importance of random statistical processes. The properties of the community are a result of the properties of single species and environmental constraints. This strand is a direct successor of the Gleasonian concept. Species³⁶ have specific properties and depend on environmental conditions (climate, soil) only. One cannot consider a

³⁶ Species are considered to be individuals. Of course there are many differences between individual members of a species but these have to be neglected. Otherwise, it would be impossible to arrive at statements of communities. Whenever one talks of species one talks of individuals and it is assumed that every individual member of a species has the same properties. So, if one uses the term *species* this is an individual characterization in contrast to *population* which especially refers to a group of individuals which is considered to be a single entity.

community to be an organism because it is a random assembly of different species and does not develop according to general laws. Proponents of this strand stress the randomness of community composition and the importance of investigating the properties of concrete species. Species properties and environmental conditions force different species to occur in the same place at the same time. Thus, a community will be established by a “random colonization” and not by interactive or deterministic processes of competing populations.³⁷

The other strand sees populations as parts of tightly knit bigger groups (e.g. communities) and assumes that the causes for demographic changes are to be found in biotic interactions like competition and predation (cf. Hagen 1989). The majority of population ecologists follow this second strand. Proponents stress the importance of deterministic processes, especially competition and predation that will lead to a special composition of communities. Thus, the community structure necessarily results from deterministic processes of interaction between populations.

The historical roots of this strand of population ecology can be found in the works of theoretical ecologists like Lotka and Volterra in the 1920s and 30s and in the laboratory and field studies of Elton (1927) and Gause (1934). Lotka and Volterra used the logistic model of single population growth from Verhulst (1845) to describe predator-prey or parasite-host relationships. These so-called *Lotka-Volterra equations* describe basic processes at the level of populations. Elton (1927) proposed the idea that communities are tightly knit groups of interacting populations, whereas Gause (1934) stressed the importance of competition. Proponents of this strand want to establish some fundamental theorems (mostly in the form of differential equations) to describe properties and behavior of populations (cf. Shrader-Frechette 1986, 79).

This form, often denoted as *theoretical population ecology* has some similarities with systems ecology: both work with supra-individual entities and use a lot of mathematics to describe these macro-level phenomena. Major proponents of theoretical population theory like Lotka, Volterra, MacArthur and May came from mathematics or physics and wanted to apply their mathematical skills to ecology. However, while systems ecology is interested in even more complex ecological systems and stresses the investigation of abiotic processes, population ecology investigates mostly the biotic interactions of

³⁷ The discussion on the formation of communities was initiated by the equilibrium theory of island biogeography (MacArthur & Wilson 1967) which explained the composition of island communities by simple population processes. A more accurate outline on the theory of island colonization will be given in the third and fourth chapter.

populations. There are, however, transitions and the borders between systems ecology and theoretical population ecology are not always distinct. Ecologists like Lotka, Elton and Hutchinson were considered to be seminal for both population ecology and systems ecology.³⁸

We can find many debates between the two strands of population ecology on the role of mathematics and the empirical adequacy of population ecological methods. There has been a continuing discussion between mathematicians and the biologists in the course of the history of population ecology during the last 80 years. It is not so much discussed whether mathematics has been useful for ecology, rather the question was how far mathematics would lead ecology astray from the real world before losing the touch with reality (Kingsland 1995, 4). The mathematicians and the physicists have been interested in equilibrium and uniformity thereby often ignoring the individual differences of biological objects, whereas biologists have stressed the individuality, heterogeneity and unpredictability. The crucial difference between these two approaches is that the biological view is historical in considering the unique and contingent objects and the “mathematical” view is ahistorical trying to find general laws.³⁹

Now, one could consider the equilibrium aspect of populations and communities to be as holistic as the approach of systems ecology (e.g. Shrader-Frechette 1986, 79). Nevertheless, there are differences. Theoretical population ecologists like Volterra or May want to understand the development of a community by means of investigating their elements (individuals and populations) and are thus reductionistic compared to systems ecologists, who want to analyze whole communities and ecosystems respectively. So, one can conclude that theoretical population ecology is more holistic than the “historical” strand of population ecology because it is investigating population processes on a higher level than the aut-ecological parameter of single species. However, population ecology being concerned with the explanation of community properties is a reductionist account whereas systems ecology is holistic in that it first investigates the community and examines individuals only in terms of their roles. In the following section, I will investigate more accurately the system account of ecology.

³⁸ Illustrations of their work can be found in books on history of systems ecology (e.g. Hagen 1992) and population ecology (e.g. Kingsland 1995).

³⁹ These different assumptions within population ecology led to a long discussion on holism and reductionism in population ecology which will be discussed in the fourth chapter.

2.2.3 Systems Ecology

Systems ecology considers nature to be divided into ecosystems that can be dealt with as units. It tries to find laws which are applicable to the whole system. This approach focuses on the flow of material and energy through ecosystems without considering the organisms that make up the system (Hagen 1989, 434). They are only important in terms of their roles as transformers of energy or matter. Like population ecology, systems ecology is a diversified approach of ecology. One can distinguish various forms of investigation. Systems ecologists are mostly interested in modeling ecosystems by means of systems analysis and simulation (cf. Darnell 1970, 9). One form stresses the capture and turnover of energy (production and productivity), another one is interested in biogeochemical cycles (especially of mineral nutrients). Sometimes, systems ecologists also apply systems analyzing techniques developed for ecosystems to populations.

The origins of systems ecology can be seen in the organicism of Forbes and Clements and in the systems ideas of Lotka and Bertalanffy. Forbes (1887) considered the lake to be a microcosm in which all complex interactions of nature are to be found. Clements (1916) regarded the community as a superorganism that developed towards a definite climax stage according to physiological laws. Alfred Lotka (1925)⁴⁰ anticipated Bertalanffy' ideas of a general system theory by assuming that biological systems could be analyzed with the same methods that a physical chemist would use to analyze a chemical system. Lotka was looking for a law of evolution that would work in the same way as the laws of thermodynamics (especially the second one), with the same degree of generality (cf. Kingsland 1995, 26ff.). This has led to the idea that energy is the main aspect to be investigated in the study of ecosystems.

Systems ecology became a distinct approach after World War II. It bases on "systems thinking" which is considered a mixture of theories and methods. These include the concept of the "open system" of Bertalanffy, aspects of cybernetics (feedback loops, automation), information and communication theory dealing with theoretical and mathematical problems of transmissions in message-carrying circuits, operations research, games theory and computer techniques for the simulation of complex systems and their processes (Lilienfeld 1978, 1). All these aspects can also be found in systems ecology. Thus, systems ecology is not regarded as a biological discipline or a

⁴⁰ Alfred Lotka is considered to be one of the founders of theoretical population ecology, but he is as well the founder of eco-energetics that often is regarded as the core of ecosystem analysis (cf. McIntosh 1985, 200).

distinct branch of ecology but it rather should be considered a merger of a complex of things called systems analysis and ecology (McIntosh 1985, 226).⁴¹

Systems ecology rapidly took precedence to other ecological approaches, at least partly because it was closely involved with concerns of American society. Systems ecologists benefited from the Cold War as most of their funding in the post war years came from the U.S. Atomic Energy Commission (AEC). They had to study the effects of radiation on organisms by analyzing the movement of radioactive material through food chains etc (Golley 1993, 3). The importance of economical influence in the rise of systems ecology is without question. Some people even argue that the ecosystem paradigm was so successful and seductive on economic grounds alone, independent of biological or philosophical considerations (Simberloff 1980, 29).

However, there were also some other non-scientific aspects that must be considered in order to understand the rise in significance of systems ecology in the second half of the last century. In 1953, the seminal textbook "Fundamentals of Ecology" of Eugene and Howard Odum was published for the first time. The Odum brothers were the most important proponents of systems ecology in the United States and played a large part in the popularization of systems ecology. Some years later, Rachel Carson's "Silent Spring" (Carson 1962) was published, which initiated long discussions on environmental pollution in the North American and European societies. Since systems ecology was interested in dealing with environmental questions, there was a close relationship between systems ecology and the environmental movement, at least in the United States. In 1961, the International Biological Program (IBP) was established. The participating ecologists were successful in being funded by arguing that the program of systems ecology would contribute to solve the environmental crisis. Systems ecological projects were funded until the end of the IBP in 1974. During this time, ecology became so widely known that the public equated ecology with systems ecology (Palladino 1991, 234). The existence of population ecology was hardly noticed by the public.

The concept of the ecosystem that was already developed before the war (Tansley 1935, cf. chapter 3.1.1.1) and became widely distributed after the publication of the "Fundamentals" in 1953. Systems ecologists considered the ecosystem to be the basic

⁴¹ Systems analysis in ecology is mostly viewed as a method, but it is not easy for the ecologist to identify whether it is a really method, a sort of philosophy or even an ideology (cf. McIntosh 1985, 232). One can consider systems analysis to be a technical application of a holist, materialist philosophy (Golley 1993, 33). As we will see in the following this uncertainties make it difficult to understand the aims of systems ecology and their methods.

unit in ecology, like the cell for molecular biology (Odum 1964). The ecosystem concept became very well known by the ecosystem researches that were performed within the scope of the IBP. The ecosystem concept was used for a better understanding of natural complexity and a way to manage the environment. This holistic concept was widely accepted by ecologists who were confronted with very complex and often unpredictable phenomena. The concept suggested that nature consisted in systems that would be stable and homogenous if not disturbed by humans. Thus, conservationists of nature that considered ecosystem research to be a way to cope with the environmental problems also accepted it. The idea that there was (somewhere) ultimate order, balance, and equilibrium in nature has given some guidance to scientists and laymen during the postwar years helping them avoid dissonance with the overall (American) culture (Golley 1993, 2, 3).

The systems approach is basically functional and technical which can be seen by the terminology used and the non-biological origin of the ecosystem approach (Hagen 1989, 435; Taylor 1988). The metaphor of "organism" used by Clements was rejected by Odum and his followers, who used the metaphor of "cybernetic machine" instead. This metaphor was combined with a conception of control of nature that could be operationalized in a far more precise way than the metaphor of the organism (Kwa 1986, 169). Thus systems ecology and the ecosystem concept correspond on the one hand to an alternative way of science, combined with nature conservation, sometimes even with esoteric views on the properties of nature represented by ecosystem. On the other hand, systems ecology is very technical and uses typical analytical methods from physics, chemistry and systems analysis. One important property assumed of ecosystems is the possibility of self-regulation due to feedback loops. The roots of this concept can be found mainly in cybernetics. The theorists of feedback systems viewed nature as a machine and tried to apply a specific technical terminology to all natural systems. The negative feedback was regarded as a very important ecological principle that could be applied to both biogeochemical cycles and to population growth (Hutchinson 1948).

The individual elements were not very important in this cybernetic view, they were considered only in terms of their specific role for the whole system. Thus, they can be regarded as black boxes that have a specific role in the dynamic processes of the ecosystem. A plant has its role as producer of biomass, an animal its role as consumer and bacteria their role as decomposer (cf. pct. 4). Ecosystem analysis measures the

quantitative amounts of energy or biomass of the boxes as a function of input-output relations. The individual properties of a species are not important. The elements are only considered in terms of their function and are exchangeable with other elements that can overtake the same role in the system. In some cases, this approach can help to manage environmental problems. A problem of cattle breeding in Australia may be used as example. Too many cattle led to an increased production of dung, which attracted many flies. Since there were no beetles to decompose the dung, flies attracted by it became a pest. Ecologists imported beetles from Africa that were dung decomposers to cope with this plague. Thus the number of flies could be reduced effectively (cf. Suchandtke 1993, 256) and the functional systems view was confirmed to be applicable to nature conservation.

Systems ecology is often regarded as a holistic discipline. The term *holism* is used to indicate that the study of ecosystems should be based on a "whole-before-the-parts" approach (Odum 1977, 1289). Odum never stated clearly what he meant by "holism", it seems to be a mixture between metaphysical and methodological assumptions. Yet this diffuse form of holistic thought was widely accepted by the public and especially by environmental activists. The concept of the ecosystem was considered to be a holistic concept because it should serve as a way to deal with complexity by conceiving of complex relationships as units. Systems ecology tries to understand natural processes without considering concrete individuals or populations. It is also considered a holistic science, because it is not interested in parts but only in complexes of smaller material entities (like individuals or populations). Nevertheless, systems ecology also belongs to the abstracting and reducing disciplines and can be considered "reductionistic" in the sense that it analyses quantitative relations of input and output of the black boxes. It is not interested in the individual as individual (Trepl 1987, 177ff.). By the black-box-approach, systems ecology tries to find laws that can be applied to all systems. Black boxes with similar input-output relations are exchangeable. Systems ecology is looking for structural generalizations that can be applied to every system. Everything is seen under *structural laws* that govern the processes of ecosystems. Thus, this approach is very similar to the concept of unification developed by Bertalanffy (cf. Introduction 1.1).

This search for structural laws was regarded as a new instrument to unify ecology. It was considered the only useful method of ecology, for it could demonstrate common features of most diverse organisms at the macro-level. By describing individual properties at the level of communities, populations or individuals, there is very little in

common between spermatophytes, bacteria and vertebrates. Because all these organisms are functionally linked according to well-defined laws in an ecosystem (cf. Odum 1971, 3f.), one can consider systems ecology to be *functional ecology*. Thus, one can say that systems ecology tries to unify ecology by means of an abstracting method which focuses on the description of analogue processes and organizations at the level of whole ecosystems.

At this point, the difference between systems ecology and population ecology approaches becomes clearer. Although population ecologists also want to describe processes at the level of complex entities (one or two populations), they try to show that the formation of more complex entities (e.g. communities or ecosystems) results from the interactions of its parts. From a methodological point of view, one can distinguish between a reductionist approach (empirical population ecology) explaining on the level of individual species and their properties, a moderate reductionistic approach (theoretical population ecology) explaining on the level of populations and a holistic approach (systems ecology) explaining and researching on the level of the community or ecosystem. However, although there are big differences, one can find transitions between the illustrated approaches. The division between the population oriented approaches and systems ecology has become even more obvious with the development of evolutionary ecology.

2.2.4 Evolutionary Ecology

Although the approach of evolutionary ecology is closely related to population ecology, I consider it as a third big approach to ecology. It tries to explain the occurrence of populations, communities and bigger functional entities by means of individual selection. One should distinguish it from population ecology because population ecology is not interested in ultimate explanations but proximate ones. By means of ultimate explanations, evolutionary ecology has the possibility to synthesize ecological and behavioral phenomena. It has more unifying potential than both systems ecology and population ecology, and, as I will demonstrate in the following, evolutionary ecology is even able to unify the approaches of systems ecology and population ecology.

Evolutionary ecology is a young “sub-discipline” of ecology and tries to understand ecological processes by means of ultimate⁴² explanations. Evolutionary ecologists are mainly interested in the question *why* special ecological phenomena proceed the way they do. They take for granted the known statement of Dobzhansky (1973) that nothing in biology makes sense except in the light of evolution (cf. Cockburn 1991, 3). Evolutionary ecologists are interested in the evolution of life histories,⁴³ of mating systems, of sex, the adaptive basis of territoriality, foraging behavior, social behavior, theories of co-evolution, questions of adaptive radiation and species diversity of communities (cf. Futuyma 1986, 303).

Although evolutionary ecology only became recognized as a distinct branch of ecology in the 1960s (Futuyma 1986, 304), ecological questions were often explicitly connected with evolutionary ones long before. Haeckel's definition explicitly linked ecology with the theory of natural selection (cf. footnote 24, 25). In 1887, Forbes argued that the whole Darwinian theory belonged to ecology. Much of early ecology was a physiological approach to adaptation. These physiologists were often skeptical about the mechanisms of natural selection, but they were concerned with the central evolutionary concept of adaptation. Ecologists around 1900 wanted to know the function of specific structures in order to interpret them as an adaptation to the environment. This is quite different from contemporary evolutionary theory. Today biologists ask *why* the organism does have this trait for one particular function and not another one (cf. Collins 1986, 260f.).

The concept of natural selection fell into disrepute in the early twentieth century with the majority of ecologists who had been influenced by the superorganism concept of Clements. The development of a community as a whole does not correspond to the principle of individual selection. Ecologists wanted to be different from evolutionary fields like systematics or natural history and stressed their own ecological account.⁴⁴ Later, systems ecologists who were interested in structural laws and functions did not care about evolutionary explanations. Genetic mechanisms and historical explanations have not had place in systems ecological thinking. Systems ecologists wanted to

⁴² The term *ultimate* refers to the typical form of evolutionary explanation (cf. Introduction 1.2.1).

⁴³ The investigation of life histories considers the different forms of life to be adaptations to the environment. Thus, each form of life is a strategy to survive. The development of insects like butterflies that develop from egg via caterpillar via cocoon to an adult butterfly is considered a strategy to manage best with the environmental constraints, whereas the life cycles of dragonflies from egg via a waterliving larva to adult insect is an adaptation to other requirements of the environment.

⁴⁴ However, there were still some ecologists like Lotka deeply interested in evolutionary questions. These evolutionary explanations were quite different from the theory of natural selection.

describe and explain *how* systems processes work at the level of the system. The third edition of Odum's "Fundamentals" (1971) mentions evolution only twice while the terms *adaptation*, *natural selection* and *genetics* are not mentioned at all (cf. Futuyma 1986, 305f.). This clearly shows the different forms of explaining in the approach of systems ecology and evolutionary ecology.

Population ecologists after the Second World War were interested in evolutionary explanations, but they faced the problem of being unable to explain group phenomena by means of individual selection. Therefore, population ecologists did not apply evolutionary theory and they favored ideas of group selection to explain the occurrence of group phenomena in populations or communities (e.g. Winne - Edwards 1962). However, there have been calls for the integration of natural selection into ecological theory (e.g. Orians 1962, 262). In the sixties and seventies, evolutionary theorists developed new forms of explanation for ecological and social phenomena. By now, it was possible to explain the social behavior of bees by individual selection and specific genetic mechanisms (Hamilton 1964). Other approaches tried to understand ecological issues by means of a genetic framework (Williams 1966). Ecologists adopting this point of view worked with evolutionary, behavioral and mainly population genetic theories. They stressed the sexual and genetic selection for the formation of ecological patterns. This type of explanation of ecological complexes and processes is called *evolutionary ecology*. Since this approach is closely related to population ecology, the term *evolutionary population ecology* would be more adequate (cf. Roughgarden 1979, vii).

Nevertheless, there are several reasons why I think that the approach of evolutionary ecology is much more than a part of population ecology. In general, evolutionary ecology stresses only one aspect of evolutionary thinking. In evolutionary theory one can distinguish two major fields of investigation, one is the analysis of evolutionary mechanisms (mostly in terms of population genetics) while the other is interested in the history of nature. Only the investigation of evolutionary mechanisms has been integrated into ecology. Although the importance of history is sometimes mentioned by ecologists, in general, evolutionary ecologists are as ahistorical as systems or population ecologists (cf. Futuyma 1986, 312).

A characterizing part of evolutionary ecology is the investigation of life histories. The different forms of life (morphology, age, forms of reproduction cycles and stages, social forms etc) will be explained in terms of adaptive utility and genetic advantages. The different forms of life are strategies to survive and maximize the fitness of the species

(cf. Korfiatis & Stamou 1994, 107f.). Evolutionary ecology is based on a genetic framework, and on investigating and modeling population genetic processes that can explain the occurrence of ecological patterns. Thus, evolutionary ecology tries to arrive at unifying explanations by means of reductionistic explanations from basic genetic units and processes of adaptation. Complex ecological units shall be explained by the genetic properties of the individuals and their adaptations. Since evolutionary ecology emphasizes the genetic mechanisms as being causes of ecological structures and functions, the differences the approach of systems ecology are obvious.

The historical account of evolutionary theory is rarely integrated into ecology. Only in the last decades, biologists have become aware of the importance of historical processes in evolution and ecology. However, one can distinguish various interpretations of the term *history* in ecology. One historical effect which is important for ecology is the influence of humans on landscapes and their ecological patterns of the last hundred or more years. Another historical aspect in ecology is the history of landscapes for thousands of years, e.g. since the Pleistocene. The third form of history is concerned with the fields of paleontology and phylogeny and their techniques. This last form of history is the important one for an evolutionary ecology and has been found in ecology only since about 1990 (Kingsland 1995, 227).

In the following, I will deal with evolutionary ecology by stressing its historical character. I will develop a conception that is different from the usual understanding of evolutionary ecology. This conception will be distinct from population ecology and it has as well the possibility to work together with systems ecological accounts. This form of evolutionary ecology will have much more unifying power by providing explanations of the biotic diversity and other ecological patterns via the history of nature. It has even the possibility to justify the population and the systems ecological approach as methodically necessary and thus can help to unify the discipline of ecology. By means of the history of nature, one can come to a form of "micro-reduction" of complex ecological entities that can be "reduced" to former simpler entities, and these entities can be traced back to earlier and simpler forms. By this method, evolutionary ecology can explain and unify diverse ecological phenomena by means of their simpler "ancestors". This conception which will be elaborated in chapter 4 is able to unify the diversity of ecological objects and also the discipline of ecology by means of a special

form of reductionism.⁴⁵ However, before dealing with it, I want to go on to investigate methodical and theoretical aspects of contemporary ecology.

2.3 Methodical Problems of Ecology

In this section, I want to give a short overview on several problems of ecological methods related to the used terminology and to experiments. First, it will be demonstrated that it is very difficult to arrive at a general and adequate terminology for ecological objects and then problems of isolation in ecological experiments which can lead to strong idealized theories will be investigated. A specific difference in form of terminology and method of experiment between physics and ecology will become obvious by means of this short overview.

2.3.1 Terminology of Ecological Objects

Ecology often is considered an immature science which lacks a consistent scientific method and which has no adequate scientific theory (e.g. Peters 1991, Hagen 1989). One important aspect of this immaturity is the uncertain terminology of ecology. Key concepts like *ecology*, *ecosystem*, *stability*, *diversity* etc can have a quite different meaning in different applications and approaches of ecology (cf. Pickett et al. 1994, 5, also cf. the list of characterizations of ecology in the first section of this chapter). This uncertain terminology illustrates the conceptual uncertainty of important ecological concepts that influences some structures of ecological theory.

The problems of terminology in ecology make it very difficult to regard ecology as a unified scientific discipline. The question to be investigated is whether this terminological uncertainty is due to the natural objects or due to the different approaches in ecology or both. Most ecological terms and concepts have not yet been defined with sufficient precision and it is assumed that the imprecise definitions of terms impede the scientific development of ecology. The basic terms should be defined

⁴⁵ In evolutionary theory there are debates between scientists stressing the lawful and necessary character of evolution whereas other biologists emphasize the historical and contingent character (Gould 1989, Beatty 1995). Proponents of contingency deny the existence of biological laws and thus make it difficult to unify biology. Often, the use of mathematical or other models involves a rejection of history in favor of a harmonious unifying concept (Kingsland 1995, 8). But as I will show in the forth chapter, a historical approach to evolution does not necessarily lead to a disunity. Although we have to deal with contingencies in a historical consideration of nature we have the possibility to come to unifying explanations in ecology since every ecological object has its roots in the history of nature. By this the diversity and complexity of ecological phenomena can be reduced to smaller and simpler phenomena. Thus one will have a specific form of unifying explanation (cf. chapter 4.3.5).

as explicitly and precisely as possible in any investigation, especially for large research projects. Thus, the solution for the problem of terminology is assumed a precondition for a sound theory in ecology and its application for experimental research and environmental conservation (Jax et al. 1992).

If one accepts this suggestion, there are two ways to solve the problem of terminology, but neither is convincing. One would come to a terminological unity of ecology by defining the meaning of the key terms. In this case, one would reach a form of methodological unity already required by Logical Positivism (cf. introduction). However, this will not be successful. Objects of ecological research are so diverse that a few explicitly defined key terms will not match the diversity of ecological objects, or the definitions have to be so broad that they are of no value for specific applications. The other way would be to explicate terms accurately for every application. This would better work for empirical purposes but one would get many different terms to describe similar ecological patterns in different applications. One could not use general terms like *community* or *ecosystem* because they are too unspecified, rather one would have to develop several new terms for different applications. These terms would match specific empirical data but ecologists would have to deal with a variety of terms. This variety of terms would lead to difficulties in establishing general ecological theories, because it is not clear whether the terms used in different theories would be compatible with each other.⁴⁶

This demonstrates that a unified terminology would not solve the problems of a unified and consistent ecological theory. Either one would have a few clearly defined terms that can be used for general theories but cannot be applied to specific ecological patterns or one would have too many terms that are hardly manageable by ecologists. Although the terminology in ecology is inconsistent, I would say it is not worth creating a unified terminology. Instead of looking for a methodological unity or an explicit definition of ecological key terms, one should rather investigate whether ecological objects provide the data that allow ecologists to establish explicit terms without idealizing too much. Ecologists need terms that cover a wide range of application, with meanings wide enough to be applied to many ecological objects, but also specific enough that every ecologist can understand what is meant by a particular term. Ecologists probably have to put up with the conceptual uncertainty of the terms, which is useful for a wide range of applications, but brings some problems in constructing

⁴⁶ These problems will be investigated in detail by means of the examples “ecosystem” and “community”.

distinct theories. A more accurate investigation of this topic will be given by means of the examination of the concepts *ecosystem* and *community* in the third chapter.

2.3.2 Experiments in Ecology

Objects of ecological research are very complex and diverse. Therefore, ecologists trying to deal with this problem have to find methods and forms of experiment that help to come to broad generalizations in order to establish ecological theories. Ecologists will mostly try to investigate ecological processes under idealized conditions. They will isolate objects from its environmental constraints and investigate a chosen system with defined limitations and controlled constraints. This method has to be used to come to measurable data and generalizable statements. Ecologists must idealize the complicated conditions of the natural system and investigate an isolated system e.g. by excluding or influencing some environmental constraints. Although ecologists are interested in the relationships of organisms with their environment, they have to choose a system for investigation and must delimit and eliminate factors influencing it from outside in order to measure specific parameters.⁴⁷ Since the influence of environmental constraints on ecological objects and the interconnectedness of ecological processes are very strong, this form of idealization has a big effect on ecological theories. Sometimes the ignorance of boundary conditions e.g. by applying an enclosure to isolate the investigated system, can lead to a wrong picture of the investigated ecological process, because the measured rates are different from the rates that would occur in the absence of the enclosure (cf. Grubb 1989, 4).

In ecology, one can distinguish three forms of experiment (cf. Diamond & Case 1986, 3f.) that use different degrees of idealized conditions. On the one hand, ecologists use laboratory experiments. These experiments have the advantage that it is possible to determine exactly the influencing parameters of the investigated system and install stable conditions. Thus, they perform their experiments under idealized conditions in order to come to testable hypotheses and repeatable experiments. With this method, it will be possible to come to general statements about ecological processes that are not too idealized, but the question is whether the results of the laboratory experiments would have been the same if the experiment had been performed in nature. The

⁴⁷ This can be illustrated by the following example: ecologists isolate a small part of a lake by an enclosure to investigate the influence of specific chemical gradients on a specific species of algae. The effects probably would be quite different without the enclosure, but they were hardly measurable under natural conditions. Thus, ecologists have to perform experiments under idealized conditions.

reproduction rate of a population of mice under controlled conditions will be quite different under natural conditions where the influencing factors may change always.

On the other hand, ecology is concerned with field observations and experiments in the field. Field experiments are not as controlled as the laboratory ones, this leads to the problem that the results of these investigations are not automatically applicable to other ecological processes. Many constraints have to be excluded or roughly estimated in these experiments because it is not possible to measure them. The control used in the field experiments is weaker than in the laboratory experiments, but one has to use stronger idealizations on the theoretical level (e.g. *ceteris paribus* clauses) to arrive at general statements of ecological processes.

It is often not possible to realize a field experiment because it would result in a big damage to nature, like the flooding of entire woods or the intensive use of one chemical agent in big lakes to analyze e.g. interspecific competition etc. Therefore, a third form of “experiment” is important for ecologists, the *natural experiment*. This is a natural perturbation that can show how nature works without human influence (e.g. a destruction of a forest by a storm or the flooding of a wood by a beaver dam). Although ecologists can detect many new phenomena and processes the *natural experiment* is not more than an observation and ecologists are not able to control the influencing factors and have to rely on even stronger (theoretical) idealizations than in field experiments. Since the effects of this form of “experiment” are not influenced by the researcher, there are no idealized conditions on the level of the “experiment”. The problem with these experiments is that they cannot be used alone for a sound theory since these “experiments” cannot be repeated and it is hardly possible to infer general statements from them.

Ecologists have to use all three forms of experiment to come to general statements on ecological processes. If one wants to find out whether laboratory experiments can be applied to nature, it is necessary to combine field and laboratory experiments. If they want to know what effect great perturbations will have, ecologists have to rely on natural “experiments”. Thus, they need quite different forms of method and idealization, and combinations of them, in order to obtain general scientific statements. Although experiments under idealized conditions are necessary to arrive at general statements, these statements and theories often cannot be applied accurately. This means that ecologists have to find a middle path between idealization and empirical adequateness. This has some impacts on ecological generalizations that in many cases will differ

from physical ones, since physicists (at least the classical disciplines of mechanics and electrodynamics) need to use neither field nor natural experiments.

2.4 Theoretical Structures of Contemporary Ecology

Since generalizations are the means by which one obtains a unified theory, I will canvass specific forms of generalizations in ecology. I will investigate important aspects of ecological theories by looking at the role of laws, models and simulations. I will start with some general problems of ecological theory, go on by giving an overview on the general debate on laws in biology, and discuss why there are no natural laws in biology and ecology. Since there are a few broad and apparently true generalizations in ecology, it is useful to distinguish between different forms of law, material (natural) ones that can only be found in physics and structural ones that can be found in biology and ecology. Then I will go more deeply into detail and investigate some candidates considered to be ecological laws. As we will see, most (material) ecological "laws" do not have a wide range of application. Ecologists themselves talk mostly of models rather than laws and I will have a look at the different forms and roles of models in ecology. Since a special way of modeling, simulation, is used as a standard tool by ecologists, I will finish this section on theoretical structures by investigating the explanatory power of simulations.

2.4.1 Theory and Prediction

Ecologists and biologists often follow the epistemological ideas of Karl Popper. So, for many ecologists there are several elements of a good scientific theory. A theory has to be consistent, it should not contain contradictions and it should be as simple and as close to reality as possible. Finally yet importantly, it must be possible to falsify scientific theories (Golley 1993, 186). This last criterion is the most important because it draws a line between a scientific and a non-scientific statement. That is why it is often discussed by biologists. Although Poppers ideas are not in the focus of interest in philosophy of science for biologists they are still very important. Only sometimes, the "popperphilia" of ecologists is considered unhelpful in finding the right forms of experiments and theories for ecology (cf. Diamond 1994, 20).

Indeed, many ecological theories do not satisfy the Popperian requirements. It is assumed that central concepts of ecology are either so inexact or so idealized that it is

difficult to arrive at useful explanations and predictions. Either the concepts are too specific to be of any theoretical value or they are too broad to be applied (Peters 1991, 273).⁴⁸ Proponents of Popperian conceptions claim that prediction and other forms of testability should be considered most important aspects for the confirmation of ecological theories. Most ecological theories cannot be falsified and they are either too specific or too general to allow accurate predictions. Ecologists should rely on covering laws or true generalizations of a limited area to obtain explanations and predictions of ecological processes (Peters 1991, 177).

Again, as we have already discussed at the problem of terminology, the question to be investigated first is whether the nature of ecological objects allows the establishment of covering laws and accurate predictions. Perhaps it is not the failure of the discipline that there are no accurate predictions in ecology. Ecologists have to use broad generalizations and strong idealizations if they want to be able to predict ecological patterns, or they have to work with a small range of application, but they will not obtain generalizations of the kind found in physics. This leads to the question of whether methods and theoretical structures in physics also should be the ideal of ecological research. Although there are many reasons why biological and ecological theories differ from physical ones, philosophers and scientists still consider physics to be the ideal scientific discipline. Indeed, ecologists often are “envious” of physics and try to make ecology a more scientific discipline by adopting physical methods.⁴⁹ Although this has changed in the recent years and the autonomy of biology is stressed (e.g. by Ernst Mayr in nearly every of his publications), the classical view is still predominant among ecologists. If ecological theories do not fulfill some requirements for physical theories, it does not follow that ecological theories are unscientific. The individuality of populations and communities is a striking and typical characteristic of ecological entities that may lead to theories with a small range. However, the apparent indeterminacy and unpredictability does not imply that ecological studies have no value (cf. Simberloff 1980, 25). Ecology is an empirical discipline providing scientific statements on nature. If the theories in ecology are not as general as in physics, this is due to the objects of investigation and not to the discipline of ecology or the incompetence of ecologists.

⁴⁸ I will investigate this problem in the third chapter by examining the concepts of *ecosystem* and *community*.

⁴⁹ “Physics envy” is a much discussed topic among ecologists (cf. Egler 1986). Only in the last years ecologists have become aware of theoretical and methodological particularities of ecology.

If ecology wants to be an exact and empirical science, it has to investigate individual objects and their properties without idealizing too much, otherwise it may lose the touch to reality. Some ecologists and philosophers stress the importance of “natural history” for ecology and want to establish a “logic of case studies” for applied ecology (cf. Shrader-Frechette & McCoy 1994). They refuse the traditional form of explanation in the Hempelian sense and they are looking for specific explanations. Ecology should use practical and precise knowledge based on natural history, which means accurate investigations on individual objects. It should use “informal inferences” that have a bigger chance of being realized and applied than hypothetico-deductive inferences based on abstract generalizations (Shrader-Frechette & McCoy 1994, 244). An ecology working with case studies has a much better possibility to predict specific processes related to these case studies. With this method ecologists have already been able to obtain successful examples of prediction in nature conservation, e.g. by the case study of the Florida panther (cf. Shrader-Frechette & McCoy 1993, 198ff.). Thus rough predictions are sometimes possible from empirical knowledge and restricted generalizations only. For example, ecologists are able to predict the species of birds, beetles or mammals of a specified area based on the results of observation only (cf. Grubb 1989, 7). Although these predictions in most cases will not match the species composition to a 100%, they are useful and can be applied in many cases but surely not always. Thus, many field-oriented ecologists will not be interested in strong idealized theories but in specific ones that are near to the empirical reality and that may help to predict specific processes.

There seems to be no question that the “logic of case studies” can be used in applied ecology, e.g. in questions of nature conservation. However, it is still not obvious whether this method is useful for basic research. If ecologists do not want to give up the ideal that ecology can arrive at general theories and predictions, a “logic of case studies” is not very convincing because the range of application is too small and there is no theoretical basis. For biologists and ecologists theories are often not more than hypotheses that have gained a certain level of acceptability. The difference between hypothesis and theory therefore is largely subjective (cf. Fahrig 1988, 129). Thus, it is difficult to determine what can be considered a theory in ecology because there are many different assumptions on it. Laws and other far-reaching generalizations have always been considered hallmarks of science. Therefore, I want to look at different forms of generalization used in ecology in order to investigate whether one can talk of laws in biology and specifically in ecology.

2.4.2 Laws and Other Forms of Generalization

The question of whether there are natural laws has been debated among philosophers of science for a long time. Mostly philosophers of physics accept the existence of laws whereas philosophers of biology deny it (for biology). According to the classical view, it is the aim of science to establish general laws (e.g. Nagel 1961, 450), and so, physics is often considered to be the paradigmatic scientific discipline providing fundamental laws which govern all physical (and biological) processes. Nowadays some philosophers even doubt the existence of physical laws (e.g. Cartwright 1983, Giere 1995, 1999). For biology, most philosophers and biologists would at least deny that the establishment of laws is the central aspect of this science. Ecologists often use the word *principle* instead of law. *Principles* are simply those generalizations inductively derived from the data of ecology. Thus, a principle is a term which can have the meaning of *law*, *model* or any other sort of generalization (Grubb 1989, 8). By using the term *principle*, for ecologists it is not necessary to decide whether there are laws in ecology.

Although the establishment of laws is not a goal for biologists, philosophers still debate on the existence of specific biological laws. If one considers laws as the hallmarks of science, the answer to the question of whether there are laws in biology is important for its scientific status and its credibility in explaining nature. According to the covering law model, every scientific explanation is a deduction from some premises, containing universal empirically based laws and some initial conditions (Hempel & Oppenheim 1948, 10). If biology does not provide laws, it cannot explain scientifically. Then, according to the *received view*, the scientific status of biology is a very uncertain one. Whether or not this is true will be investigated in the following.

First, one has to come to an understanding of the term *law*. Traditionally laws of nature are considered true statements of universal form. They have to be confirmed empirically and are required to have a wide (if not universal) range of projectability. They are expected to support counterfactual conditionals; this means that they have to be necessarily true. Having the general statement: every car is green, one can use the following counterfactual conditional: if this were a car then it would be green. Obviously, this is not the case because a car need not necessarily be a green one, since there is no reason why a car should not have another color. Accordingly, this universal statement does not support counterfactual conditionals. Although not every

conception of law includes the support of counterfactuals, in the following this will be the distinctive criterion for a law.

In the conception of law, there are different metaphysical assumptions. Some consider it as real entities that can be found in nature, whereas others invent laws to describe processes. As shown in the introduction, philosophers of biology mostly are proponents of the semantic view that consider laws to be the description of an abstract system. In this view, laws are always applicable to the modeled system but this does not say too much about their general truth, since laws are not more than the description of an idealized model. Their truth is depending on the theoretical hypotheses referring to the physical model (cf. introduction 1.2.2). The fundamental laws of physics are considered descriptions of basic physical units and their interactions.

There are many different answers to the question of whether specific biological laws exist.⁵⁰ Schaffner (1993) distinguishes between universal and exceptionless generalizations and statistical ones. The universal ones may have quite different scopes but they are causally determined. In biology, many generalizations used do not have a broad scope of application although they are causal generalizations. By virtue of their causal character, they support counterfactual conditionals (Schaffner 1993, 121f.). Most of the biological “laws” and theories claimed to be universal come from molecular biology or genetics. But these generalizations (like the genetic code or the Mendelian rules) although the best candidates for “laws” in biology, still have a number of special case anomalies and are not universally valid. The more complex biological objects the less broad is the range of generalization. Today most philosophers of biology doubt the existence of specific biological laws (cf. Rosenberg 2001, 737). For this apparent lawlessness, several reasons are provided that are concerned with the nature of natural selection, as we will see in the following sections.

2.4.2.1 The Evolutionary Contingency Thesis

Gould (1989) elaborated on the idea that biology lacks own laws, but is constrained by physical and chemical laws, by stressing the contingent character of evolution. He compared evolution with a tape that would produce different outcomes on every replay. However, this does not mean that evolution cannot be understood: divergent ways

⁵⁰ In the debates on laws it is often not specified what should be considered to be a law. As we will see one has to distinguish at least between two different forms of universal generalizations that are designated as laws.

would be as explainable and interpretable as the actual path of evolution,⁵¹ but the results cannot be predicted from the beginning. Each step proceeds for cause but it is not possible to see the end of the evolutionary process at the start (Gould 1989, 51). Gould demonstrates his ideas of a contingent and historical evolution by the illustration of the Burgess Shale and its different interpretations (Gould 1989).

The *evolutionary contingency thesis* claims that distinctly biological generalizations (e.g., all leaves are green) cannot be lawful because they are concerned with contingent outcomes of evolution (Beatty 1995).⁵² This does not deny the existence of true biological generalizations (actually “there is no tree without green leaves” is a true generalization⁵³) but it says that biological generalizations will not support counterfactuals. Although we have not yet found a tree without a green pigment, evolution could produce trees that would somehow survive without chlorophyll, e.g. becoming parasitic etc. We may find biological patterns that can be described by true generalizations but nothing in evolution necessitates their truth (Beatty 1995, 52). The proponents of evolutionary contingency accept the existence of physical and chemical laws that are valid for biological objects too, but these laws only loosely determine the outcome of evolution.

The view that biology has no specific laws seems to be quite common among philosophers of biology today. Since many biologists accept that evolution produces contingent regularities, they are often more interested in regular patterns rather than in general laws. Although it could be possible to find a universal generalization in biology (in spite of being highly improbable), the primary aim of biology is not the search for fundamental laws but for contingent regularities (cf. Brandon 1996). Consequently, biologists are not seeking for the *one* correct mechanism e.g. of speciation or population density, rather they are interested in the *relative significance* of different accounts, which are consistent with evolutionary theory and help better understand the investigated phenomenon (cf. Beatty 1997, S436).

⁵¹ This form of explanation does not correspond to the covering law model, it is more a form of historical explanation similar to the one I will develop in the forth chapter.

⁵² This refers only to a specific form of law, the material one; another conception of law (the structural one) will regard some of these generalizations as laws.

⁵³ Sometimes we may find trees with red leaves but these leaves contain as well the green pigment (chlorophyll), but pigments of other colors are more powerful. To be exact, the true statement would be: Every *known* tree has leaves with a green pigment because this generalization does not support counterfactual conditionals.

At least empirical generalizations like the Mendelian rules that are often considered to be laws (cf. Brandon 1996) are generalizations on contingent regularities and will not support counterfactuals. The distribution of genes of sexually reproducing organisms should occur according to the Mendelian "laws". The counterfactual statement: *If this were a sexual organism, it would distribute its genes according to the Mendelian laws* is not necessarily true. Indeed, there are many exceptions and there is no reason why the evolutionary process should not lead to another form of gene distribution than the Mendelian which would be just as adaptive. It is obvious that Mendelian rules describe a contingent regularity. Biologists themselves are not talking of Mendelian *laws* any more but of *rules* instead in order to illustrate that there is no universal range of applicability and that there are exceptions.

If the evolutionary contingency thesis is true, then no biological regularity can be described by a law, because every biological regularity is an outcome of evolution. These regularities described by the Mendelian rules or by some ecological generalizations can still change due to the evolutionary mechanisms and thus the generalizations are accidental and may become wrong. Although the assumption that outcomes of evolution are contingent results is widespread among biologists and biophilosophers, it is still uncertain whether the process of evolution itself is lawful. However, before investigating this problem, I first want to provide another reason why there are no biological laws.

2.4.2.2 Fundamental and Structural Laws

Biological generalizations are concerned with empirical patterns like the distribution of elephants in the African savannah. In this case, ecologists provide generalizations that do not have a wide range of application. They only refer to specific empirical patterns (like the distribution of populations of elephants) that cannot be further generalized. If ecologists want to arrive at general statements being also valid for other empirical patterns (e.g. the distribution of populations of dolphins), they must rely on generalizations not directly concerned with empirical regularities but with theoretical concepts like *fitness*, *adaptation*, or *interspecific competition*.

Fitness is one of the most important explanatory biological concepts. It is regarded as a supervenient property being realized in a variety of different structures. A bald eagle, a grasshopper, a bacterium and humans have fitness, but they do not have too much in common at the level of their physical properties. Natural selection selects for effects and not for material "relationship". The selecting mechanisms do not distinguish

between different material units (e.g. wings of a bird or wings of a bat), they only select for functions of different material patterns.⁵⁴ We do not have any biological "law" directly concerned with concrete empirical regularities. Thus, in biology broad generalizations are not concerned with the material units (the organisms) but with their functions. There will be no laws referring to basic material entities (e.g. organisms or species). If one looks at a generalization about Fs, where F is a functional term (gene, wing, leaf etc) with the following form: $(x) [Fx \bullet Gx]$, this statement is not on biological structures but on functions. The problem is that there is no physical feature common to all items in the extension of Fx, because the members of this class have been selected for their functions. Functions that are selected by evolution supervene on the physical structures. Thus, birds and insects are flying and they have wings but the wings of birds and insects do not have much in common on the level of material organization but they share the function of flying. This form of selection in evolution is the reason for the absence of fundamental (material) laws in biology (cf. Rosenberg 2001, 737f.).

However, one can find some general statements in biology and ecology which refer to functions. A distinction between two forms of law may help to clarify the debate. One form may be called *material (natural, fundamental)* while the other one can be called *structural* law (cf. Stöckler 2000). The material laws correspond to the laws of the traditional concept. They are attributed to specific material elements like atoms or quanta and their properties. This form of law corresponds to the fundamental laws of physics and it cannot be found in biology because biological entities are selected for their functions and not for their material units.

In physics, it is accepted that material laws support counterfactuals. They have a distinct ontological status because they result from the properties of the elementary particles. Laws like these cannot be found in biology for two reasons. Generalizations referring to the properties of particles (e.g. species) will not support counterfactuals because those "particles" and their properties may change during to the evolutionary process. Generalizations referring to supervenient concepts (fitness, adaptation) or functional terms (genes, wings etc) cannot be applied to the underlying basic material structures because they are selected for functions and not for physical structures. Therefore, one has to deny the existence of material laws in biology and ecology.

⁵⁴ This explains why there are so many similar structures in non-related taxonomic groups. This *convergent* evolution, e.g. wings of birds and bats or feathers of non-related birds that evolved various times have independently led to similar morphological traits from quite different initial conditions. These convergent traits can be unified by means of similar functions but not by means of their basic material structures.

Yet in biology, one can find general and valid statements. These generalizations are either accidentally true if attributed to specific biological entities or they are *structural laws* describing functional relationships or processes of supervenient concepts. These laws do not refer to basic material units but to functions of higher-level properties that can be multiple realized (e.g. the different forms of wing in order to fly). This sort of law does not say too much about the material structures of the investigated objects but explains how and sometimes why the structures survive by means of their functions.

Although there is general acceptance of the non-existence of biological (material) laws, the question whether the process of natural selection itself can be considered a lawful process has not yet been answered. Natural selection provides mechanisms of change and describes a law-governed process. In this case, there is no big difference between biological and physical generalizations (Carrier 1995). The process describing laws are not related to the contingent outcomes of evolution and their basic structures, but rather to their supervenient concepts. Since we do not have any systematic connection between the concept of fitness and its material realizations, we cannot attribute the laws for the supervenient concepts to its physical realizations. Biologists can only express very general laws for supervenient properties but none for the physical realizations of these properties (cf. Sober 1996).

If we accept the existence of a lawful process of evolution, it is difficult to decide whether the laws describing this process are distinctly biological or not. By articulating precisely an evolutionary law, the result always seems to be a non-empirical mathematical truth. While natural laws refer to specific empirical objects (e.g. atoms), evolutionary ones typically do not (Sober 1993, 71f., 1997), and the question is whether they describe empirical biological realities. Lawful evolutionary statements are concerned with an abstract supervenient property and not with a concrete physical entity (cf. Sober 1996). There is no question that these statements support counterfactuals because they are necessarily true. This sort of generalization is not concerned with empirical results of evolution but with supervenient concepts like fitness that have multiple realizations that are contingent outcomes of evolution (cf. Carrier 1995). Thus, biological generalizations and generalizations on the process of selection are structural laws and not material ones. Since *natural laws* are traditionally considered to be material laws, it is justified to say that there are no natural laws in biology. This holds also for ecology, as we will see in the next section in which I want to investigate some candidates for ecological laws in order to determine their status.

2.4.2.3 Candidates for Ecological Laws

As we have seen, there are only structural laws in biology. If one accepts the arguments for contingency of biological regularities and the ones for “functional selection”, it follows that generalizations on ecological regularities cannot be material laws. In ecology, we have apparently even more contingent regularities than in the field of molecular biology or genetics, since ecological objects, processes and their constraints are much more complex. Although every empirical biological regularity is contingent, there are degrees of contingency. Ecological patterns probably provide the highest degree of contingency because there are so many different biological processes occurring together. Additionally, they also provide the highest degree of “functional selection”; the more complex the structures, the more ecologists are forced to apply a functional consideration and come to unifications by means of analogies and generalizations concerned with functions.

Although the majority of ecologists would say that there are no laws in ecology, and they will talk of models instead of laws like most biologists (cf. Sober 1993, 15), we find some proponents of the existence of ecological laws as well. However, most of the proposed ecological laws do not satisfy the condition of supporting counterfactuals and often they are even not ecological laws but physical ones. Lists of ecological laws contain the following generalizations: a) first and second law of thermodynamics, b) rules of stoichiometry, c) principle of natural selection, d) general physical processes like diffusion etc, e) interaction of organisms with themselves and their environment. The first three are considered universal laws, the fourth is a set of laws and the fifth is just a simple observation (Lawton 1999, 178).

If we take a closer look at the list, we can see that there is no specific ecological law. There is only one biological law in the list, the principle of natural selection, and all the others are physical laws. Since the fifth is just an observation, it can be discarded anyway.⁵⁵ As I demonstrated in the previous discussion, the status of the principle of natural selection as a law is debatable.⁵⁶ If its various aspects can be demonstrated to be laws then they will be structural laws. Although Lawton (1999) stresses that ecology has “truly deep laws” he is not able to mention even one. Nobody would deny that the physical laws of thermodynamics, diffusion etc are also valid for ecology, as for all

⁵⁵ Perhaps one can find some rules for this observation, in this case, it could become a lawful generalization, but as long it is considered to be just an observation I will not deal with it.

⁵⁶ Actually, the principle of natural selection is a family of mathematical models and not one single principle. But these models can be considered to be structural generalizations.

other biological disciplines, but they are not specifically biological or even ecological. Thus, Lawton's defense of laws in ecology is ineffective.

Other candidates for ecological laws are the following: a) the dissipation of energy across any trophic transfer, b) the competitive exclusion principle c) the population growth thesis, d) energy allocated within an organism for one use is unavailable for other uses, e) genetic adaptation to one set of circumstances precludes adaptation to many other circumstances, thus all species are to some extent specialists. These "laws" lack the precision of the Newtonian law of gravitation and they are not formulated in the form of a universal statement allowing specific and testable predictions, as it is expected from laws in physics. Nevertheless, they are considered more than just accidental generalizations because they are always and universally true and forbid certain things from happening. It is considered to be overly restrictive when a law in ecology is expected to be as precise or as predictive as a physical law. These restrictions would remove the possibility for the existence of laws in ecology; therefore, one should broaden the concept of law (Loehle 1988). Thus, one can attribute laws to ecology by means of a reduced standard of lawhood. However, with this strategy we will not win anything. It would be better to emphasize the differences of ecological and physical generalizations and use different terms for them than to save "laws" for ecology.

Fundamental laws and theories in ecology appear unlikely due to the evolutionary contingency and the "functional selection". Neither particular communities nor particular species will occur again in different time and place. They are unique. Although the mathematical models of ecologists have heuristic power and help us to understand ecological systems, it is thought that they will not develop into general laws which are universally applicable (Shrader-Frechette & Mc Coy 1993, 116). I do not think that this is necessarily right. Probably there are some universally applicable structural laws in ecology, only fundamental ecological laws will not be found. That is why I will have a look at the competitive exclusion principle, which is so settled that it is considered to be a law even by philosophers (cf. Weber 1999).

The Competitive Exclusion Principle

In the following, I will give an examination of the *competitive exclusion principle*.⁵⁷ This surely is the most interesting candidate for an ecological law being one of the most settled generalizations in ecology.⁵⁸ It has provided something badly needed by ecologists, a simple hypothesis that helped to bring some order to the ecological complexity (Kingsland 1995, 169). This principle states that two competing species cannot co-exist for a long time in the same niche. When competing for the same niche one of the two species will necessarily find another niche or will become extinct. The principle is considered being evolutionarily invariant and independent of evolutionary changes. This means that it supports counterfactuals and does not refer to contingent regularities. Further, it is considered an example of a causal regularity (this principle can explain why we never will find two co-existing species living on the same niche) and an example of a distinctly biological generalization. The competitive exclusion principle is causally necessary and supports counterfactuals in the following sense: if two species living in different niches were to compete for a single limiting resource, *ceteris paribus*, only one of them would survive (Weber 1999, 80).

The principle of exclusive competition is normally connected with the definition of the ecological niche. This leads to the problem of defining *niche*. Since there are many different characterizations, it is difficult to confirm the competitive exclusion principle. If a test fails, one can recover the principle by redefining the niches for the populations tested (Getz 1998, 540). However, it is also possible to formulate the principle without the concept of the niche: *Complete competitors cannot co-exist* or: *ecological differentiation is the necessary condition for co-existence* (Hardin 1960, 1296). Both formulations are testable and indeed, there are experimental confirmations of this principle (Gause 1934). Every experiment could confirm the competitive exclusion principle - one of the species was completely eliminated, but it was not always the same one (Hardin 1960, 1293). Therefore, this principle lacks the ability to make

⁵⁷ Although the scientific status of the population growth thesis, stating that *populations in finite environments cannot grow indefinitely* is also much discussed, I will only deal with the competitive exclusion principle. This investigation is sufficient to demonstrate the role of "laws" in ecology. An examination of the population growth thesis can be found in Shrader-Frechette (1994).

⁵⁸ Like most ecological concepts, the concept of competitive exclusion has many different explications. Murray (1986) distinguishes three groups. One states that co-existing species cannot be competing. This surely is a curious assumption since the exclusion of one species results from competition. A second group assumes that the principle is only applicable to species with identical or nearly identical niches or ecologies. Since it is possible that two species could live in two non-overlapping niches with the exception of one resource (e.g. nitrogen) this assumption seems to be overly restrictive. A third group states that competitors can co-exist but not indefinitely (Murray 1986, 150). This is the most generalizable form.

deterministic predictions. It can say what will happen in general, but it cannot predict what will happen with a concrete species.

There seem to be many violations of the principle. Co-existence of species in the same niche may occur in the case of resource seasonality, immigration, environmental fluctuation etc.⁵⁹ These exceptions have reduced the domain of applicability and enhanced debates on the significance of the principle. Yet the principle itself is an important ecological one because it provides ecologists with most reasonable explanations for their observations. This principle therefore should be considered as confirmed although its basic assumptions have been greatly extended and the recognized range of its applicability has narrowed considerably (cf. Fahrig 1988, 130).

One could assume that the principle is an analytically true one that follows necessarily from basic assumptions and hence supports counterfactuals. Nevertheless, the question remains: what does the principle say about empirical phenomena? I would say that this principle is a structural law that describes supervenient properties but does not make statements on material entities of the individuals concerned. By now, another question arises: is this principle a distinctly ecological, an evolutionary or even a general analytical statement that can be applied not only to ecology but also to economy and other disciplines. Anyone who wants to earn some money must find his “niche” which cannot be exactly the same one as that of someone else. The competitive exclusion principle could be applied just as well to economy as to ecology in the following formulation: *Complete competitors cannot co-exist*. This general “law” (which corresponds to a typical structural law) would not be recognized as an ecological one but a very general one which can be applied as well to ecology. Thus, it will not be a specifically ecological law.

The competitive exclusion principle is thought to be a *causal regularity* and thus a candidate for a counterfactual supporting law (Weber 1999). Causal regularities are considered an essential factor of biological explanations. They exhibit the most important features of scientific laws, support counterfactual conditionals, and they are neither temporally bound nor spatially (Waters 1998, 20). Besides the competitive exclusion principle, there are other examples of causal regularities in ecology. Thus, ecologists try to explain succession by the tendency of broadleaf trees to grow canopies, which cast shadows on rival saplings (cf. Waters 1998). Another similar

⁵⁹ It seems to be that the violations of this principle depend on the time length used for investigation. The principle has to include the notion of time but of course it is very difficult to say how long the time ought to be in order that the competitive principle be effective.

example is Bergmann's rule, which explains why animals of related species in the cold and arctic zones are bigger in size than animals in warm regions. For energetic reasons it is useful to be larger in cold regions and smaller in warm ones.⁶⁰ Nevertheless, there are other possibilities of reaching the same effect without increased size, e.g. by getting a thick fur or by inventing some internal heating systems etc (cf. Beatty 1995, Carrier 1995).⁶¹ Thus, causal regularities can support counterfactuals but they are neither distinctly biological⁶² nor do they correspond to specific empirical patterns; they only describe functional aspects of the investigated objects and thus correspond to structural generalizations. They will only partly help to understand ecological phenomena although they explain accurately.

We can conclude that ecology has only structural laws and that these are not always distinctly ecological but ones that can also be applied to other disciplines (e.g. economics or sociology). However, this leads to many questions. If there are no material laws in ecology, what will be the consequences for the scientific status of this discipline? Does ecology have to become a science of case studies? Does one have to develop a new concept of law? Is a scientific explanation possible without natural (material) laws? These questions must be answered to determine the scientific status of ecology. I will try to do this in the forth and fifth chapter, but first I will go on to investigate structures and conceptions of ecological theories (remainder of Chapter 2) and complex ecological objects (Chapter 3).

2.4.3 Models

Biologists and ecologists rarely talk of laws rather they talk of models. For biologists models describe the rules by which a system of a given kind changes (Sober 1993, 15). The term *model* is used everywhere in ecology and it has different meanings, like most terms widely used in ecology. Models shall describe the mechanisms regulating the behavior of ecological systems. Sometimes they correspond to general rules or

⁶⁰ Since the relationship between volume and surface area increases with the size of animals, the loss of warmth will be less in large animals than in small ones and they have a better chance to survive in cold regions than small animals.

⁶¹ Although this seems to be obvious, Waters argues that these generalizations are universally true and counterfactual supporting. The salient point of his account is that he believes that generalizations are not about empirical patterns but about theoretical kinds, therefore he emphasizes the difference between biological distributions and causal regularities. Both forms of generalization have to be connected somehow. Causal regularities do not say very much about the ontology of basic parts of nature, they correspond to structural laws.

⁶² Bergmann's rule actually refers to a physical law that can be applied for biology but it will not explain specific biological patterns. Additionally, the increase of the relation from volume to surface area with increasing size only holds for spherical objects and there is no spherical animal.

even “laws”, but models describing specific ecological objects can also be found. Ecological models are mostly expressed in a mathematical form. In this way, it becomes obvious that ecological models aim at more than just describing specific patterns: they aim at the description of universal accounts in order to apply it to ecological objects. Thus, they are very similar to conceptions of "law" and often it is difficult to distinguish between "law" and "model" in ecology.

Before dealing with models in ecology, I will give an account of some aspects of the general debate on models in the philosophy of science. Since about 1980, philosophers of science have been more and more interested in models, because models seem to be more relevant for the scientific method than laws, and at least in biology the term *model* is the one mostly used. Apparently, the conception of general and universal laws is not so important for scientists (at least for biological and other complex disciplines) as for (traditional) philosophers of science. Proponents of the semantic view consider models much more important than laws. They regard science as being characterized by models and not by laws and analyze scientific theories in terms of models (cf. Lloyd 2000).

2.4.3.1 General Aspects of Scientific Models

In the philosophy of science, the term *model* has various specific meanings and one can find many different accounts for the meaning and function of *model*. Generally, a model is considered to be an idealized imitation of concrete empirical data or an instantiated demonstration of a theoretical object. Thus, models are representations of theoretical or empirical entities or both. Today one distinguishes between *scale models*, *analogue models* and *theoretical models* (cf. Bailer-Jones & Hartmann 1999; Lloyd 2000). We can find other forms of models but it seems that all other forms can be subsumed under one of the three.

Scale models are shape-true imitations of very big or very small objects of research. Small imitations of ships or planes are typical examples for this form of model. Nevertheless, there are also scale models of atoms or molecules that are much bigger than the original entities. The model will represent the object true to scale but will be much smaller or much bigger. The model represents the exact form of the object but often the functions of the original cannot be attributed to the scale model. Scale models are not only used by amateurs (small ships and planes) but are important for scientific use as well. An important scientific scale model was the DNA-model by Watson and

Crick, used for a better understanding and demonstration of the spatial and chemical construction of the double helix.

Analogue models imitate the structure of an already known real object in order to apply it or some of its properties to another until then unknown system to be investigated. This type of model helps to postulate properties and functions of the unknown object. The planet model of the atom and the computer model of the human brain are known to be analogue models (Bailer-Jones & Hartmann 1999). The assumption that an ecosystem corresponds to a cybernetic machine can also be considered to be an analogue model. Both scale and analogue models are often material models, this means that they are concrete material entities. They imitate one material structure by using another material structure. The scale model is used for imitating exactly while the analogue one is used as a heuristic means.

Theoretical models try to express characteristic properties or processes of an object in an abstract way. There are different opinions on what theoretical models are. Sometimes they are thought to be linguistic assumptions and equations (e.g. Bailer-Jones & Hartmann 1999). In this case, a model more or less corresponds with the classic concept of theory structure and the difference between model and theory is not always clear (cf. Weinert 1999, 320). A theoretical model is also considered a combination of theory and model object, and is a necessary tool in applying a general theory like the Maxwell equations to a specific area (Stöckler 1998). Usually a theoretical model is conceived of non-linguistic entities that satisfy the axioms of a theory (e.g. van Fraassen 1980, 43).

The three forms of model cannot always be differentiated distinctly, because one can find transitions between the different types. A material analogue model can become a theoretical model by idealization and abstraction. The assumptions and equations of a theoretical model can be visualized and exist in form of material models. Thus, the bowl-model of ideal gases can be both a material analogue model and an abstract theoretical model. Accordingly, many models cannot be definitely categorized. For scientific disciplines, the use of theoretical models is more important than scale or analogue models. Therefore, I will focus on theoretical models.

Logical Positivists considered models to be unimportant for scientific theories. A model had only an aesthetic or didactic or at best a heuristic value but was not regarded as essential for a successful application of the scientific theory. Today, current model theories focus on abstract non-linguistic structures like groups of group theory or

vector spaces (Giere 1999, 42). The conception of model mostly used by philosophers regards models as structures that satisfy the axioms of a specific theory (Bailer-Jones & Hartmann 1999, 854; Giere 1999, 43). A theory is considered a linguistic structure, constructed by a set of statements whereas models are non-linguistic entities, which satisfy the theory. This conception was developed in mathematics but was brought into philosophy of science by assuming that epistemological processes in mathematics and empirical sciences were similar (Suppes 1960).⁶³ A model interprets a set of uninterpreted axioms, thus the equation $y=mx+n$ can be specified by attributing specific meanings to the terms.

The term *model* is used to represent theoretical or physical structures. The direct representation of natural objects seems to be the most important aspect of modeling in science (Giere 1999). A good example for a model representing empirical structures is a city map. It is a physical entity (a paper with specific forms on it) that shows just some specific elements and neglects other ones, which are not so important for its purpose (in this case the paths and roads of the city are to be found but not the houses). Thus, a map represents specific aspects of the world by means of a material entity. Although physical models like a map are neither linguistic entities nor instantiations of linguistic entities, they have the ability to represent other physical objects. In this case, models serve as instrument for theory construction. Theory (language) is not connected directly with the world, but rather with a model. The connection with the world then is a type of similarity between a model and designated parts of the world. Different ways of constructing models enable us to represent different aspects of the world more or less accurately. Such a representing model is concerned with describing the real structures of the world. We do not have a direct connection between language and world, rather models of aspects of reality help to come to a theory. The theory can be applied to nature by means of an interpretation modeling a specified part of the world. Scientific reasoning is nearly always reasoning with models (Giere 1999).

Models then can be considered representations of theories about empirical data. The mathematical model conception stresses the aspect of instantiation whereas the just outlined "representational" concept stresses the concept of direct representation. Now, one could ask whether the "representational" view is more realistic than the model used by the mathematical conception of model. From an instrumentalist point of view, one

⁶³ It is difficult to decide whether models are non-linguistic entities or linguistic ones. Although models as instantiations of theories can be considered non-linguistic entities, they are at least correlated to linguistic entities and the distinction between models and theory is not obvious.

could imagine that these mathematical models were selected in a quasi- Darwinian process and are relevant to the empirical reality only insofar as they can be applied. In some way, they are similar to structural laws: they can be applied successfully to empirical reality, but the question remains to what extent they represent the empirical patterns of reality. One could imagine that these models fit the empirical reality in terms of their functions but they need not to represent the real empirical patterns. This view corresponds to an instrumental conception of models that is opposed to the representational.

Perhaps there is a middle road between instrumentalism and realism concerning models. Models help to learn about theories and about the world. They can be considered autonomous agents and instruments of investigation. They are derived from empirical data or from theories but they are neither data nor theories, they are in some way independent agents and can mediate between theory and empirical reality. They function as tools of investigation and are independent of, but mediate between things and can be used for different tasks. The critical difference between a simple tool and a tool of investigation is that the latter involves some form of representation: models typically represent either some aspect of the world or some aspect of our theories about the world, or both at once. The representative power of models allows them not just to function instrumentally; rather they also teach us something about the things they represent. Thus, one of the most obvious uses of models is to help to construct theories. On the other side, models are used to explore the implications of theories in concrete situations. That is why models should no longer be treated as subordinate to theory and data in the production of knowledge. Models are essential ingredients in the practice of science and as important as theory or data (cf. Morrison & Morgan 1999). Whether this view on models corresponds to the use of models in ecology will be investigated in the next sections.

2.4.3.2 Models in Ecology

The word *model* can stand for a variety of things in ecology and it is difficult to gain an overview of ecological modeling because there are so many different accounts of it. Thus, I will only outline some basic features. Although modeling techniques developed relatively late in the history of ecology, modeling is now an important tool of ecological research, and ecological theory without using models is hardly imaginable. Ecological modeling originated from Lotka-Volterra and Streeter Phelps in the 1920s, while comprehensive use of models increased in the early 1970s and today modeling is one

of the most important methods of ecology. One can distinguish between more than 4000 ecological models (Jørgensen 1999).

A model as it is used in ecology is mostly an idealized representation of the functions of a community or an ecosystem, or of their dynamic or structural properties; nearly all ecological models are expressed in terms of mathematical equations (Sagoff 1984, 10). These models are much idealized and the question to be answered is how far models can be idealized by still representing aspects of empirical reality. The problem in ecology (and other complex sciences) is that there are too many factors to be eliminated for acquiring a useful model. Therefore, models often fail to explain specific empirical ecological phenomena. In other less complex sciences it probably will be more adequate to work with mathematical models, because there is not so much "noise" which has to be eliminated to build models.

In ecology, the distinction between model and theory is blurred. The word *model* is very often used in ecology, sometimes over-used and often used in the same sense as theory. Most ecologists see theory as mathematical theory and they do not distinguish between a general equation and a model. Although there is no reason, why every ecological theory should be expressed in mathematical language (cf. Reuter 2001, 25) and although in many cases it would be better to use *theory* instead of *model* (cf. Fagerstroem 1987), *theory*, *model* and *mathematical equation* are often used synonymously by ecologists.⁶⁴

In ecology, we do not find fundamental (material) laws. We may only find structural laws like the competitive exclusion principle. The question to be investigated is whether ecological models shall represent material or functional aspects of ecological objects or both. Since ecological theories (and models) are very diverse and ecologists themselves consider them to be no more than a collection of tools (cf. Roughgarden 1984, 17), the mathematical concept of model and its instrumentalist character seem to fit well with the use of models in ecology. Whether this is convincing and whether ecological objects ought to be looked at from an instrumentalist point of view will be investigated in the next sections, but first I will investigate various forms of modeling in ecology.

⁶⁴ This already shows that the use of models in the philosophy of science does not correspond to the use in ecology. But it also shows that the philosophy of science can help to clarify ecological concepts.

2.4.3.2.1 Various Forms of Approach

Ecological modeling is considered to be the construction of a symbolic representation of the functioning of an ecological system in the form of mathematical equations (cf. Pielou 1981, 17). We can distinguish broadly between descriptive and analytical models in ecology. Descriptive models try to represent empirical data directly (e.g. in form of a distribution map of a bird species etc) or by means of statistical correlations of empirical data (e.g. the average daily sunbathing time of a grasshopper species needed to get their required temperature sum). This is an important form of modeling but usually ecologists consider models to be analytical and mathematical (cf. Fenchel 1987, 18). Ecologists try to idealize ecological systems sufficiently to represent the essential behaviors by using models simple enough to be analyzed mathematically (Hall & DeAngelis 1985, 341f.). Thus, a model is considered a structure that is presented in mathematical form and that contains an articulated set of explanatory principles and idealizations (Richardson 1986, 109).

Analytical ecological models do not need to provide a true representation of ecological data; they just have to be consistent in a rather loose sense. After passing this test, they will be subjected to a more or less irrational judgment, where simplicity, productivity and beauty are important criteria. Although mathematics should only be used as an aid in theory construction and not as a substitute for it, (Fagerstroem 1987) mathematical rigor is the most important aspect of modeling in ecology. Ecologists consider the integration of mathematics into their field to be a big contribution to the theoretical knowledge of ecological systems. Models are considered to have the same relation to theoretical problems as experiments have to empirical problems (Caswell 1988). This means they are used to represent and confirm theories.

The question whether the ecological models are appropriate to the empirical ecological processes has been discussed for years in ecology (cf. Levins 1966, Hall 1988; Hall & DeAngelis 1985, 339f.). There is a communication gap between theoretical modelers, who use mainly analytic techniques and field orientated ecologists who confine their efforts to descriptive and statistic models that differ radically in spirit and approach from the abstract analytical models⁶⁵. It seems to be hopeless to construct models representing complex natural systems by means of simple mathematical equations. Thus, this form of modeling may result in an artificial world and ignore the complexity of

⁶⁵ This discussion of the use of models in population ecology is a typical trait for population ecology and corresponds to the both strands described in (2.2.2).

nature. Many models are poor substitutes for specific empirical data, because it is nearly impossible to have models that are general and accurately applicable. Mathematical rigor is important for models but sometimes irrelevant for the virtue of a model vis-à-vis reality. Often there is an overemphasis on solving equations instead of looking at which models are best in representing nature. Thus, the judging and testing of models is too poorly developed. Modelers often seem to be very traditional, although there are many indications that certain models (the logistic curve, the Lotka-Volterra equations etc) are not suitable for many cases in which they are still used by modelers. It seems as if the models have taken a life of their own, unrelated to empirical reality (cf. Hall 1988).

The method of analytical modeling and of descriptive modeling can be characterized by a top-down and a bottom-up-approach. Either ecologists start by putting every empirical detail in their model at the highest point of resolution, trying to simplify it (bottom-up), or they begin at the lowest level of resolution that includes structures and processes which are the point of interest (top-down). Either they try to elaborate every detail by imperative of natural history or they follow the theoretical imperative to encapsulate the details by starting with a leading principle like the population growth model or the competitive exclusion principle.⁶⁶ The top-down approach often works with mathematical and analogue models and tries to apply them to nature like tools. These tools are often used to manage specific mechanisms. The bottom-up- approach on the other side stresses the importance of specific (historical) empirical data and tries to represent real natural phenomena by means of descriptive and statistical models (cf. Cooper 1998).

2.4.3.2.2 Problems of Application

Although there are quite different approaches to modeling in ecology, the importance of models is stressed in systems ecology, population ecology, and evolutionary ecology. All three approaches work with models which are expressed in a mathematical language. Systems ecology, theoretical population ecology and evolutionary ecology mostly work with analytical models while the historical strand of population biology uses descriptive and statistical models. Although theoretical population ecology and systems ecology stress the importance of modeling, there are no fixed methods of how to build and apply models. Construction and application of models require scientific knowledge and some special mathematical and computational skills. The use of models in

⁶⁶ Here it becomes obvious that the separation of “laws“ and “models“ in ecology is not clear at all.

population ecology in explicative or predictive modes is dependent on the experiences of individuals, their skills and their worldviews (Getz 1998, 541; Grimm 2001, 45). Thus, modeling in population ecology is more an art or skill than a rigorous science. It is more concerned with fixing what is wrong with existing models than with finding new and correct models (Getz 1998, 550). The precision of models in population biology will, by and large, never approach the precision of those used in the physical sciences, because the variability of the constituent elements of the entities to be modeled in ecology is inherently greater in ecological than in physical systems (cf. Getz 1998, 541).

Theoretical population ecology and systems ecology often use differential equations and apply them to different systems. Models of population ecologists try to analyze competitive interactions and other population processes while systems ecology is concerned with the modeling of energy or chemical cycles. Population models make a strong distinction between biological and physical factors and try only to explain the biological ones. Systems ecologists have always wanted to include the abiotic parameters into their models (cf. Palladino 1991, 230). Population ecology tries to describe populations in terms of their age distributions, physiological states, and densities. It recognizes multi-species systems. The environment is allowed to vary but the species are treated as genetically homogenous, so that, by and large, evolution is ignored (Levins 1966, 421). Modeling in population ecology faces the same problems as in systems ecology: there are too many parameters to measure; the equations used are often analytically unsolvable. These problems could be solved by either sacrificing generality for realism and precision or sacrificing realism for generality and precision or sacrificing precision for realism and generality.

In the sixties and seventies systems ecologists tried to model whole ecosystems. They wanted to completely describe entire systems and make testable predictions for them in order to develop concepts of conservation, but they failed. They assumed that ecosystems behave like gigantic cybernetic systems that can be dealt with by the same methods as cybernetic machines. After the end of the International Biological Program (IBP) in 1974, the impossibility of this program and its inapplicability to nature conservation became obvious. Thus, most ecosystem ecologists adopted reductionist methods in ecosystem studies. However, they continued using the ecosystem models for organizing data and generating questions. They were no longer interested in describing states of nature realistically (cf. Golley 1993, 189). Ecosystem models were

not used to represent physical patterns but as an instrument for theory construction and hypotheses generation. However, the realistic aspects still can be found in contemporary models of ecosystem. They are considered complex adaptive systems with a high number of feedback regularities enabling organisms and populations to survive and reproduce in spite of changes in external conditions. Ecosystem properties emerge as a result of many simultaneous and parallel processes. Although it is possible to examine the parts by reduction to simple relationships, the interactions of parts form a whole that behaves differently from the sum of the components (Jørgensen 1999, 77).

In the next section, I want to go into the Lotka-Volterra equations in order to illustrate the way of analytical modeling by a case study.

2.4.3.2.3 The Lotka-Volterra Equations

The important and still ongoing debate on the role of mathematics in population ecology is often discussed by looking at the role of the logistic curve (cf. Kingsland 1995, 214f.). This equation was reformulated to the Lotka-Volterra equations.⁶⁷ The first assumption of an infinite growth of populations can be expressed with the following simple equation, the Malthusian model, which assumes an exponential increase in population size with time:

$$dx/dt = rx$$

(x = population number and r = a constant rate of increase)

Some ecologists consider this simple equation to be a law, but mostly it is called a *model*. It is the basic principle for the different formulations and applications of the Lotka-Volterra equations. The model starts with strong idealizations: an indefinitely growing population (by neglecting immigration and emigration). Actually, there is no existing population that exhibits infinite growth; therefore, the equations have to be modified by adding some limiting parameters. Thus, we come to the logistic curve. The label "logistic" comes from Verhulst (1845). It should describe how the early states of growth would increase exponentially until the time when the crucial resources become limiting. Now, the growth tends asymptotically to a limiting value. Thus, the logistic curve has a typical sigmoid form.

⁶⁷ The equations themselves are often called *model*, according to the philosophical terminology a model would be an application of the Lotka-Volterra equations, but for pragmatic reasons I will sometimes use the ecological terminology. Yet one can consider the specified equation (x= number of individuals etc.) to be an interpretation of the general equation. Thus it corresponds to the mathematical conception of model.

Sometimes this curve is described by the following equation:

$$x = K / (1 + e^{-at})$$

(x = number of individuals, t = time, K = upper asymptote, r = maximum rate of increase, a = constant of integration).

Nevertheless, usually the model is expressed in a differential form:

$$dx/dt = rx ((K-x) / K)$$

K represents the *carrying capacity* or *equilibrium number* for the population in a specific area. It depends on the area of the population and indicates the maximum number of individuals in a population which can survive. Somehow, the density of the population is controlled but it is not obvious which factors are responsible for density control. Often it is assumed that the population controls its density and that the control factor is a function of x^2 although there is no biological reason for it (cf. Wangersky 1978). Since cause and effect do not occur simultaneously in biology, we have to include a time lag ($t-\tau$) and come to the most general form of the single species growth model.

$$dx/dt = rx ((K-x) / K)_{(t-\tau)}$$

Many parameters must be included into this model to describe the growth of a single population more accurately, like specific mechanisms of density dependent control of population growth. Thus, the model of single population growth submits too many changes before it can be applied to a specific population.

The fundamental model of population growth is not only used to describe single population growth, it is also the basic equation for predator-prey and other competition models for several populations. The predator-prey model consists of two equations representing two populations influencing each other:

$$dx/dt = rx - \alpha xy$$

$$dy/dt = \beta xy - Dy$$

(x = the number of prey organisms, y = number of predators, α is a constant that links the prey mortality to the number of prey and predators, whereas β links the increase in predators to the number of prey and predators and D is a constant of mortality for the predators).

Although there were several contributors to the development of these curves (for a detailed history of this development cf. Kingsland 1982), this pair of equations is known as the Lotka-Volterra equations (cf. Simberloff 1980, 18). They are still very important for contemporary ecology and must be studied by every student of population ecology.

These models describe the well-known cycle which arises from the fact that an increase of predators is followed by a decrease of prey and that a decrease of prey results in a decrease of predators. The decrease of predators enables the population of prey to increase again and the cycles begin again. The equation describes a mechanism on the level of populations. Actually, there is no predator-prey system described exactly by these equations. However, these simple models can illustrate some important mechanisms that are responsible for population cycles. One has to include the damping factor for the population growth of predators and the time lag in the effects on the prey in order to get the models a little more precise. Thus, we come to the following equations:

$$dx/dt = rx ((K - x)/K) - \alpha xy$$

$$dy/dt = \beta xy - Dy_{(t-\tau)}$$

One has to consider many other factors that ought to be included for the application to specific cases. The equations can also be applied to describe parasite-host systems, other competitive systems etc, but we must always specify some parameters. It is only for much idealized populations that this form of equations can be applied.⁶⁸

These equations had a big impact on the theory of population ecology and they were considered the most important theoretical development for general ecology (Hutchinson & Deevey 1949). However, the field oriented ecologists considered these equations as too simplistic to be of any value. Theoretical ecologists in the sixties and seventies were highly interested in improving the Lotka-Volterra equations, but the results were largely irrelevant for empirical ecologists. Thus, they sometimes tried strongly to oppose against theoretical modeling and compared mathematical ecologists with the drunkard who has lost his watch in the dark but looks for it very carefully under the lamp because that is where the light is (Levandowsky 1976). There seems to be a strong traditionalist power which forces population modelers to hang on to the standard way of abstract modeling and not to look for new ways which are empirically more

⁶⁸ For an accurate investigation and the different applications of the Lotka-Volterra models see Wangersky (1978).

adequate (Getz 1998, 544). Accordingly, the Lotka-Volterra equations are a typical example which demonstrates the discrepancy between the “natural history view” and “mathematical” one in ecology.

2.4.3.2.4 Functions of Ecological Models

Most forms of ecological models correspond to the standard interpretative view of models. They can be considered interpretations of basic structural assumptions mostly formulated in the form of differential equations for specific populations. Although ecologists themselves often do not distinguish between models and mathematical equations, one can apply the view that models are instantiations of basic equations to the practice of ecologists. As demonstrated, by means of the logistic curve, the basic equations have to be modified in order to be applied to specific ecological objects. The application of models can be used as a test for the validity of ecological theories.

Ecological models often serve as instruments to test and apply general theories. In this application, they also serve as representing tools for empirical data. However, the main interest of the modelers is not a realistic representation of empirical data but a way to confirm theories by means of the criteria of simplicity, beauty and productivity of models. Other forms of models starting with a bottom-up-approach are more interested in representing reality and individual aspects of ecology.

In systems ecology and in theoretical population ecology and the “non-historical” evolutionary ecology, models are used in a *top-down-approach*. The empirical population ecology and the historical evolutionary ecology work with *bottom-up-models*, starting with empirical, historical data. They are more interested in representing empirical data than in finding general theories. They use models mainly for theory construction in order to understand natural processes. In both aspects of modeling, models are important parts of ecological explanations. On the one side, the explanation will be provided by a general theory on the other side, an explanation is provided by the individuals and their behavior. Nevertheless, this form of explanation cannot cover a wide range of ecological objects. Ideally, both forms of modeling should work together.

A combination of both approaches can be found in *individual based modeling* which can avoid the problems of analytical models without being pure descriptions of empirical data. Sometimes the explanations do not fit the empirical data and they do not predict ecological processes. This is similar to models of weather. In these models, it is known that small changes in the influencing factors can lead to large changes of the

complex system. This had a big effect on ecological strategies of modeling. In the eighties, ecologists began to develop fuzzy sets, neural networks, cellular automata and individual based models (cf. Breckling & Reuter 1996). Ecologists noticed the failures of the analytical, process-oriented models and developed individual based ones in order to explain complex behaviors from its individual parts. With this form of modeling, they were able to combine descriptions of macro-phenomena with historical, singular data. This form of modeling has become very common recently because it avoids some of the basic problems of traditional ecological modeling. These models are often used for simulations that can help to imitate processes of complex systems and the genesis of their properties, as we will see in the following section.

We can find different approaches of individual based modeling. Cellular automata models can be used to model the emergence (used in the trivial sense) of a spatial pattern from particular local interactions. Although this form of modeling is not yet frequently applied in ecological contexts, it is considered a promising new approach (cf. Breckling & Reuter 1996). Most cellular automata models are used in studies of vegetation dynamics. Cellular automata are the spatial counterparts of the simple classical models of population dynamics (the logistic equation and its different forms). In the cellular automaton model, each cell represents a patch of space for one individual. If a cell is empty, it can be occupied by local reproduction by one of its neighbors. If a cell is occupied, either it can become empty because the individual dies or it becomes empty as a result of competitive interaction. From these basic assumptions, one can model a spatial pattern of population dynamics and compare the result with the dynamics of some observed whole populations (van der Laan 1996). By means of computer simulations, one can calculate the effects of the different parameters in the model.

2.4.4 Simulations

Simulations are used in many scientific disciplines. However, there is no accepted definition of "simulation" (Stöckler 2000, 359). One could define computer simulations as a method devoted to the modeling of complex systems by means of the cellular automata syntax (Rohrlich 1991, 516). Another definition considers a simulation to be a process of imitating important aspects of the behavior of systems in real time, compressed time or expanded time by constructing and experimenting with the model of the system (Neelamkavil 1986, 6). It is more a broad concept of how to behave with

models than a specific method. Thus, simulation is a method of generating and imitating the development of complex systems by using and starting from basic simple data and assumptions

Simulations in ecology are often considered a form of model and ecologists talk of simulation models. One can distinguish between model and simulation in that simulation is a process that uses all forms of models (analytical, descriptive, statistical and object-oriented ones) to imitate the behavior and development of ecological systems by integrating temporal and spatial changes. The first ecological simulation was developed in the mid-forties by Gordon Riley for marine ecosystem primary and secondary production (cf. Swartzman & Kaluzny 1987, 1). He tried to imitate a natural process by an artificial process generated from some basic assumptions and changing parameters influencing the objects of simulation. By applying different parameters, he could create a process that simulated the behavior of the complex system.

A computer simulation can be considered a tool in deducing the evolution of the states of a system in cases for which an analytical solution cannot be applied successfully. The basis of a simulation is a model of the system and the rules of time evolution. The computer is used to calculate solutions for these rules. These solutions are mostly visualized as processes in space and time (Stöckler 2000, 360). There are several reasons why simulations are very helpful in analyzing complex systems. The regularities of interaction can often be described by rules for the assumed initial states of a specific complex system. The simulation illustrates whether these rules provide the means to explain the behavior of complex systems. Simulations may help to develop an understanding of the most important features of higher-level states to describe the system. The visualization of the system development by computer simulation enables us to understand the basic patterns of the process without being forced to explain every step of calculation performed by the computer (cf. Stöckler 2000).

Simulations mostly need a great deal of calculation power and thus good simulations were impossible before the introduction of computers with huge calculation capacities. Simulation models are the only tool presently available for translating a collection of hypotheses of ecological processes into a representation of how an entire ecological system works. Simulations start with a collection of hypotheses, in the form of equations (an ecological model) and describe how the major elements of the model (state variables) change over time or space. The models are mathematical descriptions of the mechanisms that control the various model processes. This is opposed to

empirical models where a relationship between the process and controlling variables is established without considering the underlying mechanisms (Swartzman & Kaluzny 1987, 1).

Ecological theories are much more concerned with the structural demonstration and in the simulation of complex processes than with focusing on the details of causal nets. In a simulation, it is possible to interpret many ecological phenomena as results of iterative and recursive processes and functions of elementary parts (Breckling & Reuter 1996). Contemporary ecological simulations often start with individual based models operating on a basic level of ecological interactions like organisms of a population or populations of a community. A realistic representation of these (known or assumed) interactions allows one to simulate the behavior of a complex system from the behavior of its individual particles.

By means of the simulation, the integration of different ecological levels of organization can be demonstrated. Simulations can show us whether the assumptions on the processes of the basic ecological organization at the level of individuals or populations may be true in comparison to the simulated behavior with the observation on the level of the complex natural system (cf. Breckling & Reuter 1996). Computer simulations start from simple assumptions (e.g. fish in a shoal will behave in a way that they will be not nearer than 5 cm and not further than 20 from each other) and apply several parameters to them (fish swimming in different directions) in order to “explain” the complex behavior of the shoal by means of its individual elements.

Although ecological simulations mostly start with the basic elements of a system and their properties, it is not a typical bottom-up approach because these basic assumptions are not always empirically based. The assumptions can be tested by comparison of the simulated complex behavior with the natural behavior of the complex system. If the simulated behavior corresponds to the one in the natural system, one can assume that the initial assumptions and the used parameters have been correct but one cannot test the individual behavior of the elements of the system. However, a simulation does not belong to a typical *top-down-approach* because the basic assumptions are based on individuals and can only be applied to a limited range (e.g. a concrete fish shoal). Thus, it is difficult to decide how far the results of a simulation can be generalized (for other fish schools or groups of birds or insects). However, they provide hints of how the behavior of a complex system could have been developed, although one cannot be sure and the basic assumptions cannot be transferred easily

to other systems. Thus, ecological simulations are in between a top-down and a bottom-up-approach.

Traditional ecological models provide several problems. Conspicuous defects of models are seen in the assumption that environmental conditions do not change with time, that population growth rates respond instantly to changes and that the space occupied by interacting populations is homogenous and sufficiently small for interactions that every organism can interact with another one in the same manner (Pielou 1981, 17). With simulation models, some of these problems can be minimized. It is possible to find out by trial and error which of these changing factors can be neglected and which ones have to be taken care of. In simulations, one has the possibility of testing the *ceteris paribus* clauses or the null hypothesis, which says that the simulated behavior of complex systems occurs due to random processes. Another advantage of the use of computer simulation is that it is accessible to nearly every ecologist, even those with relatively little mathematical background (cf. Hall & DeAngelis 1985, 344). This is surely also a reason of why the use of simulations in ecology is so widely distributed.

Simulations are tools to test hypotheses about the behavior of individuals that may lead to the behavior of complex systems. If this works, one could consider a simulation to be a form of a *how-possible* explanation (cf. introduction) that explains how the behavior of a complex system could have been developed from the behavior and from some specific parameters of individual parts of the system. It is not an explanation according to the covering-law model because prediction is not possible and because it is only a *how-possible explanation* and not a *how-actual* one. A simulation can generate the complex behavior but it cannot *explain* the genesis of the behavior of the system, because we are not able to realize the calculations and the change of parameters at every level of the simulation. Nevertheless, a computer simulation can help us to *understand* in general the systems genesis from basic conditions. It has a strong heuristic power. If there is a successful simulation, we have strong hints about the decisive factors for the development of a complex system. Now ecologists have to test whether real individuals follow the assumed rules, which were used in the simulation.

Thus, simulations seem to be only a test for hypotheses and they will not tell ecologists something new. In case ecologists test null hypotheses against assumed decisive processes of competition, a simulation can tell us whether the null hypotheses or the assumed deterministic factors or both can be responsible for the genesis of complex

behaviors or community properties.⁶⁹ Simulations that rely on hypotheses and simplified approximations of the behavior can provide useful explanations (cf. Simon 1969, 17). Although simulations can result in phenomena, which could not have been predicted from the initial assumptions of the simulation one cannot say that the “emerging” properties of a complex system are new ones. By means of a successful simulation, one can show that the properties of a higher level are outcomes of some basic assumptions and the properties of lower levels.⁷⁰ Thus, they may be surprising outcomes but they are not really new ones.

Simulations are like typical explanations in ecology, biology or social sciences. They do not rely on natural laws, rather they rely on rules with a small range of application (a fish shoal or the distribution of a plant species) but they do not provide general explanations of the complex behavior of animals that live in groups or general explanations of the distribution of plants. The mechanism provided by a simulation can explain the behavior of specific systems but no general ecological processes. Simulations can give strong hints at the possibility of an ontological reductionism concerning specific systems. If it is possible to demonstrate that the behavior of a complex system results the properties of its elements and that this result resembles an observed ecological system it will be obvious that it is somehow possible to deduce the systems behavior from the behavior of its parts. However, we cannot know whether the simulation really represents the ecological mechanisms, although being high probable. Although simulations are important instruments in ecological research they can never replace the semantic and epistemological role of experiments. Successful simulations can only demonstrate the possibility of the provided explanation but they cannot confirm it as experiments do. Simulations increase our understanding of ecological processes and they are tools to arrive at unifying explanations by illustrating that an ontological reductionism is possible for the explanation of higher-level phenomena of specific ecological systems.

⁶⁹ The discussion of whether specific community patterns are a result of random colonization (null hypothesis) or of interspecific competition (deterministic factors) was at least partly decided by means of computer simulations (for a more accurate account see chapter 3 on communities).

⁷⁰ Ecologists often consider the behavior generated by a simulation to be “emergent”. But this form of emergence is only a weak one and combinable with reductionistic explanations of complex systems. In fact, a simulation shows the possibility of an ontological reductionistic explanation by demonstrating that the complex behavior can be generated from one of the components of the system.

2.5 Conclusions

Ecology is a pluralist discipline in which I distinguished three basic approaches according to their ways of explaining. These approaches are population ecology, systems ecology and evolutionary ecology. Although the assumptions and methods of these approaches are very different, one can consider ecology to be *one* discipline since the proponents of the different approaches are interested in the same objects of research. As will become obvious by the remainder of the book, the strong divergences of systems ecology and population ecology are rather rhetorical and historically institutionalized than unbridgeable. Each of the approaches has various sub-approaches that are also quite diversified. This leads to problems of terminology, terms like *community* or *ecosystem* are used for a variety of different objects of research. In addition, one can find different types of experiment that demonstrate the difficulty to manage the complexity of ecological objects.

The main aspect of this chapter has been the dealing with theoretical structures of ecology. I demonstrated that biology has no fundamental (material) laws due to the contingent character of evolution and because evolution selects for functions and not for material units. Thus, ecologists either use accidental generalizations based on the properties and interactions of basic material units or they use structural laws or generalizations that may be general applicable. These generalizations sometimes base on analogies or they refer to supervenient concepts like *fitness* and *adaptation*. Ecologists themselves do not talk of *laws* but rather of *models*. The term *model* in ecology is a universal term with a variety of meanings and functions that can designate a form of theory, a way to represent a natural object or a way to represent theories. Most ecological models are formulated mathematically. There have been long disputes on the extended use of mathematics in ecology. In the last years the use of complicated mathematical models changed, ecologists are using simpler models which are not always formulated mathematically and which describe the basic behavior of the components of a complex system. Computer simulation techniques are often a successful way to imitate the complex natural processes of an ecological system. This method has led to a shift to the conception that the complex behavior of systems can be explained by its constituting parts. Simulations correspond to typical forms of explanation in ecology and biology; they can show how it was possible that a complex system and its properties evolved from given initial states of its components underlying specific forms of interaction.

3 Conceptions of Complex Ecological Units

In this chapter, I will deal with conceptions of complex ecological units. One can distinguish between two types of how to deal with them. One view tries to apply the ideas of Bertalanffy's general systems theory to the objects of ecology. Thus, the ecosystem, being the most important concept of this systems theoretical approach will be in the center of my investigation in the first sections of this chapter. Another form to deal with complex units is by means of the concept of *levels of integration* stressing hierarchical aspects of ecological organization. Several units of lower (micro) levels will be integrated into a new unit on a macro level (cf. pct. 2, 99). In the second part of this chapter, I will investigate the level of community because this level is the connection between population and ecosystem and because both systems and population ecology approaches use the community as central object of investigation. Although the systems view and the level of organization view are combinable in some ways, they stress different aspects and should be separated. Besides, the level of organization concept is easily combinable. I will start with the investigation of the systems view of ecological entities.

3.1 Ecological Systems

Systems ecology has been strongly influenced by general systems theory. Therefore, I will shortly deal with general systems before looking at ecological ones. In systems theory one often distinguishes between real and ideal systems. An *ideal system* consists of abstract schemes helping to organize our perceptions and ideas. Typical abstract schemes are a philosophic system and a system of laws; they do not correspond to physical entities. A *real system* corresponds to material entities that are interacting in a causal manner. Examples for this sort of system are the central nervous system, the solar system and other natural systems. General systems theory is interested in real systems. One can use the following definition for a real system: a system is a specific part of the physical reality in which interactions and processes take place (Bischof 1995, 13).⁷¹

⁷¹ "Ein System ist ein konkreter Ausschnitt aus der physischen Realität, in dem Interaktionen stattfinden, also Prozesse ablaufen" (Bischof 1995, 13).

Every entity that is constituted by various elements interacting with each other can be regarded as a system. Systems have a specific structure and their elements have a formal order (cf. Steinbacher 2000, 1579). The behavior of one component of a system in a specific relation is different from the behavior of this component in another relation. This leads to interactions of the elements in the system (Bertalanffy 1968, 56).⁷² The interactions and the resulting processes are often regulated by internal or external control (cf. Krieger 1996, 12). Systems can be simple or very complex, which means that they may contain a large number of parts interacting in a non-simple way. Thus, the term *system* refers to small or large sets of elements interacting in a simple or non-simple way.

Ludwig von Bertalanffy (1949, 1968) developed a general theory of systems, which had a strong impact on thinking about biological and ecological systems. *General systems theory* should develop and formulate principles that could be applied for every system. These principles should be formulated in a mathematical form and they should be applicable to every system independent of the nature of their individual elements. Thus, any system will be determined by some form of equation (Bertalanffy 1949, 115).⁷³ Accordingly, one can regard a system as a form of model that describes complex interactions by instantiating (and often visualizing) a formal theory. The theoretical structures shall represent empirical processes. The system that realizes these structures can be applied to nature and help to describe it. It can also serve as a confirmation of theories and as a means of constructing new hypotheses (cf. the part on models in ecology, section 2.4.3.2). These systems serve as tools to represent aspects of investigated empirical data and they can be examined by means of systems analysis. Thus, systems are models of complex real interactions constructed by the human observer. A theory of systems provides the tools to analyze those systems by means of mathematical descriptions (cf. Breckling & Umbach 1996, 5).

There are several properties of systems that make them useful concepts for ecology: they can be nested because they are not bound to a specific scale. Thus, big systems can contain various small ones. Accordingly, systems are parts of hierarchical

⁷² „A system can be defined as a complex of interacting elements. Interaction means that elements, p , stand in relations, R , so that the behavior of an element p in R is different from its behavior in another relation, R' . If the behaviors in R and R' are not different, there is no interaction, and the elements behave independently with respect to the relations R and R' .“ (Bertalanffy 1968, 56)

⁷³ A system is the „Anzahl von in Wechselwirkung stehenden Elementen p_1, p_2, \dots, p_n , charakterisiert durch quantitative Maße Q_1, Q_2, \dots, Q_n . Ein solches kann durch ein beliebiges System von Gleichungen bestimmt sein.“ (Bertalanffy 1949, 115)

structures. Systems on the same level are not distinctly separated, they may overlap.⁷⁴ For biological systems, there are some specific aspects. Living systems maintain themselves in a steady state, they can avoid the increase of entropy and they may even develop towards states of increases of order and organization (Bertalanffy 1968, 41). Biological systems do not only have import and export of energy but of material as well, that means that they are open systems (cf. Bertalanffy 1968, 121). Although one may also find open physical systems (like the water cycles) and one can also demonstrate “self-organization” for complex physical systems, e.g. the “Bénard instability” that will lead to a specific movement of molecules in a liquid layer after reaching a threshold value of temperature (cf. Stöckler 1991, 338), these properties seem to be more typical for biological systems than for physical ones. However, the properties of self-organization and the occurrence of fluxes of energy and matter are considered important factors of ecological systems. The openness of ecological systems makes it difficult to determine the boundaries of these systems, as we will see in the following.

In ecology, one should distinguish between the terms *ecological system* and *ecosystem*. The first term is a very broad one and can comprise every system investigated by ecologists (cf. Kitching 1983, 7). In this case, pure biological systems like predator-prey systems must also be regarded as ecological systems. Although those systems are typical objects of ecological research, the concept of *ecological system* is not adequate. Since ecology is defined as the investigation of interactions between organisms and their biotic and abiotic environment (cf. chapter 2), one should be more consistent and characterize ecological systems as consisting of biotic and abiotic elements. Then, an ecological system is every system containing living beings and their abiotic environment from the smallest scale (bacteria and their medium) to the biosphere (all organisms of the earth with their environment). Any biological system like individual, population and community will become an ecological system by including abiotic factors of the environment. Whereas the term *ecological system* can be used for every system that includes interacting biotic and abiotic factors, it should be distinguished from the term *ecosystem*. This term is used much more frequently in the ecological literature than the other one and mostly in a more specific meaning.

⁷⁴One predator-prey system can overlap with another predator-prey system, so the system of fox and rabbit can overlap with the system fox-hare (Kitching 1983, 4). It also can overlap with yet another system like host-parasite systems that will have an influence on the first system. If rabbits are heavily parasitized they will be an easy prey for the foxes. Thus the predator-prey cycles will change according to the influence of the parasites. Similar forms of overlapping can be found in many other ecological systems.

Accordingly, one can consider ecosystems to be a class of ecological systems, as we will see in the following.⁷⁵

3.1.1 The Ecosystem

In every approach and every textbook on ecology, one will find the term *ecosystem*. This term has become a ubiquitous abundance and is to be found in basic and applied ecology. Although the concept of the ecosystem is one of the most famous concepts of ecology,⁷⁶ the meaning of the term is not clear at all. There are many different meanings attributed to the term *ecosystem* and it is used for different applications. Without further specifications, it is not at all obvious what is meant when ecologists talk of *ecosystem*. That is why, in the following, I want to clarify the meaning of the term by looking at some historical stages first, and then by investigating contemporary characterizations and applications. There are many background assumptions referring to ecosystem properties which also play an important part for their characterization, these will be investigated in a third section. At last, I want to draw some implications on how to deal with the concept of ecosystem.

3.1.1.1 Short Historical Account

In contemporary ecology, we can find many definitions and characterizations of *ecosystem*. Most of them are very general and can be applied to many different ecological entities. Although the importance of the ecosystem concept for ecology is stressed, there are no rules of how to apply the term *ecosystem* to nature. For a better understanding of the diversity of meanings of *ecosystem* and their relevance for ecology, I will give a short historical account before examining the difficulties of the contemporary ecosystem concept. By the help of this historical consideration, it will be easier to understand why the contemporary concept of ecosystem is so diverse and includes so many different notions that it seems hardly comprehensible.

⁷⁵ Although there are some ecologists who do not distinguish between ecological system and ecosystem (cf. Kormondy 1984, 2, Odum 1971, 8), one can notice a quite distinct difference between these forms of system in the ecological literature. Ecologists distinguish explicitly between the organization of ecosystems and of organisms (cf. Breckling & Müller 1996, 24). But it can hardly be denied that an organism is an ecological system, because there are interactions between biotic and abiotic elements in an organism. Thus, ecosystems are a class of ecological systems.

⁷⁶ The British Ecological Society made an enquiry among its members asking them which concepts of ecology were the most popular ones. 69 % of the respondents considered the ecosystem to be the most popular concept of ecology (Cherrett 1988, 5).

The term *ecosystem* without which today's ecology is hardly imaginable was coined relatively late in the history of ecology by A. G. Tansley (1935).⁷⁷ Tansley used the term in a technical sense and his basic concept is still applied today. He demanded a more empirical method in vegetation science and wanted to avoid the errors of the Clementsian school which considered a plant community to be an organism, a view that lacked an empirical basis (Tansley 1935, 295). Tansley regarded a plant community as a system that could be integrated into the array of physical systems, ranging from the atom to the whole universe. These *ecosystems* do not only include the complex of organisms but also the whole complex of abiotic factors of the environment, the habitat factors in the widest sense. Ecosystems are considered basic units of the biosphere but they are only partly natural, because they have to be isolated arbitrarily by the ecologist from the continuum of the biosphere. By this, Tansley referred to the philosophical view of Levy's (1932) who described the general method of science as mentally isolating natural systems for the purpose of study in a way that the series of isolates may become the actual objects of research. The isolated systems are parts of larger ones, they can overlap, interlock and interact with each other. The process of isolation is partly artificial, but it is the only possible way to proceed (Tansley 1935, 299f.).

The term *ecosystem* was developed in order to come to a better understanding of plant communities than by the use of the concept of *superorganism*. *Ecosystem* was used as a technical term designating a complex of interacting living beings and abiotic factors. However, it was not obvious how to apply the term. Although Tansley stressed the artificial character of ecosystems, he did not provide suggestions of how to isolate them from the continuum of the biosphere and how to use them for ecological research. The first application of this new term in ecological research came only several years later. In his seminal paper on "The Trophic-Dynamic Aspect of Ecology" Lindeman (1942) investigated trophic cycles of the "Cedar Bog Lake" in Minnesota by considering it to be an ecosystem. Lindeman explicitly referred to Tansley (1935) and regarded ecosystems as systems composed of physical-chemical-biological processes which could take place at any scale in space and time. The basic processes in these systems are trophic dynamics, the transfer of energy from one part of the ecosystem to another (Lindeman 1942, 400). In his conclusion, he stated that by means of food webs one

⁷⁷ Although the term *ecosystem* is a new one, the notion of an ecological system can be found before Tansley, e.g. in the work of S.A. Forbes (1887), or Möbius who investigated a complex entity of living beings and their environment. In this section, I will only deal with some aspects of the history for an extensive account on the history of the ecosystem concept cf. Hagen (1992) and Golley (1993).

could illustrate the impossibility to separate the biotic community from its abiotic environment. Therefore, the ecosystem has to be considered a more fundamental ecological unit than the community is. The organisms within an ecosystem belong to different trophic levels. Ecologists considered them under specific functional (energetic) aspects. They play their roles as producers, primary and secondary consumers, decomposers etc). All of them are dependent on the solar radiation as a source of energy (Lindeman 1942, 415). This investigation had a big impact on the following researchers interested in studies of complex ecological units.

In 1953, the seminal textbook “Fundamentals of Ecology” was published by Eugene and Howard Odum. From that time on, the ecosystem concept became central to ecology. Tinsley’s technical term has been transformed to a broad conception that could (and still can) be found everywhere in scientific and popular literature on ecology (cf. Golley 1993, 1). Proponents of the “new” systems ecology regarded the ecosystem as the fundamental unit of ecology. It was compared in its significance to the species for taxonomy and systematics (Evans 1956) or the cell for cytology (Odum 1964). Eugene Odum explicitly wanted to have a broad concept of the ecosystem, he was not much interested in the conceptual clarification but in establishing a concept that demonstrated specific properties of nature. The term *ecosystem* should designate every group of organisms in a specific area interacting with their physical environment in a way that an energy flow would lead to a clearly defined trophic structure, biotic diversity and material cycles (Odum 1971, 8).⁷⁸ The main function of the ecosystem concept is the emphasis of the obligatory relationships and interdependencies of ecological entities that represent functional units. The broadness of the concept has the advantage that it can be applied to very different ecological entities like a pond, a lake, a forest, a flowerpot and even a space shuttle and its staff (Odum 1971, 9). All these different systems show similar forms of interrelations (energy and material cycles) that justify it to use the term *ecosystem* for all of them. The partly artificial character of ecosystems has mostly been neglected and ecosystems were considered to be naturally given units.

From the 1960s until the 1980s, the concept of ecosystem of the “Fundamentals” was very abundant in the United States. Ecologists mostly considered ecosystems to be

⁷⁸ „Any unit that includes all of the organisms (i.e. the „community“) in a given area interacting with the physical environment so that a flow of energy leads to a clearly defined trophic structure, biotic diversity, and material cycles (i.e. exchange of materials between living and nonliving parts) within the system is an ecological system or *ecosystem*.“ (Odum 1971, 8)

defined parts of the biosphere at any scale characterized by processes that were results from the integration and interaction of biotic and abiotic elements. The predominance of the Odumian concept was not only due to scientific but also to economic and political reasons (cf. chapter 2.2.3). The rise of systems ecology and the ecosystem concept was promoted by the funding of the AEC (Atomic Energy Commission). Additionally, there was another important sociological aspect that favored the predominance of the ecosystem concept. The assumption that the problems of pollution could be solved by “curing ecosystems” has led to a wide acceptance of the ecosystem concept in the (non-scientific) population. Ecosystem research was funded throughout the IBP (International Biological Project) from 1961 until 1974. These different aspects of ecosystem research led to an interesting combination of nearly esoteric views (everything is connected with everything, the earth is a living being, ecosystem health etc) with analytical and technical assumptions (everything can be controlled, functions must be analyzed accurately and explained with mathematical rigor etc) and both views were integrated in the ecosystem concept. Thus, there are quite different assumptions and sometimes even contradicting “weltanschauungen” which can be found in the ecosystem concept.

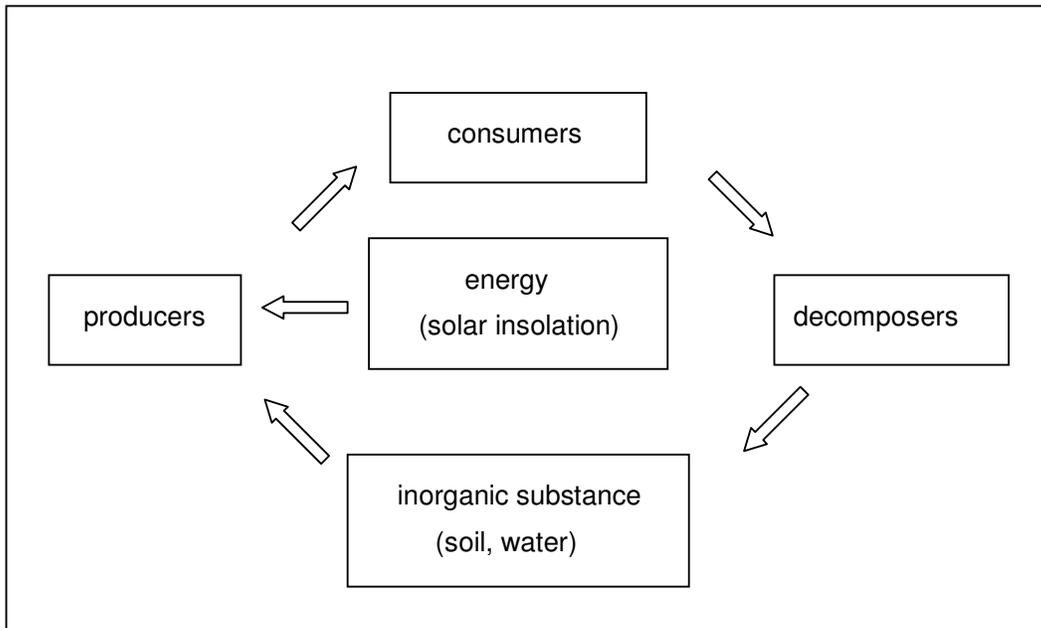
After the end of the IBP (International Biological Program) in 1974, ecosystem studies gradually lost their exceptional status and became normal scientific work of ecologists. In the 1970s, the view that ecosystems were real discrete entities of nature with characteristic structures turned into the imagination that the ecosystem concept is just a useful method of organizing the complexity of nature (Golley 1993, 166). Thus, the understanding of *ecosystem* was again closer to Tinsley’s notion, who already stressed the instrumental aspect of *ecosystem*, whereas Odum’ and similar concepts during the IBP regarded ecosystems as real parts of nature. Today, ecologists consider ecosystems to be a complex of interacting organisms and their environment. One can find aspects in it, a realistic and a constructivist one. On the one hand, it is regarded as an abstract model describing processes and functions of the investigated natural object. On the other hand, it is considered a specific part of nature. Often, both understandings are used simultaneously. This makes it quite difficult to understand what is meant by *ecosystem*. To be sure, the meaning of ecosystem should be specified by every application. In any case, the borders of the systems are defined by the observer (cf. Breckling & Müller 1996, 10).

This short historical sketch shows that many of the contemporary problems of the ecosystem conception can be understood by its historical genesis. In the contemporary ecosystem concept, one still can conceive aspects of Tansley and Odum; there are aspects of natural conservation, technical analogies and computational modeling. In addition, there is still the problem of how ecosystems can be isolated from a continuum in a manner which is acceptable and understandable for everyone. Obviously, ecosystems are no “natural kinds” in the sense of distinct characterized natural units, they are rather units defined by ecologists for specific methodological aspects. Nevertheless, the question remains whether they are purely instrumental constructs or whether they have specific real properties. To come to a better understanding, I will look more closely at contemporary conceptions of ecosystems.

3.1.1.2 Characterizations and Applications

Most contemporary ecologists characterize ecosystems as structures of interaction of different organisms and their abiotic environment (e.g. Klötzli 1989, 288; Leser 1984, 356). These interactions can be found between the abiotic components of climate and soil and the biotic components which are characterized by producers (green plants), consumers (animals) and decomposers (microorganisms etc) (cf. Walter & Breckle 1983, 1). Every biological system is dependent on other biological systems and abiotic constraints, and it will somewhere find its place in an ecosystem (cf. pct. 2). In Germany, the characterization of Ellenberg (1973, 1) has had a big impact: an ecosystem is a structure of interaction between living beings and their inorganic environment. It is open but to a certain degree, it has the ability of self-regulation.⁷⁹ This conception of ecosystem can be applied in two ways. On the one hand, we can use it for real parts of nature but, on the other hand, it can be used for abstract models representing ecological processes occurring on any scale. Often, both approaches will be used together perhaps with an emphasis on modeling ecological processes.

⁷⁹ „Ein Ökosystem ist ein Wirkungsgefüge von Lebewesen und deren anorganischer Umwelt, das zwar offen, aber bis zu einem gewissen Grad zur Selbstregulation befähigt ist.“ (Ellenberg 1973, 1)



Picture 2: Abstract diagram of an ecosystem with a closed cycle of energy and matter. Every organism or group of organisms can be considered the way that energy and matter fluxes will take place. Now, one can specify the ecosystem, distinguish between different forms of producers, composers, and decomposers. One can measure the quantities of energy and matter inputs and outputs, one can look at specific nutrient cycles (e.g. nitrogen or oxygen), one can investigate the stability of the system in dependence of its species diversity etc.

The ecosystem is considered the fundamental organizing unit of ecology and has been compared in its significance for ecology with the cell for cell biology (Odum 1964) or the species for taxonomy and systematics (Evans 1956). It has been regarded as basic functional unit in ecology, without which life could not be maintained on earth (Odum 1971, 8).⁸⁰ Yet, ecosystems may have any size and the borders must be determined by the researcher. For this reason an ecosystem can be a little water filled hole in a tree or a big community like the Atlantic Ocean or the rain forest with their abiotic parameters. They can be isolated and thus be quite independent from others, but they can also be integrated into other systems which will be dependent on each other (cf. Stöcker 1977).⁸¹ Since the dimensions of ecosystems are defined by the observer, a special complex of nature can be considered both, an ecosystem and a part of an ecosystem (Gluch 1977, 171).

⁸⁰ „The ecosystem is the basic functional unit in ecology, since it includes both organisms (biotic communities) and abiotic environment, each influencing the properties of the other and both necessary for maintenance of life as we have it on the earth.“ (Odum 1971, 8)

⁸¹ There are only degrees of independency, because there will be no system that is not influenced by others.

One can try to limit the systems by spatial or functional (flows of matter or energy) aspects. The first notion accepts the given borders and elements found in nature, whereas the second considers a part of nature by constructing different systems in order to investigate specific questions. Both approaches often fall together for the practicing ecologist (Weidemann 1994). There is no method with which one will find sharp borders and there are no criteria of how to determine an ecosystem in nature. Ecosystem boundaries are usually determined for the convenience of the investigator rather than based on a known functional discontinuity with an adjacent ecosystem (cf. Likens 1992, 9). Functional limitations do not allow better borders than spatial demarcations because one will never find a closed cycle of energy or matter except on the level of the biosphere (by including the sun as source of energy). Although it might be possible to find relatively distinct natural borders of an ecosystem like a lake or a forest, one will always find some species that belong to the water and to the land or to the forest and to the adjacent field. However, for pragmatic reasons one has to delimit the investigated ecosystem. Every ecosystem study should begin by a diagram of the system of interest and by determining the boundaries of the system. Although ecosystems are open, they have to be regarded as effectively closed for the purpose of the study, only driving variables (like temperature etc) and sources or sink of the material from outside the system have to be considered (Kitching 1983, 14). Therefore, it seems to be impossible to understand the borders of an ecosystem as naturally given. Most ecologists will consider them as arbitrarily chosen by ecologists according to the objectives of investigation (cf. Breckling & Müller 1996, 10; Jørgensen 1992, 23; Tansley 1935, 300).

Every system that is open to material and energy flow and that contains at least one living being, can be considered an ecosystem (Dale 1970). In this case, there would be no difference between an organism and an ecosystem. Nevertheless, contemporary ecologists clearly distinguish between organisms and ecosystems. The elements of ecosystems and their interactions are much more variable than the elements of an organism. Compartments of an ecosystem are not bound to the system the fixed way the elements of an organism are bound; they just *somehow* have to be in accordance with their environmental requirements. Ecosystems consist of historically developed individual parts that can be grouped together with regard to some specific unifying aspects.⁸² Quite often, the same elements can be found in different systems, this is not

⁸² There are no fixed criteria for the unifying aspects and they can be chosen arbitrarily by the scientists.

the case in organisms (Breckling & Müller 1996, 24). Thus, we can regard an organism as an ecological system but not as an ecosystem. There are similar processes in organisms and ecosystems which will lead to a flow of energy and matter but an organism is not an ecosystem because the relations of its elements are too fixed. Hence, we can regard an ecosystem as a subgroup of ecological systems that contains at least two organisms.

The functional characterization of ecosystems does not take the individual elements into consideration but only their functional roles in the processes of interaction. Although the chosen ecosystems may have quite different levels of complexity and very different material elements, the term *ecosystem* can be used because it describes structural uniformities like energy flows or material cycles that can be quantitatively measured. Whether one takes the rain forest or a nest of birds, one should be able to describe those systems with the same structural equations or diagrams of matter or energy cycles. Sometimes one distinguished between a trophic and an energetic standpoint. The trophic standpoint stresses the significance of the components whereas the energetic emphasizes the processes of the system. Proponents of the trophic standpoint describe cycles of matter by a) inorganic substances in material cycles, b) organic compounds linking the biotic with the abiotic, c) climate regime, d) autotrophic organisms as producers (plants that can transform energy and inorganic material into organic material), e) phagotrophs as consumers (animals that eat plants or other animals), and f.) saprotrophs as decomposers (bacteria and fungi reduce organic material to inorganic components). From the energetic standpoint, an ecosystem can be analyzed by a) energy circuits, b) food chains, c) diversity patterns in time and space, d) nutrient (biogeochemical) cycles, e) development and evolution, and 6) control (cybernetics) (cf. Odum 1971, 8). Both considerations overlap and cannot be clearly distinguished, they try to describe ecosystems by means of structural (functional) aspects.

Contemporary ecosystem studies have diverse aims and applications and emphasize the constructive character of the contemporary ecosystem concept. There are many different approaches and not everyone tries to understand ecosystems in terms of energy or matter balances only. Objectives of modern ecosystem investigations can be found in 1) a structural analysis by classifying and monitoring of species, b) a functional analysis by investigating the outputs of ecosystem components (e.g. flux of energy, biomass production, nutrition cycles), and 3) systems analysis by investigating

stability, self-organization, evolution, resiliency and models of ecosystems (Klötzli 1993, 289). One can consider these approaches to be 1) a form of natural history (classifying and monitoring), 2) a balance or budgetary approach and 3) a modeling and simulation approach (cf. Likens 1992, 10). Complete studies of ecosystems should make use of all the different approaches to unravel complexity and to develop an ecological understanding and provide useful information for decision makers and managers (Likens 1992, 24).

3.1.1.3 *Properties and Background Assumptions*

Since the ecosystem concept can be applied to nearly every group of living beings and their environment, there are many different properties that are attributed to ecosystems. In many cases, these properties are only guesswork and should be better regarded as background assumptions on ecosystems than as empirically confirmed properties. According to these “properties”, one can find many different aspects by which ecosystems should be investigated. Cyberneticists and proponents of control theory see the ecosystem as being characterized by a complex self-controlling feedback loop. From the information theorists’ viewpoint, the ecosystem is a communication channel. Ecosystems are also considered a form of network organization working analogously to electrical circuits. A thermodynamical consideration uses the conceptions of self-organization and emergence as guiding principles for ecosystem research (Müller 1997).

As already illustrated, systems ecologists have used many technical analogies to describe ecosystems. Ecosystems have often been compared to cybernetic machines and there is an ongoing debate on this topic. Proponents of the cybernetic view argue that the movement of energy-matter in the biosphere is characterized by feedback loops, and that informational processes modulate this movement. They assume that the biosphere is in harmony and equilibrium and suggest that it could only have evolved the way it did, because ecosystems are cybernetic systems (Patten & Odum 1981, 894). Cybernetic systems have three important essential properties: a) they are open to energy and often to matter but closed to information and control, b) the information is communicated by facts but they take on meaning in a certain context only, c) the basic building block of a cybernetic system is a feedback loop that regulates the transformation of matter or energy because the regulator has access to information concerning the state of the system (McNaughton & Coughenour 1981, 987f.). Adversaries of the view that ecosystems are cybernetic entities assume that

elements of ecosystems are not connected by an information network like elements of cybernetic machines. Although it is possible that small systems within a bigger ecosystem can interact by informational means (e.g. foxes and hares, flowers, and bees), there is no reason to assume this for whole ecosystems because they are quite different from organisms or small communities (cf. Engelberg & Boyarsky 1979, 321).

The assumption that ecosystems are cybernetic systems is closely related to the notion of autopoiesis and homeostasis. Ecological systems are composed of living systems and their environment. Living systems are often called autopoietic, which means that they create and maintain themselves (Weidemann 1994, 24). Self-organization and self-regulation will lead to homeostasis or other forms of final equilibrium in ecological systems. This equilibrium will be reached by the development of ecosystems. This development is an orderly process of directed and predictable processes that culminate in a stabilized ecosystem with a maximum protection from perturbations of the environment (Odum 1969, 262).⁸³ By this assumption, Odum used the term *ecosystem* in a way that was much closer to the Clementsian concept of community than to Tinsley's technical term. Like Clements' community, the ecosystem would come to a stage of maturity (the climax) via several determined states of succession. This *climax* will stay forever if not disturbed by influences from outside (Odum 1969). The development of ecosystems is gradual, they become more and more integrated and their states become more and more sensitive. The climax is the most complete steady state providing an equilibrium, which will be reached under given conditions (cf. Gluch 1977).

The equilibrium view of nature was widely abundant among ecologists until the mid of the twentieth century. Already Tansley wanted to explain the harmony of nature by the properties of ecosystems. Natural selection of incipient systems will select systems with a stable equilibrium that will survive longest (Tansley 1935, 300). Beginning in the middle of the 20th century, the view that ecological systems are in equilibrium has been gradually changed into a non-equilibrium view. This change is sometimes considered a paradigmatic change in ecology. Odum and his successors tried to establish harmony and equilibrium of nature and ecosystems again, but contemporary ecologists mostly will tend to a non-equilibrium view. Many nature conservationists and proponents of

⁸³ "In a word the "strategy" of succession as a short-term process is basically the same as the "strategy" of long-term evolutionary development at the biosphere - namely, increased control of, or homeostasis with, the physical environment in the sense of achieving maximum protection from its perturbations." (Odum 1969, 262)

applied ecology, however, still propose an equilibrium view of nature. Thus, both notions of ecosystems can be found today. The discussion on equilibrium in ecosystem has led to the question whether humans (as obvious destroyers) should be regarded as parts of ecosystems. Although humans were often excluded as disturbing factors in the seventies and eighties, today they are mostly included in ecosystems considerations (cf. Jax 1999). From a scientific point of view, there should be no question that humans are parts of ecosystems but the debates on the role of humans in relation to ecosystems demonstrate the difficulty exclusively to consider the ecosystem concept by its scientific aspects.⁸⁴

However, there is still another group of properties attributed to ecosystems. It is assumed that ecosystems as wholes react differently to inputs than their components. Hence, ecosystems have properties that cannot be found on the level of its elements (individuals, populations etc). These “emergent” properties are sometimes considered the central criterion for the definition of an ecosystem (Breckling & Müller 1996, 13). According to this criterion, it is not possible to consider all aspects of an ecosystem exclusively by energy fluxes because many interrelations will be neglected by this abstraction being important preconditions for the understanding of emergent properties of ecosystems (Breckling & Müller 1996, 27).⁸⁵ Emergent properties of ecosystems are those that cannot be predicted from the observation of the components of that unit (Salt 1977, 145). A true system or emergent property results from the interactions of elements and is qualitatively different from the properties of the elements. Emergent properties are not predictable from the behavior of the isolated parts (Loehle & Pechmann 1988, 887).⁸⁶

⁸⁴ Many scientists adopted ideas of harmony, stability etc. from nature conservationists and therefore it is difficult to distinguish between basic and applied ecology and between strategies for nature conservation and empirically confirmed statements on ecosystems.

⁸⁵ „Es hat sich gezeigt, dass es nicht möglich ist, alle wesentlichen Aspekte ökologischer Prozesse dem Aspekt des Energieflusses unterzuordnen, weil durch die damit verbundene Abstraktion entscheidende Zusammenhänge verlorengehen, die eine Voraussetzung für das Verständnis vieler emergenter ökosystemarer Eigenschaften bilden.“ (Breckling & Müller 1996, 27).

⁸⁶ The way “emergent properties” are used in ecology is not in contrast to the possibility of reduction. Emergent properties are considered to be features of ecological systems that result from the properties of the parts and their interactions (e.g. Müller 1996, 166). This is a weak form of emergence. Although ecosystem properties cannot be predicted from the properties of the parts, it can be shown, e.g. by computer simulation that emergent properties are results of initial conditions and the specific behavior of the individual parts and specific calculation processes. Thus, the term “emergent” does not contradict a reductionist account of ecosystems because the properties of ecosystems can be “reduced” to its parts and their properties by means of computer simulation. I fail to see why “emergent properties” shall express something specific for ecosystems. Since the term *emergence* has other notions as well (like irreducibility) and will thus often lead to confusion, I will try to avoid the term *emergence* in the following, although it will not be possible to do it in a strict way. If the term “emergent” is used, it will always be used in its weak sense, as a result of interactions of systems components.

In this part of the chapter, I have given a short overview on assumed properties of ecosystems. These properties are very different and it is impossible to integrate them to arrive at an intensional definition of *ecosystem*. Although one can find some widely assumed properties of ecosystems like “emergence” or “self-regulation” one will not find a property of ecosystems which will be accepted by every ecologist and which can be confirmed empirically for every ecosystem. Since ecosystems can be found at any scale and can comprise any amount of biotic and abiotic factors, it is highly improbable that there are specific properties shared by every ecosystem. Small ecosystems like seed distributing ants may have properties of cybernetic machines but surely not the ecosystem of the lake Michigan. Thus, I plead that it will not be possible to come to general and accurate statements concerning ecosystems and their properties. However, the term *ecosystem* has played and will play an important role as an ecological key term although it corresponds to a broad and imprecise concept. It seems that ecologists mostly know what they are talking about when using the term “ecosystem” although it is not possible to specify its exact meaning.

3.1.1.4 Implications

As we have seen, the term *ecosystem* has no fixed meaning and a very broad range of application. There are quite a lot of different properties attributed to ecosystems and *ecosystem* can designate many different things. The concept of ecosystem has a variety of meanings. This makes it difficult, if not impossible, to explicate the term according to Carnap’s method.⁸⁷ I do not think that it is possible to explicate *ecosystem* without neglecting important aspects of reality. One could explicate *ecosystem* in specific applications by means of functional or spatial accounts but one would always lose some aspects that are combined to the general concept.

Obviously, the application of the ecosystem concept to nature is pragmatic and dependent on the perspective of the researchers. Although ecosystems are regarded as basic units of the biosphere, the biosphere is accepted as a continuum. Thus, one could consider the limitation of ecosystems to be necessary for methodological reasons only, because it is not possible to investigate the whole biosphere. Ecologists have to investigate parts that are not too complex and that clearly exhibit the processes of the biosphere.

⁸⁷“By the procedure of explication we mean the transformation of an inexact, prescientific concept, the explicandum, into a new exact concept, the explicatum. Although the explicandum cannot be given in exact terms, it should be made as clear as possible by informal explanations and examples.” (Carnap 1962, 3)

The broad concept of ecosystem can be useful to learn something about nature although it does not designate a part of nature from an ontological point of view. The properties attributed to ecosystems (e.g. emergence, homeostasis) should be more regarded as metaphors that help to better understand and organize nature than that it makes any statement about nature. Then, the application of *ecosystem* is useful as a methodological concept only which does not say much about the properties of nature. In many cases, it will serve as an analogue model: one takes properties of another object, e.g. a cybernetic machine as a heuristic means to get to know something about the nature of ecosystems. Nevertheless, it is nothing more than a heuristic means and thus intensional characterizations of ecosystem via specific properties will become impossible. Thus, we have to stay with an extensional characterization. The extensional characterization designates *ecosystem* as corresponding to all the different units in ecology which are considered specific ecosystems.

Thus, one can conceive of an ecosystem as every ecological system investigated by ecologists with the exception of the organism. This means, that beginning from two organisms and their environment, like people in a house or birds in a nest, until the system of the South American rain forests and the whole biosphere, every designed ecological unit can be considered an ecosystem. Accepting this, people in a space shuttle and all organisms in a virgin rainforest or in a bird's nest must be regarded as ecosystems. However, this conception of ecosystem is so broad that it must be specified for every specific investigation. Ecologists interested in specific systems must explain where the borders are and why they want to consider the chosen system to be an ecosystem and not a bigger or smaller one. Since there are no criteria for this, one should stay with the broad concept of ecosystem which has to be specified by every application.

3.1.2 Ecosystems and Holism

The concept of ecosystem is mostly combined with a holistic worldview, but in most cases, there is no specification of what is meant by *holism*. Ecosystem ecologists often talk of unspecified "emergent" properties of ecosystems and assume that the whole is more than the sum of its parts. This holism is often considered a conception which is in contradiction to reductionism. By means of the ecosystem concept, I want to investigate what form of holism is provided by ecologists and I will show that the provided holism will not necessarily contradict with reductionistic accounts of complex

ecological units. Most forms of holism which are represented by ecosystems ecologists fit quite well with reductionistic accounts of explaining the behavior of complex ecological units.

In the introduction, I distinguished three forms of reductionism, the ontological, the methodological and the meta-theoretical (cf. section 1.2.3). The ontological reductionism says that all living beings and their complexity can be explained by means of the behavior of non-living and much simpler units and their properties. There are no specific forces that lead to the properties of a complex unit. Thus, the occurrence of complex systems and their properties can be explained by its composing parts and their properties. The methodological form of reductionism states that one should always investigate and explain on the lowest level possible, that means on the level of the components of systems and not on the level of the entire system. The last form, the meta-theoretical reductionism, is interested in the reduction of theories of complex entities to theories of its parts by means of a formal account. Biologists are often not very much interested in this last form of reductionism, and therefore, I will not deal with it. Besides most biological and ecological theories are not articulated in a way that they could be reduced by formal means to simpler theories.

One can also distinguish between different forms of holism. Obviously, there are a metaphysical or ontological and a methodological form. Proponents of ontological holism state that there are complex entities with properties of their own that cannot be reduced to the properties of their parts. Some holists will even state that the whole determines the properties of the parts. Proponents of a methodological holism say that natural phenomena should be investigated and explained as wholes. One can distinguish between three different forms of this holism: a) the properties of a whole cannot be explained by the properties of its isolated parts, b) the properties of the parts cannot be determined when isolated but just in relation to the whole, c) one must always consider every aspect and all interactions of a complex whole to avoid a single minded emphasis of some aspects (cf. Stöckler & Haferkamp 2000, 563).

What form of holism is to be connected with the ecosystem? The ecosystem concept of Odum can be considered a form of ontological holism. Ecosystems were thought to develop as wholes; they have specific properties as homeostasis that cannot be explained by the properties of its parts, the parts are rather determined by the whole and not vice versa (Odum 1977). This ecosystem concept will be in conformity with a methodological holism as well. Ecosystems shall be considered and explained as

wholes. Every component has its functional role in the processes of the system and is dependent on the system. Since the properties are dependent on the whole system, the properties of the parts cannot be determined if isolated, i.e. properties of isolated parts will be different from the properties of the same parts that are not isolated. Most properties of individual components can be determined independently from the whole ecosystem by means of aut-ecological investigation, but those which are important for the system processes can only be demonstrated by investigating the whole system. Although ecosystem ecologists have stressed that of all factors of a system should be integrated into the investigation they consider ecosystems only by their functions and try to abstract from the individual elements. Hence, one can conclude that the Odumian ecosystem concept corresponds to a methodological holism in the forms a) and b) but not to c). Since ecologists are only interested in the functions and structures of ecosystems as wholes and do not take the individual components into account, the ecosystem is investigated single-minded under functional aspects. In case one understands holism in terms of form c), the Odumian ecosystem concept can be considered a form of methodological reductionism.

Contemporary systems ecology regards ecosystems as human constructs which help to organize nature. In this case, we can no longer speak of an ontological or metaphysical holism although, in many cases, it is not easy to determine whether the statements on holism and emergence are made from an ontological or a methodological point of view. Apparently, ecologists are not very much interested in ontological questions. However, in any case, modern concepts of ecosystems belong to forms of methodological holism. Since modern forms of ecosystem research do not investigate ecosystems under functional aspects only but also take categorizing and monitoring into account, it corresponds to all three forms of methodological holism. Often *holism* is used merely to say that as much variables as possible have to be considered to understand the object of study (cf. Wilson 1988, 270). Systems will be investigated holistically and shall be explained on the level of the whole, but not only by functional means. This form of holism does not contradict an ontological reductionism that considers the continuous biosphere to be composed of individual units and their properties by the long process of evolution. Although contemporary ecosystem ecologists may not be interested in ontological reductionism, they have to accept the combinability of this form of reduction with the methodological holism represented by them. Thus, the debate on reductionism and holism simply becomes a debate on methodological issues and loses many of its controversial aspects. Most proponents

of an ontological reductionism will not be in favor of a methodological reductionism (cf. introduction) so that there will be no problem for a proponent of a reductionistic conception of nature to investigate and explain on a complex systems level. Nevertheless, the question remains whether it is possible to explain the system properties by its components, their properties and initial conditions only.

Therefore, the stressed differences between holistic and reductionistic views in ecology do not seem to be contradicting, they are combinable. Even if ecologists state that a reduction of an ecosystem to its material elements and their properties is impossible because the interactions of elements result in system properties, which are not properties of the individual elements (e.g. Weidemann 1994), they have to accept that there is nothing very “new” on the level of the complex system. The systems properties result from the composing parts and their properties, their interactions and some initial conditions. Successful simulations of “emergent” properties by means of computer simulations also demonstrate that there is nothing new on the systems level that does not result from the components and basic assumptions. That is why one must at least accept the possibility that the properties of the complex system can be explained by the composing elements and their properties. Certainly, some properties of the whole are results of overlapping and interactions of the properties of the parts, but although they cannot be predicted in advance, they can be reductionistically explained afterwards.

Perhaps it would be better to talk of “systemism” instead of holism. In holism, the thesis that everything is connected with everything else is weaker in systemism; here the thesis would be as follows: everything is connected with *some* other thing(s). In contrast to holism, systemism is not as anti-analytical as some strong forms of holism. Since ecologists are interested in analyzing systems, one should not talk of an individualism-holism controversy but rather of an individualism-systemism controversy (Mahner & Bunge 1997, 177). This seems to be a convincing suggestion, because the irrational side of a metaphysical holism would no longer be invoked. Systemism should be considered a pragmatic form of holism. In a pragmatic sense, the whole is more than the sum of its parts, so that we are not able to infer the properties of the whole from the properties of their parts and the laws of interaction. However, this does not contradict the possibility of ontological reduction. It is possible to be an in-principle reductionist and at the same time a pragmatic holist (cf. Simon 1969, 86).

3.1.3 Unifying Power of the Ecosystem Concept

The ecosystem concept is sometimes considered the central and unifying concept of ecology (Odum 1969). Nevertheless, the previous demonstration has shown that the analogy of the ecosystem with the cell or the species as the central unit of a scientific field (cf. Evans 1956, Odum 1964) is not justified. The concept of species and the concept of cell refer both to clearly limited natural entities.⁸⁸ Cells in an organism are clearly distinguished by their membranes and they are much less variable than elements of an ecosystem or small ecosystems in a bigger one. The borders of ecosystem will only be determined by ecologists according to their objectives of research. Cells and species are considered basic entities of complex wholes, but since ecosystems can be hierarchically integrated into each other, they cannot be regarded as basic units of bigger entities. If they provide a unity, it has to be different from the one provided by basic material entities like cells or atoms.

The ecosystem concept should have the ability to unify the different biological disciplines of botany, zoology, limnology etc by integrating the objects of these different disciplines into one object of investigation (Odum 1977). The ecosystem ecologist needed to analyze botanical, zoological, limnological and abiotic factors that were formerly investigated by proponents of different disciplines. By the investigations of fluxes of energy, or matter, the different objects were considered under a unified aspect. When investigating nutrient cycles, one had to take plants, animals and microorganism into account because they represent the roles of producers, consumers and decomposers. By this functional approach, zoology and botany had to be tied together and the ecosystem concept helped to find to a unified method in ecology. Since everything in a system was considered under matter or energy fluxes, one can regard this form of unification as a form of methodological reductionism. Only structural laws and functional descriptions were used to organize specific features of nature as units.

The unifying power of the Odumian ecosystem concept only relates to methodical aspects. Contemporary ecologists are not interested any more to explain everything in terms of energy or matter cycles. One will find as well other approaches to ecosystem research like “natural history” (cf. p. 102). Hence, one cannot say that contemporary ecosystem researchers use one method of ecosystems investigation only; they rather

⁸⁸ Although this is not quite true, because there are difficulties to find exact borders, especially for the species concept, the borders of cells and species are by and large provided by nature whereas the borders of an ecosystem only depend on the researcher who determines them.

use a plurality of methods to make statements about ecosystems. In most cases, they will no longer be interested in a unity, provided neither by structural nor by material laws. Since the contemporary ecosystem concept is viewed from a constructivist account, it may be a useful and successful unifying concept for a team of researchers investigating specific aspects of nature, but for other ecologists, the same “ecosystem” may be irrelevant, because they are interested in other questions and will choose other limitations and characterizations for the system investigated. That is why they have to choose another concept of ecosystem to arrive at a unified account of their research object.

If one looks for a material unit in ecology that corresponds to the cell or the species, these units have to be material parts with fixed boundaries. Such a unit has to be quite different from the broad concept of ecosystem. A unified explanation of ecological patterns and processes by means of basic material units can only be achieved by a consideration of the evolution of these parts that resulted in the contemporary diversity of ecological patterns and processes. One can imagine that, during the process of evolution, some individual units were connected so that they in their further evolution would evolve together. It is possible that those “co-evolutionary units” have some of the attributed properties of ecosystems. One has to look at the genesis and composition of complex ecological levels by means of material units and only a combination of ecological levels and their composition and ecosystems as functional units will lead to a unified understanding of the complexity of ecological objects. However, before dealing with this question in the next chapter, I will investigate ecological levels.

3.2 Ecological Levels

In the previous sections, I dealt with the method to regard complex ecological units as systems. There is another way to deal with ecological complexity that is often mixed with the systems view. This is the concept of “levels or organization” or “levels of integration”. This concept suggests a hierarchical organization of ecological levels in a way that a higher level integrates several lower ones. Ecological levels of integration can be listed in the following hierarchy: organism, population, community, ecosystem, landscape, biome, biosphere (cf. Allen & Hoekstra 1992, 7; Breckling & Müller 1996, 9). In many textbooks, the ecosystem is considered a level of integration including the community and its abiotic environment (cf. pct.1, 28). In this understanding, the meaning of *ecosystem* is more restricted and the application is simpler than in the

systems view because obviously populations will not be regarded as ecosystem. While the distinction between community and ecosystem is at first quite obvious (an ecosystem being the community plus physicochemical factors), it is still difficult to determine the borders between different communities and hence ecosystems. The distinction between organism (an individual living being), population (a group of individuals of the same species that live in the same area with the ability of genetic exchange), community (a group of several populations living together in the same habitat), and ecosystem (the community and its abiotic factors) is more or less convincing; but the distinction between the higher levels of integration: ecosystems, landscapes and biomes is hardly possible.⁸⁹ A landscape is the integration of several ecosystems, but since the borders of an ecosystem are not clearly defined one cannot distinguish between ecosystem and landscape, they may sometimes be one and the same (see below).

At first, the distinction between community and ecosystem as ecological levels seems to be obvious. However, it does not seem to be very useful to distinguish between community and ecosystem as objects of investigation. This distinction may be helpful in some ways but it is impossible to study an ecological system in isolation from its abiotic environment. That is why one should not regard the ecosystem as a separate level of organization. There is actually no reason to assume that ecological energetics and nutrient dynamics belong exclusively to ecosystem research, rather than to community studies, as is usually the practice in textbooks on ecology. The investigation of these fluxes simply represents supplementary means to a better understanding of the community structure. That is why they do not justify the establishment of a new level of organization (cf. Begon et al. 1986, 592; Wissel 1989, 202). If one wants to stress the difference between biotic and abiotic factors, one has to do this on every level of organization. In this case, one would distinguish between a population and a population plus its abiotic environment (perhaps one could talk of *population ecosystem*). Nevertheless, this is not accepted as a new level of organization. Thus, there is no reason why this should be the case on the level of the community. Since ecologists have always been interested in the investigation of biotic and abiotic factors on every level of complexity the use of the term *ecosystem* fails to characterize a specific ecological level. Every ecological investigation of organisms, populations or

⁸⁹ As we will see in the next section of this chapter there are also problems concerning the distinction of the levels of integration of population and community.

communities should consider abiotic factors. That is why it is not necessary to create a specific level for them.

It is obvious that the use of the term *ecosystem* designating a hierarchical level of integration has no justification and it even contradicts in some way the general use of *ecosystem* from the systems theoretical point of view. We can already find fluxes of energy and matter at the level of the organism. There is no reason for the establishment of a specific ecological level called *ecosystem* based on the community. Therefore, it would be useful to abolish the term *ecosystem* with this meaning. If one wants to use a consistent hierarchy of integrative ecological levels it should then be as follows: organism, population, community, landscape, biome and biosphere. In this hierarchy, every higher level comprises its lower levels. Although there are still some problems with to an empirical distinction between the different levels, it is a consistent hierarchy of ecological levels of integration. Since the level of community is the focus point of population ecologists and systems ecologists, in the following I will deal with the community level.

3.2.1 The Community

In this section, I will investigate some aspects of the concept of *community*. As I have argued in the previous section, every ecological level should include the abiotic environment so that *community* will replace the term *ecosystem*. The community level is the main object of investigation by system and population ecologists. Systems ecologists investigate interactions among the organisms of a community and the transformation and fluxes of energy and matter and consider it a system, population ecologists focus on distribution and abundance of organisms that constitute communities. Both approaches are interested in interactions of different species and their environment which is considered the domain of community ecology (cf. Lawton 2000, 131). Thus, the community is the central ecological level for the systems approach of ecology and for the population approach and, as we will see as well for the evolutionary approach. I will begin investigating the general conception of the community level, then I will go on to examine holistic and reductionistic characterizations before dealing with specific problems of the plant community because the community concept is used mostly by plant ecologists and not so much by animal ecologists. Since there is a specific way of unifying the diversity of plant diversity, I will stick on phytosociology. In the last section, I will investigate forms of typological and

populational (evolutionary) thinking in community ecology that correspond to holistic and reductionistic approaches.

3.2.1.1 The Community as an Ecological Level

Community ecology deals with patterns and processes that involve groups of coexisting species in one locality (cf. Lawton 2000, 17). One can distinguish between two general conceptions of community. The spatial characterization regards a community as an association of all populations in specific spatially defined boundaries like those of a pond or a forest. However, *community* can also be characterized by means of interactions of different populations, e.g. seed dispersal of specific plants by specific birds or ants. In this case, members of a community need not always be in the same area (cf. Ricklefs 1993, 407f.). Often, both aspects of community conceptions are used together and the same problem as with the ecosystem concept arises: a key term of ecology does not have an unambiguous meaning. In the following, I will mainly focus on the spatial account of community because the aspect of interaction largely corresponds to the systems view which has been examined in the last sections.

I will focus on the spatial or geographical conceptions of community. Here, one is confronted with the problem that communities are very heterogeneous in relation to their temporal-spatial scale and their structure. The structure of a community is determined by species richness and their relative abundance. One will probably never find two geographical areas characterized as communities that show the same set of species. They may be very similar but by way of exception, they will provide the same array of species. Supposing, there were two forest communities of beeches, they will have a different community structure (some species will occur in one but not in the other community) although both are considered a community of beeches. This structural heterogeneity makes it very difficult to regard communities as discrete natural units and not just arbitrarily chosen objects of investigation. *Community* used in this way, is just a term designating spatial units that contain many different co-occurring species. However, this characterization seems to be too general to be of any use. For this reason, I want to clarify the different meanings of this concept.

The spatial and temporal scale of communities can immensely vary. Communities can be found in a small seasonal pond in the African savannah, e.g. groups of protozoan or small fish. In this case, the spatial scale of the community is quite small and the temporal scale of community existence would be a short one because of the seasonality of the pond. Nevertheless, the community can also be a South African

savannah. In this case, ecologists will investigate large mammals like elephants and antelopes or birds, the spatial scale of the community is much larger and so is the temporal one. This means that the scale of community depends on the group of organisms mainly studied by community ecologists. This must always be an important preconsideration before the spatial borders of a community can be determined (cf. Fenchel 1987, 97).

Now, the problem arises, whether the community can be considered a distinct ecological level. The term *community* is used for the organisms in the Amazonian rainforest, in the Atlantic ocean, the living beings co-occurring in one big tree and also for all species living and feeding on cow dung. Since there are different scales for communities, depending on the size of the organisms mainly investigated, one will often find one community existing in another. If ecologists investigate the community of a South African savannah this scale is the adequate one for the investigation of big mammals. However, it would be impossible to investigate all protozoans which live in small seasonal ponds of the South African savannah living in the same area as the mammals. Nobody will regard all protozoans of seasonal ponds in a savannah as one community. Every pond rather will be considered a community including populations of different protozoan species. In this case, the community of a South African savannah includes several pond communities. This means that the spatial account of communities is not used to designate one distinct level of integration but several.

Since the community is not one single level of integration but represents several levels, it will be difficult to distinguish the community criterion from the level of landscape. If we accept the conventional hierarchy of ecological levels, a landscape consists of several contiguous communities. A landscape is considered a geographical area that can be overviewed from one point. The landscape criterion is the most tangible of the bigger ecological units, because one must only look at them in order to perceive them (Allen & Hoekstra 1992, 55). In this case, a community can be both larger and smaller in scale than a landscape. There is no criterion for a distinction between community and landscape. Obviously, the levels of ecological organization do not correspond to the levels characterized by different scales. The conventional ecological levels are no good models for the ecological phenomena we find in nature (cf. Allen & Hoekstra 1992, 7). Therefore, the scale of a landscape may be smaller than the geographical region of a population of elephants. This shows that the concept of "levels of integration", at least

in its conventional form is only a rough classification but no convincing concept with which to organize the ecological complexity.

Although all organisms of a spatially determined community should belong to this community, for pragmatic reasons, ecologists only investigate several groups of organism of the community. Therefore, the much-discussed question arises, how many species are necessary to constitute a community as an object of investigation. Most ecologists tend to say that a community has to consist of species rich mixtures of many different taxa.⁹⁰ However, in practice ecologists only investigate taxonomically related groups of a specific area like mammals, birds or beetles and consider them to be communities. Other species occurring in the same area are neglected. It is almost impossible to study entire communities with all the co-occurring species. There are no ecological reasons for the sticking to the investigation of phylogenetically related groups but only pragmatic ones:⁹¹ ecologists must be able to determine the species they are investigating. If they want to investigate all insects of a specified area but have to learn to identify the different families, genera and species of insects first, they will need years. Thus, they have to focus on specific taxonomic groups they know or that can easily be determined (like dragonflies or grasshoppers). It may be possible to find somebody who knows all the species of a small piece of a North European meadow or lake but in complex communities, like tropic forests, nobody will be able to know all the species of a defined area. One needs a lot of time and many taxonomically skilled ecologists who are able to identify the species in case one wants to investigate a whole community (in a specified area). Since this is impossible for normal scientific research,⁹² communities are mostly conceived of several taxonomic groups (e.g. mammals, birds, dragonflies, grasshoppers or beetles) of a specific area. This shows that the general concept of a spatial community including all co-occurring populations cannot be applied to research.

Another problem of the spatial community concept is the question whether communities are distinct entities with obvious borders or whether community borders

⁹⁰ A taxon is a group that includes phylogenetically related organisms or species. Taxa are hierarchically organized: Thus we have the taxon *species* (e.g. the Common Swift *Apus apus*), several related species belong to the *genus* (e.g. the Common Swift *Apus apus* and the Alpine Swift *Apus melba*). Several genera form the *family* (in this case the family of Swifts, *Apodidae*), the families are grouped to an *order* (*Apodiformes*) that organize a *class* (birds, *Aves*).

⁹¹ This may change by taking evolutionary aspects of ecology into account (see below) but in most cases the characterization of a community by taxonomically related groups is made for pragmatic reasons only.

⁹² In fact there is a huge and ambitious project the national park *Smokey Mountains* in Tennessee. Ecologists want to catalogue all the species occurring in this entire community (cf. Breuer 2001, 33). But this is an exceptional case.

are arbitrarily drawn from a continuum by ecologists for purposes of investigation. Sometimes we may find obvious borders when there is a forest and a regularly sowed meadow or a pond with no flooding but with regard to the difference between savannah and steppe or savannah and forest, it will be difficult to draw the borders. In those cases, there are large transition zones and one can hardly say where one community ends and where the other begins (cf. Looijen 1998, 136). This boundary problem increases by the investigation of moving animals. Since there are many migrating animals and animals like eagles or buzzards which have a wide range encompassing several spatially defined communities it is difficult to decide to which community these birds belong. A pragmatic solution could assume that they belong to several communities. However, this would once again demonstrate the inapplicability of the concept of “levels of organization” and it demonstrates the difficulty to apply the spatial community concept to animals.

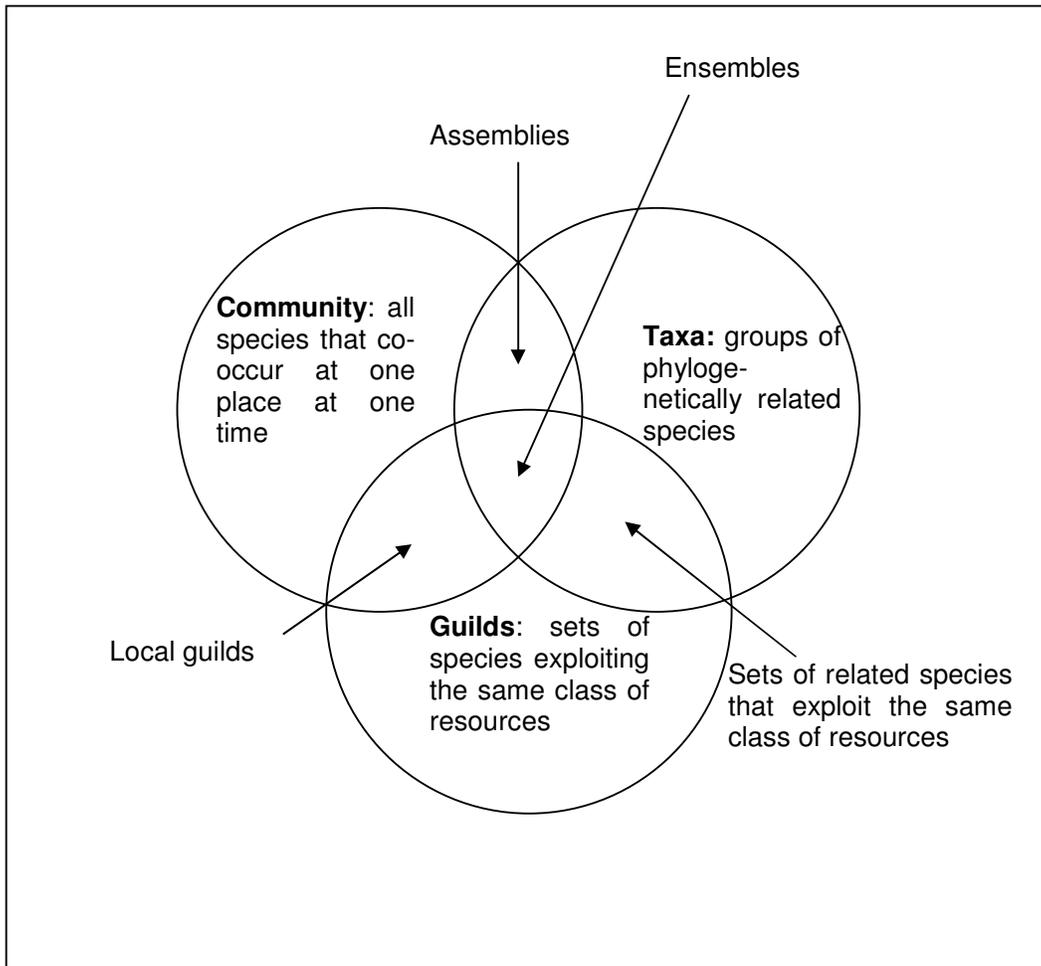
Animal communities are in most cases considered to be determined by strong ecological interactions between individuals or populations (Fenchel 1987, 103). Those conceptions of community structures refer to guilds⁹³ or to other more or less well defined ecological groups of populations being characterized by predator-prey relations, pollinator systems or other mutualistic interactions. This form of functional understanding of communities is mostly used for the study of animals, but as we will see in the next section competition and other functional explanations have a big impact on the conceptions of plant communities too. However, it is difficult to determine exclusively communities by means of interacting populations. Apart from the obvious interactions, like predator-prey or pollinator systems and food chains, it is often not known whether there are interactions between co-occurring species or species that meet. Therefore, ecologists mostly conceive of communities by functional and spatial accounts. In this case, a community can be considered a set of interacting populations in a given area (cf. Fauth et al. 1996, 285). However, the problem remains the same, in any bigger area, as for example, a lake or a bog we will find some neutral species which are not interacting with others. A rabbit normally will not interact with a bumblebee although it might be possible that via several interactions the abundance of

⁹³ A guild is a group of species regardless of its taxonomic position that uses the same class of environmental resources in a similar way (cf. Root 1967, 335). Examples of a guild are seed distributing animals (birds, ants, bats etc) or cavity nesters.

bumblebees may be influenced by the rabbit.⁹⁴ However, it is possible that the interactions of specific species have a big impact on the whole community. So the trophic structure of food webs can sometimes be controlled by only one species. In some marine communities, the sea stars (*Pisaster*, *Heliaster*) are so called *keystone predators*. If they are removed, the preyed mussels (*Mytilus*) can grow until they cover the entire area of the community. This leads to a strong elimination of diversity and complexity of the foodwebs in this community (Paine 1966). However, there are not always keystone species in community foodwebs. These examples demonstrate the difficulties of a characterization of communities by means of interaction only. This shows even more that the black box view of systems ecology does not help to designate specific communities because, in those cases, the individuals have to be taken into account.

By now, it has become obvious that ecologists do not use one concept of community but several. In the following diagram originally presented by Fauth et al. (1996) a conceptual clarification of the different applications of the term *community* is given. The terms *community*, *guild*, *assemblage* and *ensemble* are often used synonymously although they were all developed to describe specific community patterns. The areas of investigation which ecologists consider to be communities can often be divided into three distinct sets: *taxa* which are phylogenetically determined, *communities* which are geographically determined and *guilds* which are determined by the resources their members use. In the intersections of these sets, we can find the objects most widely investigated by community ecologists. Local guilds are the members of a community that are using similar resources, assemblages are phylogenetically related species using the same geographical area, and ensembles are phylogenetically related species that live in the same geographical area and use the same class of resources. This probably is the most investigated “community” by community ecologists. There is no name for the intersection between taxa and guilds: related species that are using the same or similar resources. This diagram offers an operational characterization of concepts which shall help to identify and communicate the objects of ecological studies that are often designated as communities (Fauth et al. 1996).

⁹⁴ This will be the case if one only looks at the roles of individuals in systemic processes like a nutrient or energy cycles, but it is impossible to confirm the interactions of all species in a community.



Picture 3: Terminology distinguishing the different concepts that are synonymous for “community” (after Fauth et al. 1996, 283). For further explanation, see text.

This diagram shows that concepts of *community* are very diverse. The geographical account and the one by interaction are typically ecological, whereas the taxonomic aspect of communities is used for pragmatic reasons. Ecology is interested in interactions and not in phylogenetic relations, but taxonomic accounts help to organize the variety of possible interactions in a spatially characterized area. That is why taxonomic accounts are important and nearly always used (except in black box approaches of system ecology) and they seem to have a big impact as well for the conceptual foundation of *community*. It would be nice to separate the different notions clearly but it seems impossible if one does not intend to construct an ecology without

practical relevance.⁹⁵ However, *community* is an important criterion for organizing ecological objects although it can mean different things. However, not only the characterization of communities is difficult, the demarcation of community from other levels is not without problems either. As mentioned above, it is nearly impossible to draw lines between community and landscape as long as communities are spatially determined. In addition, I do not think that a distinction between landscape and community is necessary, because these terms are only used operationally. Therefore, it does not make a big difference for any specific research project whether one talks of *landscapes* or *communities*, as long as ecologists know what they are looking for.

3.2.1.2 *Holistic and Reductionistic Characterizations*

From the previous illustrations on communities follows that the concept of *community* has many different characterizations and definitions. Now, I want to have a look at holistic and reductionistic accounts of communities. We can find a wide array ranging from holistic to reductionistic conceptions. Communities are, for example, regarded as 1) distinct ecological units characterized by interacting living beings of a specified area,⁹⁶ 2) species occurring in the same area with the possibility of interaction⁹⁷ or 3) whatever lives in a habitat (lake, forest etc) and is investigated by ecologists.⁹⁸ These three assumptions can be interpreted as a strong ontological holism, a moderate ontological holism and a methodological holism of communities (Looijen 1998, 137).⁹⁹

⁹⁵ One can find very rigid definitions of community like the following: "A concrete system is a biocoenosis or community iff (1) it is composed of organisms belonging to at least two different biospecies (i.e., iff its composition is multispecific; or (2) it is composed of (at least two) different biopopulations of unspecific organisms." (Mahner & Bunge 1997, 171) This definition cannot work because it is too specific (a community often does not have the same borders as its populations so that it can not be composed of entire populations). Additionally most ecologists will not accept this definition because they assume a community to contain various species). Only an open and operational characterization of community will be satisfying (cf. Palmer et al. 1994). Although there are all these terminological difficulties in ecology and ecologists are always debating on the correct use of terms, in practice most ecologists seem to know what they are talking about. Thus it is difficult to say whether this terminological uncertainty really impedes practical ecological research. Yet it will become difficult if one requires a general applicability of these concepts. There is no doubt that the terminological uncertainties and different applications impede a general and distinct explication of ecological key terms like *community* and *ecosystem*, but in spite of this, ecologists are able to investigate their objects of research and write papers on them.

⁹⁶ "An assemblage of populations of plants, animals, bacteria, and fungi that live in an environment and interact with one another, forming together a distinctive living system with its own composition, structure, environmental relations, development and functions." (Whittaker 1975, 1f.) "One or more populations with similar [life habits and] resource demands co-occurring in space and time." (Mc Naughton & Wolf 1973, 550)

⁹⁷ "A group of interacting species that occur in the same area." (Ricklefs 1973, 590). "A group of species living closely enough together for the potential of interaction." (Strong et al. 1984, VII).

⁹⁸ „Whatever lives in a habitat (lake, forest, sea floor) that some ecologist wants to study." (Cohen 1989, 181) "Any assemblage of populations (of plants and animals) in a prescribed area or habitat." (Krebs 1972, 379)

⁹⁹ The previous quotations have been taken from Looijen (1998, 136).

Conceptions that consider communities to be distinct units characterized by interactions of all its members are holistic, they seem to correspond to a form of ontological holism. The role of interaction is stressed and by doing so, the community is regarded as a whole. This view corresponds to the classic systems account I dealt with in the section on ecosystems. The view that regards communities as co-occurring species in an area that is investigated by ecologists can be considered to be a form of ontological reductionism because every group of individuals of one species is considered to be one single element. One can also attribute a weak methodological holism to this view, because it deals with several populations at once. The third view regards communities as species that occur in the same area and that have the possibility of interaction lies somewhere between the other two views. On the one hand, it denies a distinct community given by nature, on the other hand, it at least accepts the possibility of interactions that may lead to a natural community.¹⁰⁰

Although there are some community ecologists holding a strong ontological holism, most contemporary ecologists are reductionistic in their ontological assumptions on communities. Today, the debate on holism and reductionism in community ecology is about the question whether communities have emergent structures. Since the whole has different properties than its isolated parts these properties are characterized as emergent.¹⁰¹ Species number and species composition are often considered community properties and the question is, whether they have to be explained by means of interaction between populations or whether the community structure can be explained by the individual adaptations of species to their environment (cf. Looijen 1998, 137). Although there has been a strong dispute between the two parties, they both belong to a reductionist population ecological approach (cf. section 4.1.2).

Generally, communities are conceived of as a set of populations. However, the borders of the populations and the borders of the community coincide only rarely. That is why the community should be regarded as a set of individuals from different populations. This seems to be accepted by the majority of community ecologists (Allen & Hoekstra 1992, 43), at least in empirical research in spite of most textbook characterizations of community. Thus, communities should be considered sets of coexisting individuals of different species that occur in the areas of intersection of populations of these species (cf. Looijen 1998, 157). Apparently, the majority of community ecologists accept a

¹⁰⁰ As we will see in the next chapter the discussions between holism and reductionism in ecology often refer to the question whether there are interactions between populations or not (cf. section 4.1.2).

¹⁰¹ The term *emergent* is always used in its weak form (cf. Footnote 107).

reductionistic understanding of communities, consisting of individuals and not of interacting populations.

Although we can find a lot of holistic terminology in community ecology, most ecologists consider communities to be entities whose properties originate from the properties of the individual species. Since the occurrence of a species in a community is due to contingent factors, we cannot find any lawful generalization on the micro-level. The description and explanation of community patterns generally occurs on the macro-level by means of structural laws. This is due to pragmatic reasons and does not necessarily correspond to a holistic account of communities from an ontological point of view. Thus, most contemporary ecologists deal with operational characterizations of community. An investigation into the different characterizations of *community* revealed that there was only one that assumed a community to be a distinct unit given by nature (Palmer & Whyte 1994). The other characterizations are purely operational or pragmatic in that they are useful applications to the object of research. However, one cannot totally exclude the possibility of interactions of populations¹⁰² so that the medium view seems to be the most general form of characterization of community: a group of individuals of different species living closely enough together so that they have a potential of interaction (cf. Strong et al. 1984, VII).

Originally, the term *community* was developed for associations of plants and their properties. Spatial conceptions can much better be applied to plants than to animals, because interactions between plants are much less obvious than between animals or between plants and animals. Methods for the investigation of plant communities are much more elaborated than for animal communities. While the general concept of a community and for an animal community has to be very broad, the concept of the plant community is more explicit. Systematizations of plant communities are even a widely used instrument to come to a (methodological) unification of the diversity of plant groups by means of a syntaxonomical hierarchy as will be investigated in the next section.

¹⁰² I will deal with some examples that suggest the existence of interactions in the section on island biogeography (cf. section 4.1.3).

3.2.1.3 Plant Communities: *Syntaxonomy*¹⁰³ as a Tool for Unification

The concept of community mostly refers to a community of plants. The classic concept was developed by Clements (1916, 1936). He considered a plant community to be an organism that developed from the bare soil via several states of growth (seres of succession) to a mature and unchangeable stage of vegetation (climax). This *succession* is regarded as result of interactions between populations that are constantly being out-competed during the developing process of the community. Similar views were proposed by Forbes (1887), Thienemann (1918) and Lindeman (1942) (cf. Looijen 1998, 123). It is possible to establish a natural system of plant communities according to their climax stages (Clements 1936, 253).

Basically, there are three ways of recognition and characterization of specific plant communities. They can be categorized according to their habitat or biotope that is a geographical area including its abiotic constraints (climate, soil structure, and altitude). Another categorization according to the “physiognomy” of vegetation characterizes communities by the appearance of the growth forms of its plants (e.g. large trees, tall or small grasses etc). The last method characterizes a plant community by means of its composition of species. The number of species and their relative abundance constitute a plant community (cf. McIntosh 1985, 130). The first approach has to deal with the difficulty to recognize the different environments or biotopes. This will probably work for distinct biotopes like ponds or a defined area of bog, but if one looks at a shrubby meadow gradually transforming into a forest, it is nearly impossible to determine the boundaries and it is thus difficult to determine the place where the investigation should begin.

The second approach, that is based on physiognomy regards communities as discrete entities characterized by a specific appearance, e.g. a tall grass prairie or a coniferous wood. The roots of this physiognomic approach can be found well before the term *ecology* was coined in 1866. In 1806, Alexander von Humboldt already tried to characterize landscapes (that he considered to be vegetational units) by the “total impression” of the vegetation and its physiognomy. One can understand this *physiognomy* as an early form of vegetation science (Trepl 1987, 104f.). After the beginning of scientific ecology, the physiognomic approach in community ecology

¹⁰³ This form of taxonomic hierarchy is called *syntaxonomy* because it is something like a “metahierarchy” of simple taxa. *Syntaxonomy* looks for similarities of taxa in order to generate a new taxonomical structure.

vanished but elements of it can still be found in contemporary characterizations of landscapes.¹⁰⁴ Today, the exclusive approach to communities by physiognomy is considered unscientific, but it still plays an important role in the recognition of plant communities: The appearance of a plant community is characterized by horizontal and vertical structures. A meadow with nothing but short grass has a very simple structure whereas the rainforest with its different layers is very complicated. The structure of a community depends on different forms of growth like trees, flowers, moss or lichens. The problem with this approach of community determination is that we may always find plants with a different physiognomy in between the community. Therefore, there are always some shrubs or grasses in a forest characterized by big trees, and it will be hard to decide whether they belong to the physiognomically determined “tree”-community. Therefore, it is impossible to consider communities to be distinct entities by the physiognomic approach (cf. Looijen 1998, 142).

The third approach is at present most widely used at least in Europe. It is called *phytosociology* or *vegetation science*. It investigates the vegetational aspect of ecosystems by means of structure, the function of species, their fitness and the historical development. Vegetation science is often connected with nature conservation by the establishment of conservation management plans (Wilmanns 1989, 9). Vegetation science describes plant communities by means of species composition and their relative abundance. It determines all the plant species and their abundance in different areas, compares the data and finally comes to units that provide specific arrays of species. By this method, vegetation science has the possibility to constitute distinct natural communities based on comparable data. The basic idea of these systems states that the distribution of species is determined by environmental conditions. In places with more or less the same conditions, the same or similar species associations will be found (cf. Looijen 1998, 142). Thus, one does not start determining the community by an investigation of environmental constraints or a physiognomic characterization but with lists of species and their abundance. By doing so the habitat factors of the community also become known and its physiognomy can be determined by the predominant species and their numbers in much more detail.

¹⁰⁴ In fact this “total impression” of Humboldt (“Totaleindruck”) still serves as a criterion for the landscape today. This again shows one problematic aspect of the conventional concept of “levels of integration”. Landscape and in many cases plant communities are typologically determined entities which means that they are very differently constituted than organisms and populations which are functionally determined, thus it is difficult to put them into the same hierarchy (cf. Loehle 1988).

Similarities in species composition and relative abundance of species in different communities can lead to similarities of communities that can be expressed in a hierarchical classification system. This system is a means of unifying the vast amount of different groupings of plants. In Europe, one can find several views on how to establish the classification systems but the systematization of Braun-Blanquet (1964) is still predominant. One starts by listing all the species occurring in a “more or less homogeneous area” and estimates their abundance. The resulting lists will lead to a diversity of different plant communities (Wilmanns 1991, 28f.)¹⁰⁵. These different communities can be systematized according to the abundance of distinct species in the different areas. Plant communities are characterized by so-called *character species* that are exclusively bound to a specific area and characterize an *association*, which is the orienting unit in the classification of plant communities. There are also *differential*, *faithful* and *accompanying species* in the association. Differential species of a specific association can also be found in the contiguous associations, but they are still typical for the association in question. Faithful species regularly occur in the association but they can also be found in other associations. Accompanying species are not typical for the association but there are always some of them in an association (cf. Wilmanns 1989, 28 f., Sitte et al. 1991, 859f.).

The hierarchical syntaxonomy can be regarded as a way to arrive at a unified account of plant diversity in nature. The hierarchical ranks demonstrate the grade of similarity of species composition in different communities. The higher the hierarchical rank, the less are the similarities of species in the different communities. The hierarchical system of syntaxa is based on four principal ranks – *association*, *alliance*, *order* and *class* (Barkman et al. 1986, 145). The association is characterized by character species, several associations will be grouped together into an alliance by means of common character species in the different associations. The alliances providing the same character of differential species can be grouped together into an order and the orders again into a class. Therefore, every plant community can somewhere be grouped into this hierarchical system. Thus, the associations Bromo-Hordetum (with the character species *Bromus sterilis*, *Lepidium graminifolium*, *Hordeum murinum*), Bromo-*Erigeron*etum (*Bromus tectorum*, *Conyza canadensis*, *Senecio viscosus*), Urtico-Malvetum (*Chenopodium murale*, *Malva neglecta*, *Urtica urens*) and several others

¹⁰⁵ Here again, we find the physiognomic approach. “A more or less homogeneous area” can only be determined by its physiognomy.

belong to one alliance etc and several alliances belong to one order etc (Wilmanns 1989, 99).

The European ecologists interested in plant communities tried to understand the properties of plant communities not from the climate alone but also from the environmental conditions of a certain area. A specific plant community (with a specific species composition) belonged to each type of environment. Concrete plant communities (phytocoenosa) were considered to be instantiations of certain types (phytocoena). The community was considered something like a natural kind (Looijen 1998, 123). Thus, one could conceive of the syntaxonomic hierarchy as a picture of a real pattern given by nature. However, contemporary vegetation science considers communities and the hierarchical ranks rather to be theoretical constructs than units provided by nature. The method of vegetation science described seems to be a good means of establishing ecological units because one can use an analytical method. Of course, there are several limits to this method. Sometimes one can find typical compositions of species widely distributed that do not show any character species but they are also considered associations, sometimes as fragments of communities (Wilmanns 1989, 36). With those phytosociological conceptions, one cannot work unambiguously. This at least shows that concepts of vegetation science cannot be applied to every plant "community" in nature. That is why one can conclude that the syntaxonomic hierarchy is a methodological unification suitable for gathering an overview of the variety of plant groupings. It has many empirical applications but often fails to describe adequately plant communities. Most characterizations and classifications of communities should therefore only be considered to be a tool and not to be an end in itself (cf. Cooper 1998, 556).

In the United States, this is different. According to the Clementsian concept of community, the ecological limits of distribution of each population coincide with the distribution of the community as a whole. There are distinct borders in communities. That is why one talks of a *closed community* definitely characterized by its climax vegetation. Thus, many classification systems of communities have been developed. They became more and more split until there were absurd levels of distinction.¹⁰⁶ Most vegetation scientists left the Clementsian concept and adopted a concept of communities which is in favor of the *open community* developed by Gleason (1926).

¹⁰⁶ This still seems to be the case in the competing schools of phytosociology in Europe, although they use different methods than the Clementsian school.

Species are distributed independently of others that co-occur in a particular assembly. At present, this concept is predominant in the United States. The differences perceived in the continuum of communities are due to changing gradients (altitude, soil properties, climate), but there are no reasons for considering communities to be distinct natural units (cf. Ricklefs 1993, 410). If one accepts the open community concept, a hierarchical syntaxonomical order of communities is not possible because one cannot separate one community from another. In this case, the methodological way to a unity will not be successful although it may be useful in specific investigations.¹⁰⁷

Communities should not be considered discrete natural units. Most characterizations are operational and applicable in specific contexts only but they do not serve as a general means to demonstrate what a community of plant is. These (sometimes very different) operational characterizations force ecologists to accept the different scales of communities. That is why one should accept communities as arbitrarily defined structures which can have a wide variety of meanings. Perhaps it would be easier to abolish the term *community*, but it seems that ecologists stick on traditional concepts and they rather will give them new meanings rather than inventing new ones. This has the advantage that one does not have to deal with a variety of terms which would be the case if all the different entities characterized as *community* would be designated by a specific term.

However, I will go on using the term *community* because it is the term always used in the literature and there is no need for the invention of a new terminology. This would only lead to more confusion. I want to go on investigating different ways of looking at ecological units by means of evolutionary aspects. This is a precondition to come to an evolutionary understanding that will lead to a new account of natural units.

3.2.2 Typological versus Populational Thinking

In 1984, Ernst Mayr made an interesting distinction between populational and typological thinking in evolutionary theory. These ways of thinking led to quite different conceptions of evolution. Population thinking stresses the gradual changes of individuals of the same group and their genetic composition. This form of reasoning has its origins in systematics. Systematicists have often dealt with different specimen of

¹⁰⁷ Most botanical investigations of applied ecology that analyze an area will work with concepts of phytosociology and characterize communities by means of character species etc. In this case there are widely used applications of phytosociological concepts that have a big impact for strategies of nature conservation but I doubt the scientific value of these characterizations. It is a practical way of dealing with complexity but it does not tell us too much about nature.

one and the same species expressing different traits which contradicted a fixed conception of species. Population thinking emphasizes the gradual changes in nature and it looks at plant and animal breeding in order to find the mechanisms of these changes. Typological thinking on the other side considers natural units to be fixed and unchangeable or changeable according to determined stages only. In systematics, typological thinking was replaced by population thinking by the acceptance of Darwin's evolutionary theory but there has always been a friction between populational and typological accounts. From its beginnings until today, the history of evolutionary theory can be regarded as a continuous discussion between typological (assuming fixed types, saltation instead of gradual change etc) and population thinking (stressing a gradual change in the evolution of species). Virtually every controversy in the field of evolutionary theory has been a controversy between typologists and populationists (Mayr 1984).

One can also use these methods of thinking for ecology in order to characterize the different conceptions of ecological units. Thus, the dispute on the status of communities or other ecological units can be regarded as one of typological versus populational thinking. Although this distinction is not very common and the typological account of biology does not play a big part in ecological research (at least not officially), this form of thinking has always had a big impact on ecological research and ecological theory. Typological thinking tries to find stable types in nature by constituting units on very different levels like species, populations, communities or ecosystems. These units are fixed types that will only change as a whole according to specific laws. Thus, typological thinking and forms of holistic thinking are interwoven. This way of thinking can be found in the Clementsian account of plant community, in Odum's ecosystem concept and also today in some contemporary accounts of phytosociology. Populational thinking follows the tradition of Gleason and of Darwin and corresponds to the approaches of population ecology and evolutionary ecology. Gleason looked at the elements of complex ecological units and their properties whereas Darwin tried to explain the changes of traits and properties of these elements.

In the last few decades, typological thinking in ecology has been gradually replaced by populational thinking. This can be illustrated by the changing concepts of succession and climax. According to Clements (1916), succession is a series of changes leading to a climax which is determined by and in equilibrium with the local environment. Although being still important for community ecologists contemporary concepts of the climax

differ to a considerable degree from the original Clementsian concept. Climax communities correspond to the climate regions (e.g. tundra and taiga in the polar zones), but the climax stage is not uniform at all and one may find very different plant communities (cf. Sitte et al. 1991, 863f.). Other conceptions conceive of climax communities as dynamic states often with regular cycles of change (cf. Ricklefs 1993, 445). However, this shows that the concept of climax and thus of community is not static at all and corresponds much more to the open community concept of Gleason.

If one cannot consider communities and other complex ecological entities as natural units, the populational account of Gleason seems to be the right one to be applied to ecology. Thereby there will be no bigger units in nature than the single species (understood as individuals). The development of a community is due to random effects and the properties of the individual species. It will not change as a whole but only because of changes of individuals and their properties. Since the properties of single species change by means of mutation and selection, we have to bring evolutionary theory into account in order to explain the structure of complex ecological entities. Moreover, with the help of this form of reasoning, we can develop a more unified theory of communities and we are even able to understand why it is sometimes justified to talk of ecological systems as real natural units. At first, this does not seem very promising because evolution is a process that leads to contingent results and ecological generalizations base on contingencies. Thus, it seems impossible to institute unifying explanations based on generalizations on basic material entities (e.g. species). Yet I think there is a way to arrive at unifying explanations by means of an evolutionary ecology that emphasizes the historical account which will be demonstrated in the next chapter (cf. section 4.3.5.).

3.3 Conclusions

In this chapter, I have investigated different conceptions of complex ecological units. I distinguished between two forms of how to consider complex ecological entities. On the one hand, one can characterize these entities by means of a systems account, on the other hand by means of the concept of levels of integration. Both views are combinable and often mixed. This probably is due to the uncertain terminology and the different ways of determining of complex ecological objects that are used in both views. The main problem of all these concepts is to find units in nature that can clearly be separated from other units. Considering the ecosystem and the community concept, it

has become obvious that both do not have a settled meaning and that they are applied to a diversity of different objects. They are either spatially characterized or functionally or both. In the last forty years, there has been a shift from an understanding of ecosystems and communities that regarded them from an ontological point of view as given units provided by nature to a methodological understanding of these entities that regards them as purely operational and as mental constructs to organize the diversity of ecological objects. This methodological characterization became especially evident by means of the example of syntaxonomy in plant communities.

Most contemporary ecologists will follow a reductionistic concept of ecosystems and communities in that they consider them to be arbitrarily chosen complexes that are composed of individual elements with properties resulting from interactions of individual parts. However, I want to demonstrate in the next chapter that there is still the possibility that specific interactions in populations may lead to complex ecological entities being characterized by material units. As we will see, it is only possible to arrive at this form of ontological understanding of complex ecological units by means of populational thinking and integrating evolutionary and historical accounts.

4 Unifying Concepts in Ecology

In this chapter, I come to the main aspect of this book. I will discuss by what means it is possible to come to a unified ecology. As already elaborated in the introduction one can distinguish between a methodological and an ontological form of unity. The methodological way of unifying ecology can use a method e.g. by investigating every process in terms of energy changes or by using analogies for the description and explanation of very different systems, e.g. by means of cybernetic properties that are assumed to be found in every ecosystem. The ontological way of unifying wants to establish a unity of ecology by demonstrating that the diversity of ecological systems and the complex processes can be explained by their basic (material) elements and their properties. Both forms of unifying are to be found in ecology, but they face several difficulties and cannot establish unifying explanations that are valid for the entire field of ecology. This will be shown in this chapter before dealing with ways that are more successful to provide unifying explanations for the entire field of ecology.

I first want to look at forms of unifying explanations that are used in population ecology and systems ecology. In population ecology, there have been several debates on the form of explanation. Some authors have stressed the holistic and deterministic processes that will lead to stable complex community properties whereas other ones want to show that these properties are random results from the behavior of single elements. I will investigate two examples in population ecology to demonstrate these forms of explanation. Although population ecologists sometimes make a big difference between holistic and reductionistic explanations, it will become obvious that both forms of explanation are combinable with a form of an ontological reductionism that will lead to unifying explanations based on material units.

Then I want to investigate the forms of unifying explanation that are used in systems ecology. They often use explanations by means of analogies and are looking for methods with which to explain any ecological process by means of specific systems properties. I will investigate the role of analogies and hierarchies and their unifying explanatory power. Systems ecologists often stress the importance of holism (although without specifying what they are talking about) and I will demonstrate that they use pluralistic forms of explanation and investigation but that these explanations do not contradict an ontological reductionism.

In the last part of this chapter (4.3), I will investigate the relations of evolution and ecology. It will then become obvious that a unified ecology is not possible without the integration of evolutionary ideas into ecology. I will first look at the interdependencies of evolutionary theory and general ecology, and then investigate the role of historical thinking in evolutionary and ecological explanations. In further sections on this topic, I will illustrate some suggestions of how complex ecological entities could have been evolved before developing my own account of how it will be possible to come to a unified ecology by means of evolutionary ecology. I will demonstrate that it is possible to come to unifying explanations of the ecological diversity by a form of ontological reduction using the historical aspect of evolutionary theory. By this, also a unity of the discipline of ecology will be provided because the results of the research of population ecology and of systems ecology are important preconditions for explanations of evolutionary ecology. The population and the systems ecology approach are not only justified but also necessary to arrive at a general understanding of ecological processes.

4.1 Population Ecology

In this section of the chapter, I want to deal with explanations of population ecology. As already described in the second chapter, there are two forms of population ecology, one being often considered as holistic whereas the other is regarded as reductionistic (cf. section 2.2.1). I first want to give a general overview on the meaning of holism and reductionism in population ecology and then I will investigate how it can be combined with philosophical terminology and concepts. After this, I will deal with two examples of population ecology. The Lotka-Volterra equations with their emphasis on competition are a typical example of a deterministic explanation of community phenomena by means of its composing populations. I will also deal with a second example, the *equilibrium theory of island biogeography*, which is still one of the most encompassing theories in ecology which has resulted in a long debate on reductionism and holism in ecology.

4.1.1 Holism and Reductionism in Population Ecology

Debates on holism and reductionism can be found in nearly all areas of ecology. The terms *holism* and *reductionism* are mostly used in an unspecified way and it is not

always easy to understand the meaning of the terms applied. In general, the application of the terms by ecologists is different from the one used in philosophy of science and one can only try to translate ecological applications into the terms used in philosophy of science. That is what I want to do for the concepts of holism and reductionism.

In philosophy of biology, there is a distinction between three different forms of reductionism (cf. section 1.2.3). The ontological reductionism assumes every biological phenomenon to be an outcome of interactions of basic physicochemical entities. Transferred to ecology, reduction from an ontological point of view states that every complex ecological entity and every complex process is composed by individual parts and their properties in a way that complex ecological systems can be explained by them. From a methodological point of view, reductionism claims that scientific research or explanations should be always performed on the most fundamental level possible. Meta-theoretical¹⁰⁸ reductionism is concerned with the question whether complex theories and laws of one branch of science can be considered to be special cases of theories or laws of a more fundamental discipline (cf. Ayala 1974, viiif.). Meta-theoretical reduction is interested in the formal reduction of theories of different disciplines and corresponds to Nagel' s account of theory reduction.

I will investigate whether the philosophical terminology on reduction is combinable with the concepts of reductionism used by ecologists. In general, biologists are not interested in meta-theoretical reductionism, besides biological and ecological theories are not formulated in a way that a formal account of reduction can be performed. There are, however, some claims that theory reduction might possibly be applicable to a number of areas of ecology (Loehle 1988, 98), but these suggestions have not generally been accepted by other ecologists and philosophers (cf. Shrader-Frechette & Mc Coy 1988).¹⁰⁹ Only one exception is claimed: it seems that the Lotka-Volterra equations can be formally reduced to niche theories (cf. Looijen 1998, 177f.). Whether this formal reduction is successful will be discussed in the next section.

The debates on reductionism and holism in population ecology are mostly debates on methodological questions. Ecologists discuss on the fundamental unit of ecological

¹⁰⁸ This form of reduction was originally designated as "epistemological" (Ayala 1973, viii), but I will use the term *meta-theoretical* because *epistemological* which may lead to confusion (in doing so I am following a suggestion of Kochanski's 1979, 80).

¹⁰⁹ This refers to the problems of laws I dealt with in the second chapter (cf. section 2.4.2). Since there are no material laws in ecology, a meta-theoretical reduction is irrelevant.

research and on which research strategies ought to be followed. They further discuss whether communities or even ecosystems should be studied as wholes, or whether they should be investigated by means of their parts. They want to know whether the explanation should be given on the macro- or on the micro-level. These questions must be distinguished from the ontological question, whether communities and their properties are constituted by their individual units and can be exclusively explained by them (although not in a formal manner). Often, ontological, methodological and ethical questions (e.g. that the reductionist way of research has led to a damage of nature and that we need a "holistic" approach in order to conserve nature) are not distinguished. The appeal for holism seems to integrate all these aspects (cf. Loehle 1988; cf. the discussion in the ecological journal *Oikos* (forum) 1988, 267 - 281).

Most ecologists and most biologists will admit the ontological thesis that there are no specific forces leading to complex units with new properties. Nevertheless, many of them will also stress that there are specific properties of complex biological and ecological systems that cannot be predicted from the properties the elements. Thus, the properties of the whole cannot be reduced to the properties of the elements; the new properties rather emerge on the level of the whole resulting from interactions of the parts (cf. the next two sections). Ontological anti-reductionism has been weakened during the last few years. There appears to be a growing recognition that processes occurring at the level of the individual can form the basis for the construction of a theoretical framework with which it is possible to interpret the properties of populations or communities (cf. Koehl 1989, 49).

As I argued in the introduction, in many cases a reductionistic explanation for a complex unity does not make sense if one wants to understand the properties of the complex level. If one wants to explain the behavior of migrating birds and understand their formation of flight, one will not understand it by looking at their cells, their genes or their atoms. Although it could be possible to explain the complex behavior by means of basic units, one will not understand the specific form of behavior on the level of the group of migrating birds. In this case, explanations on the macro level are much more to the point of interest and explanations on a lower level would blur the specific questions. This problem will become more obvious in the following two sections and by the examples given there.

First, I want to deal with a philosophical investigation on holism and reductionism in ecology (Looijen 1998). This investigation results in the claim that reductionism and

holism are mutually dependent research programs. Looijen wants to demonstrate that the major distinctions commonly assumed between holism and reductionism in biology (e.g. emergence versus reduction or phenomenological explanations versus explanations by basic mechanisms) are not contradictions at all. He considers reduction to be an epistemological issue that belongs to logical relations between different statements which should not be confused with ontological reduction. He states that holism and reductionism should be regarded as mutually depending research programs rather than as conflicting views of nature or of relations between sciences. Holistic programs play an important part as guiding principles for reductionistic approaches. Before starting with the reductionistic research, one has to know the results of the holistic programs that can be completed by reductionist research (Looijen 1998).

The interdependence of holism and reductionism is certainly an important point, but only in relation to methodological aspects. Looijen claims that reductionism in its radical form is a failure. He thinks that radical reductionism denies the existence of properties of higher levels of organization and denies as well the importance of studying them. He argues that one cannot start a reduction if there is nothing that can be reduced, so that one first needs some holistic explanations which can be complemented by reductionistic explanations at a more basic level. The holist research program serves as a guide program which points the way to any problem that cannot be resolved by it. In this case, one needs a reductionistic supply program that provides the guide program with the solution (Looijen 1998, 83f.).

I am not sure, whether this argument only refers to methodological or also to ontological questions of reduction. From an ontological point of view, there is no reason why a reductionist should not accept the existence of macro-levels and their properties. In many cases, the macro-level is the first perception of the researcher and it would be stupid to deny its existence. An ontological reductionist does not have to deny the fact that higher levels have properties; he simply states that these properties are not emergent in the sense that they are new and cannot be explained by the composing parts and their properties. The task of the ontological reductionist program is to demonstrate that the whole is not more than the sum of the parts, their properties and, in some cases, their interactions. However, this is quite different from the methodological question on which level ecologists should research and explain. There is no doubt that ecology needs a diversity of different methods on all levels to arrive at better

descriptions of ecological complexes and to better understand natural phenomena but, from an ontological point of view, this fits well into a strong reductionistic account. This will be demonstrated in the next two sections by case studies.

4.1.2 The Lotka-Volterra Equations

The Lotka-Volterra equations are central for population ecology. They are used to describe processes of competitive exclusion and predator-prey or host parasite systems. They start with the assumption that the growth of population is a deterministic process which can be described by the logistic model for population growth expressed by the following equation:

$$dx/dt = rx ((K-x) /K)$$

A change in the number of the members of a population (dx) is dependent on the birth rate (r) and the carrying capacity (K) of the area in which the population lives. If the birthrate r increases, the population growth will exponentially increase until the equilibrium with the carrying capacity is reached. This leads to the typical sigmoid curve of population growth. This form of population growth can be found in nearly in every population, e.g. a population of bacteria in a petri-dish starting to grow very slowly with just a few specimen which will, however, grow faster and faster until it will reach exponential growth. If the bacteria cover all the medium of the petri-dish, the growth rate will slow down and will come asymptotically close to a fixed value. There are some factors that control the density of populations and these factors at least partly depend on the carrying capacity of the environment.

The logistic model of population growth is a simple mathematical equation. This is an advantage, because a lot of population ecologists can use them without being mathematically trained, but it is also a disadvantage, because there is hardly a situation in population ecology which can adequately be described by these equations. It is a deterministic model which does not consider random processes. Nevertheless, random processes occur almost everywhere in ecology. The simple model for population growth was extended by Lotka and Volterra. They incorporated some aspects of interspecific competition into the model and used it for two populations. Thus, they developed the following pair of equations, predicting either competitive exclusion or stable coexistence of two competing species (cf. the section on models 2.4.3.2.3):

$$dx/dt = rx - \alpha xy$$

$$dy/dt = \beta xy - Dy$$

(x is the number of prey organisms, y is the number of predators, α is a constant that links the prey mortality to the number of prey and predators, whereas β links the increase in predators to the number of prey and predators, D being a constant of mortality for the predators).

The Lotka-Volterra equations are considered holistic models in that they explain on the level of the population and not on the level of the individual. They can be used relatively successfully for an explanation of a variety of phenomena in population ecology. That is why they may well become the first general and unifying model in ecology (Looijen 1998, 177). They tell us how species influence each other on the level of populations or even communities but they do not say anything about the underlying micro-level processes that explain the competition between the populations of species. They can thus be considered a form of holistic explanation.¹¹⁰ The question is now whether there are processes and elements that can explain the behavior on the macro-level described by the equations. There are some modern niche theories providing these explanations. Modern niche theory is a family of models specifying the competition on resources and the mechanism of resource exploitation by two or more species. Looijen performed a meta-theoretical reduction of these equations to a specific model of modern niche theory. He stresses that the Lotka-Volterra equations served as a holistic guideline for the niche theory, whereas the niche theory is a reductionistic supply program for the Lotka-Volterra model (Looijen 1998, 184f.).

Although this meta-theoretical reduction seems to be possible, it seems unlikely that the modern niche theory will be a sufficient means to explain the structure and dynamics of communities. The generalizations of modern niche theories are also structural generalizations. They only apply to resource utilization but do not look at specific properties of a certain species. Therefore, it is not a reduction to a material but to a structural generalization. This reduction does not tell us anything about the basic entities of the populations involved. One needs a theory about the environmental requirements and tolerances of specific species (a habitat theory) to come to statements with a better empirical basis (Looijen 1998, 235). Thus, one can talk of a reduction of a special model to a more general theory referring to structural

¹¹⁰ This form of holism is a methodological form which can not found in any other scientific disciplines. It does not seem anything especially ecological. This means that every explanation and description on a macro level is holistic research.

generalizations but not of a reduction to a theory of fundamental (material) generalizations of basic population units.

The Lotka-Volterra equations belong to abstract laws which only specify the behavior of systems of idealized objects fulfilling certain functional conditions implicit in those laws. These laws (which may be expressed by the niche theory mentioned by Looijen) cannot explain everything, because we need empirical data for the fact that the objects, at least approximately, satisfy the specified functional conditions. It is possible that the models of ecological systems in terms of ecological natural kinds will provide information that is quite unrelated to the prevalence of organisms of the kinds in which we are interested. No physiological explanation of the fact that lynxes eat hares will provide an explanation why a particular lynx eats a hare (Dupré 1993, 107 - 120). Thus, ecologists are not able to explain community phenomena by means of fundamental laws but only by means of structural ones.

A reduction of the Lotka-Volterra model to material units is not possible, which will be demonstrated by the following example. According to the holistic model describing predator-prey systems, the cause of the death of the rabbit is the high number of foxes. The cause of the low level of the rabbit population is the high level of foxes. In case of a micro-reduction, it should be possible to deduce the complex behavior of the populations from the behavior of the individual. The individual fact may be as follows: rabbit *r* was eaten because he passed through the capture space of fox *f*. The fact that a rabbit was eaten by a fox does not help us to understand the oscillating of hare and fox populations. The micro-level is often inadequate for the explanation of population phenomena and that is why one has to deal with upper-level explanations. No micro-reduction will explain the death of a specific rabbit, because the mutualistic interactions only occur on the level of the population and not on the level of the individual. If the hare is eaten, then it will be over (Garfinkel 1981, Chapter 2).

I do not think that this argument is correct. One cannot reduce the population level to single individuals but to several of them (if there were only one rabbit the fox would not survive either) and it would then be possible to derive a pattern of a macro-level from a pattern of a micro-level. Only by reduction of a specific population cycle will we find an explanation. It will be impossible to reduce the general equations which claim validity for every predator prey system to material units. This reduction does not work because one has to deal with contingent outcomes of evolution and it is not possible to reduce contemporary population phenomena to their contemporary material units. If one

wants to establish generalizations which are valid for all populations, one must use structural generalizations or one can only establish rules for a specific population cycle (cf. next section). Generalizations based on material units and their properties are either accidental or they are not biological (i.e. ecological) but physical (cf. section 2.4.2).

4.1.3 The Theory of Island Biogeography

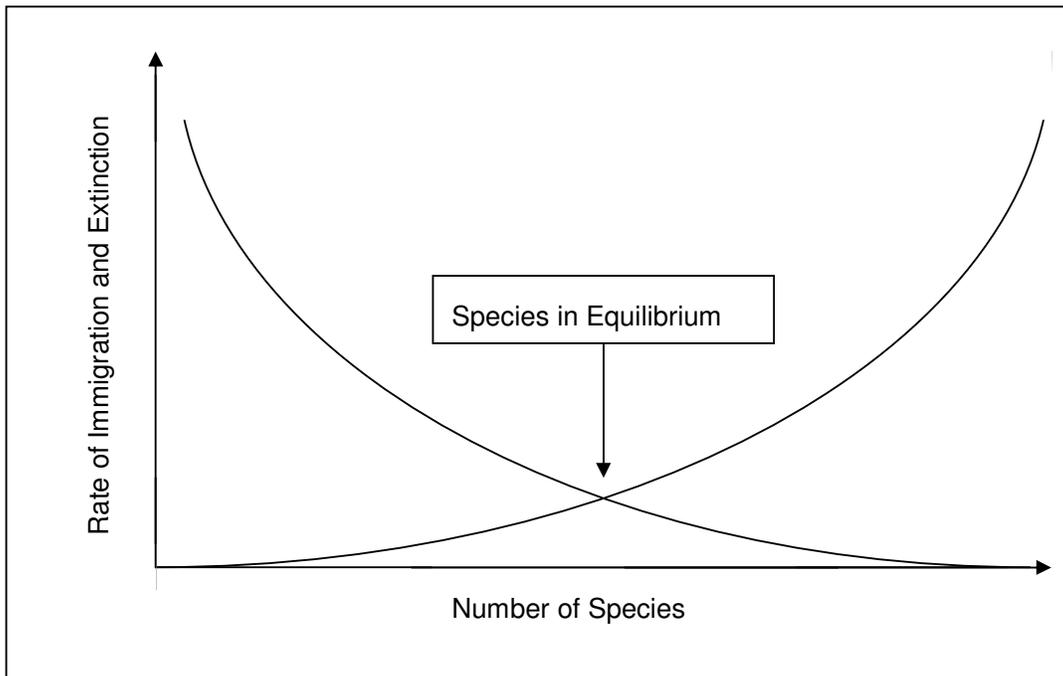
In this section, I want to look at one of the most important theories of population ecology and the debates on holism and reductionism initiated by this theory. The *equilibrium theory of island biogeography* is a general theory of population ecology which wants to provide a unifying explanation for some community properties resulting from the behavior and competition of their populations. This theory was developed by the mathematician and ecologist Robert M. Mac Arthur and the taxonomist and zoogeographer Edward O. Wilson (1967). They aimed at a unified explanation of island biogeography which they considered the same as island ecology (Mac Arthur & Wilson 1967, v). They provided an explanation of how communities on islands were established and how they could maintain their specific properties (species number and their abundances).

Mac Arthur and Wilson (1967) developed a dynamic picture of communities which was in contrast to the static picture which until then has been prevalent in the minds of ecologists and naturalists. They were interested in giving a general explanation of the long-known relationship of area size and number of species. As had been known for a long time, the bigger the area in size the more species were to be expected, at least under similar environmental conditions. The authors investigated communities of small islands. These islands were clearly spatially determined areas, with only one community.

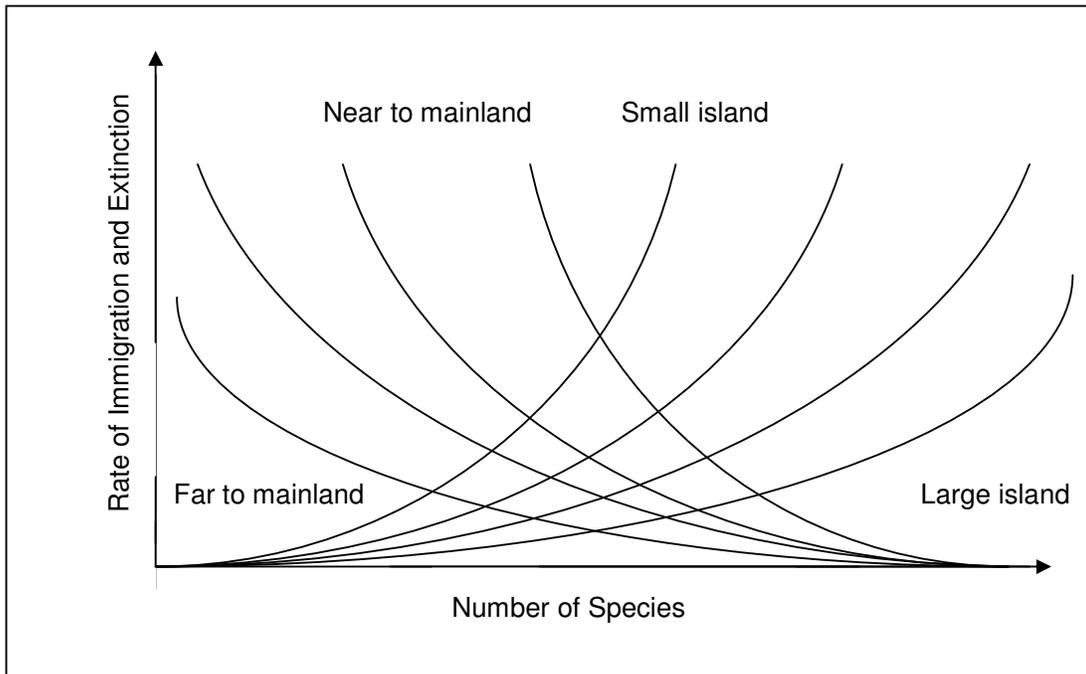
The authors conceived of island community structure as a result of a dynamic equilibrium between the immigration of new species and the extinction of those that had colonized before. The basic idea of the theory can be graphically demonstrated (see pct. 4). The immigration rate (I) of species is high when the island is empty and it will continually decline when the niches of the island become gradually occupied. This curve goes down asymptotically to the value of zero immigration in case all niches of the island are occupied. Of course the extinction rate (E) is zero when the island is empty and it will increase the more species colonize the island. The successful

colonization of new species will lead to an increase in competition and also to an increase in the extinction rate. The point of intersection of the curves of immigration and extinction indicates the equilibrium number of species of the island community with a constant rate of immigration and extinction.

The shape of the curves will be different according to the distance of the island from the continent: the larger the distance, the lower the immigration rate, the I-curve will be flatter and the equilibrium point will be reached by a smaller number of species. The extinction rate is dependent from the area size of the island, the larger the island, the lower the extinction rate. The equilibrium point will be reached in large islands with far more species than in small islands. Thus, large islands near the continent will have much more species than small islands which are far away from the mainland (cf. pct. 5).



Picture 4: The Equilibrium model of species of a single island (after Mac Arthur and Wilson 1967, 21).



Picture 5: Equilibrium models of species on several islands with varying distances from the mainland and varying size. Accordingly, the equilibrium points are shifting (after Mac Arthur & Wilson 1967, 22).

The theory of island biogeography explains the diversity of species of a community by means of a holistic explanation. Like the Lotka-Volterra equations, this explanation proceeds on a macro-level. The successful immigration and the extinction of species in a community are considered to be macro-level phenomena which are results of interactions between the different populations of the community. The explanation stresses the equilibrium in the number of species and the environmental conditions (area size, distance of continents) of a community. These data refer to the whole community and not to single species (cf. Looijen 1998, 207).

Although this model is holistic, it is combinable with an ontological reductionist account, because this form of holism explains and describes only methodically on a macro-level. The theory of island biogeography in its holistic form is one of the best ecological theories and one of the few that could be confirmed experimentally. The ecologists chose six small islands, poisoned all terrestrial arthropods and waited for the recolonization of the island (Simberloff & Wilson 1969, 1970). By doing so, they could confirm the theory of island biogeography. However, the theory lacks many explanatory details concerning the factors determining immigration and extinction of single species. Like most ecological theories, this theory supplies explanatory information but does

not provide details about causal mechanisms and fundamental regularities governing the mechanisms (cf. Cooper 1990, 175). Thus, the theory can integrate many phenomena into a theoretical model and heighten our understanding, but it fails to refer to the actual causal details. It is a theory with typical structural generalizations.

Every community is different and one will not find two of them with exactly the same species and the same pattern of colonization. The theories of community ecology are contingent upon the organisms involved and on their environment. Community ecologists can understand the local rules of engagement for interacting species in one given place and at one given time. In almost every place and in the same place at another time, species assemblages are sufficiently different, which makes it very difficult, if not impossible, to apply the local rules to other populations and communities. This is due to the contingent details (different properties of species). Ecologists may find generalizations applicable to other communities on a macro-level but not on the level of intense local studies. One can thus only compare different local guilds and population assemblages of different sites on a macro-level. However, to arrive at those generalizations, one has to neglect many details, and thus the generalizations of community ecology are often rough *ceteris paribus* generalizations and can be applied to macro-level phenomena only (cf. Lawton 2000, 47f.).

This problem of community ecology corresponds to the problems of ecological laws in general (cf. section 2.4.2). In ecology, there are no fundamental laws. The existing general statements refer to macro-levels. They are *structural generalizations* describing the behavior of macroscopic and complex entities. Nevertheless, these structural laws do not provide statements about the material units composing the complex level. Structural laws help to organize and understand complex processes but they do not tell us anything about specific properties of the basic elements. That is why ecologists use structural laws on a macro-level which help to arrive at unifying theories. The unity to be reached is methodological and helps to organize and explain complex ecological processes.

The equilibrium theory of island biogeography initiated a long debate on holism and reductionism in population ecology. The two strands of the population ecology approach (cf. section 2.2.2) vary in their assumptions on how to explain community phenomena. One strand stresses deterministic factors in their explanations; the other uses random factors to explain specific community properties. One school is interested

in explaining the community pattern by means of interactions of populations whereas the other wants to explain these patterns by the properties of singular species only.

The first strand, following the ideas of Mac Arthur tried to conceive of community phenomena by means of interspecific competition of populations which will necessarily lead to a specific community pattern. One of the main proponents is Jared Diamond (1975), who established some deterministic *assembly rules* for populations which structure a community. From this, it follows that ecological communities result as stable and integrated entities. The species of a community are selected by competition between several populations; they will be co-adapted in relation to their niches and abundances. They will thus be interwoven with the other populations in a tightly knit structure. This structure will provide new “emergent” properties, e.g. the possibility to resist invasions of new species (Diamond 1975, 343). Good examples of this form of community are the Darwin’s Finches. They have occupied all niches of the Galapagos Islands and no invader from outside has a chance to colonize there. Ecologists consider this form of explanation which stresses competition and determinism to be holistic (cf. Looijen 1998, 199ff.).

Simberloff (1978), however, denies the existence of assembly rules and argues for a random colonization. One should first test a null hypothesis by assuming that the actual distribution pattern could have developed differently from the assumed rules of the investigated process. A null hypothesis is often combined with the assumption that patterns in nature developed randomly and that there are no deterministic and lawful processes. Null models are used to describe the system in the absence of the action of the postulated causal process. They try to imitate the behavior of hypothetical non-interactive communities (Quinn et al. 1983, 609). This view is often referred to as reductionistic, in contrast to the view defending assembly rules which is considered holistic.

By means of computer simulations, random colonization models of islands have been calculated (Simberloff & Connor 1981). The results clearly demonstrated that a random colonization could lead to community patterns very similar to those assumed to have developed according to interspecific competition and assembly rules (Simberloff & Connor 1981). Thus, the arrangement of species in a community alone cannot lead to the conclusion whether it resulted from competition or from random colonization. Sometimes both forms of explanation are possible. This, once again, demonstrates that

biologists mostly have to work with *how-possible explanations* and only rarely with *how-actual explanations* (cf. section 1.2.1).

The debate on assembly rules and random colonization has lasted for more than ten years. It has been a very polemic discussion and has not really led to a result. Diamond concretized his statements by relating the assembly rules of populations to the guild only and not to the whole community of an island. It is hard to deny that there are no interactions on the level of the guild (that is what it has been defined for: a group of co-occurring species sharing the same or similar resources; they have to interact). At least there has been an agreement on three aspects: 1) patterns in the species composition of guilds are not completely at random, 2) community patterns can often be explained in terms of properties of individual species and characteristics of the island and 3) there are only few cases, in which competition theory is a necessary ingredient of the explanation of composition and number of species in a community (cf. Looijen 1998, 232).¹¹¹

Obviously, communities are very diverse and the ways that lead to communities can be manifold. That is why one must be aware that field observations may often show that certain taxa or systems are more in conformity with theory than others are. However, the examples for interspecific competition which lead to community structure are as good as examples for the random colonization model. In the case of the Darwin's Finches, at least, it could be shown that differences observed in beak lengths were explainable and only predictable by means of interspecific competition (Grant & Abbot 1980). This is one of the best examples of competition and co-evolution between species (see below in the section on co-evolution section 4.3.4). The occurrence of the beak differences cannot be explained by the properties of the single species only.

Although these two positions in ecology have been referred to as holistic (interactions of communities) and reductionistic (random colonization), this difference does not seem to be obvious. Both views assume that communities are composed by populations or individuals. At first sight, the question, whether the process of community development occurs according to deterministic processes of interaction or to random colonization, has nothing to do with questions of reductionism and holism, both forms explain the community properties by means of its composing units, their properties and their interactions. There are some differences in the form of explanation, but it is difficult to see what is reductionistic and what is holistic in them. From an ontological point of

¹¹¹ For an extensive survey of this debate cf. Looijen (1998, 211 - 232).

view, both forms can be considered reductionistic. However, they explain on different levels. Whereas one strand explains on the level of species (individuals), the other explains on the level of populations and their interactions. One can, perhaps, distinguish between certain degrees of a methodological holism. The explanation by means of assembly rules operates on a higher level than the explanation by random colonization. In addition, it seems to be possible to use successfully both forms of explanation in different investigations although the possibility of ontological reduction is not denied.

The outcome of interactions between populations is often regarded as resulting in emergent properties of the community. In this case, the term *emergent* only means that properties on the levels of the whole cannot be predicted and explained by the properties of the individuals alone but only by the properties of the individuals or populations and their interactions. This use of *emergent* does not at all contradict an ontological reductionism. The community properties may be unpredictable by the properties of the isolated species, but they can afterwards be explained by an investigation of the properties of the different species. One can even try to anticipate community properties from specific interacting individuals and their properties by means of computer simulations.

So, one can conclude that, seen from an ontological point of view, the approach of population ecology is reductionistic. The claims on holism and emergence only refer to methodological problems and a weak form of emergence can be combined with ontological reductionistic accounts. Both forms of the population ecology approach accept the thesis of ontological reduction. They arrive at unifying explanations by reducing the processes and properties of complex levels to lower ones, thereby trying to find a unity of ecology by means of a common matter (in this case species (individuals) or populations).

Since the units of complex levels are contingent results of evolution, generalizations on them are structural or accidental. If population ecology explains with "material" generalizations, it will be able to provide a unity from an ontological point of view. However, this unity encompasses only one single community, sometimes perhaps several but it will not encompass all or most population phenomena. This is not possible because of the contingent results of evolution and because evolution selects for function, therefore ecologists have to deal with supervenient properties like fitness etc (cf. section 2.4.2.2).

As we have seen, the population ecology account will arrive at unifying explanations but they will only be valid for a small range of population phenomena. Now, I want to look again at systems ecology and examine the forms of unifying explanations used and to investigate their range of application.

4.2 Systems Ecology

Population ecology is often considered a reductionistic research program and is opposed to systems ecology as a holist research program (e.g. Hagen 1989). As already demonstrated, holism, in relation to the ecosystem concept, can have quite different meanings (cf. section 3.1.2). One can distinguish between four forms of what is considered to be holism in systems ecology: a) an assumption which considers ecosystems to be whole units with laws and organizational principles of their own, b) a demand for holism which stresses the importance of embedding a problem into a larger context and of reflecting upon the consequences of research (e.g. in order to avoid environmental harm), c) a black box approach that is characterized by input-output relations and by neglecting the individuality of the component species of the whole system, and d) the approach of systems analysis which wants to include every component and its properties into the system of investigation (glass box approach) (Loehle 1988, 101).¹¹²

If one wants to combine these views on holism in systems ecology with philosophical concepts, some forms of “ecological holism” will vanish. Approach b) is much more an ethical imperative how to perform research than a form of explanation. It is a statement neither on properties of nature nor on methods of explanation. It is an ethical imperative with a methodological implication. It cannot be used for the question of the unity of ecology. Form d) is an approach which wants to investigate everything that can be found in a system by means of systems analysis and by the use of a mechanistic method. This can be considered a form of ontological reductionism: it uses

¹¹² “1) The view that ecosystems are integrated, interconnected systems with their own laws and organizational principles. It is not necessarily denied that reductive explanations are possible, but merely that they are so impractical that the higher level system should be studied phenomenologically.

2) The practice of embedding a problem in a larger context. Thus when designing a waste-treatment pond, holism might mean keeping in mind that migratory ducks might use the pond and be killed. It is this type of holism that ecologists complain is lacking in civil engineers and urban planners.

3) A black box approach which includes questions such as: What is the nutrient loss response of a whole watershed to acid rain? The watershed is treated as an input-output system without detailed concern for mechanisms or particular species. This is an empirical approach that does not necessarily seek laws or principles (in contrast to 1)

4) Detailed systems analysis such as ecosystems models that are mechanism oriented. This approach is holistic because it includes all components and processes.” (Loehle 1988, 101)

reductionistic explanations by means of basic mechanisms and a holistic method by integrating all aspects of the system. Form a) seems to correspond to a methodological holism and perhaps also to an ontological holism, but this is not obvious. In systems ecology, ontological assumptions of holism seem to have vanished during the last few years (cf. section 3.1.2). Approach c) seems to be the most typical form of holism in systems ecology. By neglecting the individual components and by only viewing them in terms of their roles, it wants to provide structural laws with which to explain similarities in different systems. This form can be regarded as a methodological reductionism which observes all aspects of ecological systems in terms of its function. This view will mostly be combinable with an ontological reductionism, too.¹¹³

As in population ecology, one can also find several disputes on holism and reductionism in systems ecology. Some systems ecologists criticize ecosystem modelers as being reductionistic. Computer models of ecosystems are sometimes considered to be a form of large scale reductionism that requires a dual reductionistic-holistic strategy (McIntosh 1985, 225). The typical method of systems ecology to arrive at a unity of ecology, however, seems to be the use of functional explanations and analogies which help to establish models that can be used to describe most different ecosystems. Although this view can be combined with an ontological reductionism, it is a very different way to unify a scientific discipline. For this reason, it would be useful not always to use the term *holistic* in systems ecology because this will only lead to confusion. One should rather talk of analogies and models with different degrees of integration which will lead to the establishment of structural generalizations on high hierarchical levels.

In the following two sections, I want to investigate into this form of system ecological explanation and its success concerning unifying explanations. I will first look at the way analogies are used to describe ecological systems. This approach is similar to Bertalanffy's account of explanation in general system theory. In the second part, I will look at the form of hierarchical systems ecology which wants to find a new way to the unity of ecology by means of a theory of hierarchy.

¹¹³ The blackbox account is sometimes considered to be a crypto-reductionism because it uses a method which is in practice reductionistic (cf. Bergandi et al. 1998, 192). This is a form of methodological reductionism, which is typical for many forms of systems ecology claiming to be (ontological) holists.

4.2.1 Unification by Analogies

The assumption that every ecosystem can be characterized by a black box model can be considered a form of methodological reductionism, perhaps also to be an ontological holism in that it assumes that the system properties cannot be reduced to those of its parts. The predominant proponent of this of systems ecology was Eugene Odum. His ideas on systems ecology share much with the systems conception of Bertalanffy. One should come to a general conception of ecosystems by considering ecology under the aspect of fluxes of energy, by abstracting from individual elements and by just looking at their respective roles. Thus, every ecosystem could be understood as an input-output black box model.

Fluxes of energy and matter can be quantitatively analyzed and described by mathematical equations. The general equations should be valid for every ecological system and one can thus arrive at a unity of ecology via structural equations describing functional processes of diverse ecological systems. Some functions of ecological systems are thought to be so general that they should be found in every system.

This form of methodological unity lies in the tradition of the systems theory of Bertalanffy (1949, 1968). Bertalanffy considered the hope to reduce the different levels of reality to the level of physics to be far-fetched and futile. A better way to arrive at a unification of science would be via analogies and structural laws which can be applied to a diversity of systems (Bertalanffy 1968, 48). Systems ecologists have tried to apply Bertalanffy's conception of systems to ecosystems. They wanted to arrive at a unity of ecology by means of a methodological reductionism, because everything is reduced by this method to the description and analysis of functions. By this method, one can come to analogue models that can be applied to every ecosystem. Perhaps one should rather talk of unifying by analogies instead of using an unspecified concept of holism. Systems ecology explains systems properties by means of functional analogies and isomorphic structures of different ecosystems which can be described by the same structural laws. The main aim then is to find structural laws which can be applied to every ecological system independent from its internal composition.

This "analogism" has weakened during the last few decades and at present, most ecosystem ecologists favor an ontological reductionism although they talk of "holism", "emergent properties", "self-organization" etc. A contemporary way of systems ecology to arrive at a unity of ecology is by means of hierarchy theory which claims not to be interested in questions of holism and reductionism and which tries to find new forms of

explanation in systems ecology. Whether this is a successful way to arrive at a unity of ecology will be examined in the next section.

4.2.2 Hierarchy Theory – A New Form of Unification?

Biological and ecological processes appear to be hierarchically organized and one can find several hierarchical concepts of ecological objects. However, as we have seen, the concepts of hierarchy used in ecology (levels of organization, syntaxonomy) are diverse and lack of consistency. Probably one has to develop a special type of explanation and theory applicable to hierarchical systems (cf. Shrader-Frechette 1986, 91). Indeed, one can find several approaches trying to establish theories of complex organized hierarchical systems (e.g. Koestler 1969; Simon 1962, 1969; Weiss 1971). "Hierarchy theory" in ecology started with Pattee (1973), Allen & Starr (1982), O'Neill et al. (1986), and Allen & Hoekstra (1992) and is, up to now, be mentioned in much of ecosystems literature.¹¹⁴

Most conceptions of hierarchical systems base on Simon's concept of hierarchy (Simon 1962). He considered a complex system to be made up of a large number of parts interacting in a non-simple way and providing a hierarchical structure. Most of the complex structures of the world are enormously redundant and redundancy can be used in order to simplify their description by means of hierarchical levels. Complex systems are composed of simpler systems. They will develop from simple systems very rapidly if there are stable intermediate forms which can be found again on every higher level. Thus, one will hardly find complex systems that are not hierarchically structured. That is why a good way to formulate a non-trivial theory of complex systems is by way of a theory of hierarchy (Simon 1962).

The concept of *hierarchy* is important for complex disciplines but the term has no settled meaning. A traditional understanding of *hierarchy* is provided by the following definition: A hierarchy is a collection of ordered levels with a control relationship between a node of one level and the set of nodes connected to it on the next lower level. Nevertheless, in modern hierarchy theories the term *hierarchy* is often arbitrarily redefined in order to suit the need of the respective author (cf. Arras 1991, 5f.). The conception of "hierarchical system" is a little clearer. It is mostly regarded as being composed of interrelated subsystems, which themselves consist of several

¹¹⁴ Hierarchies play an important part in every approach to ecology, but as will become obvious, "hierarchy theory" is developed for a new conception of ecosystems and used as a new instrument for systems analysis. So, it belongs to systems ecology.

subsystems. This form of nested hierarchy ends at the lowest subsystem (Simon 1969, 196).¹¹⁵

It is simple to transfer these ideas to the community and the ecosystem concept. Every community can be considered a hierarchical system composed by several small (more or less stable) subsystems (atoms, cells, individuals, populations) and thus provides redundant structures which can be ordered into a nested hierarchy.

In ecology there is no consensus on the meaning of the terms ‚level‘ und ‚hierarchy‘, either of them is used in a variety of ways (cf. Mahner & Bunge 1997, 177). For this reason, it is difficult to consider “hierarchy theory” to be a theory.¹¹⁶ It rather seems to be an approach with various conceptions in the diversified approach of systems ecology that refers to hierarchies. Some proponents of “hierarchy theory” consider it to be a collection of tools providing useful methods for the design and the control of open ended-systems which will probably never become a closed theory (Patten 1973, 132). At least until today one can say that "hierarchy theory" is no theory but a collection of more or less elaborated ideas referring to hierarchical structures. Even so, it is used as a “theory” by many ecologists interested in theoretical questions helping to clarify problems of hierarchical structure in ecological systems. “Hierarchy theory” is one approach of systems ecology to deal with complex ecological systems. Although it is not (yet?) mainstream in ecosystems research, it is widely distributed by systems ecologists interested in the theoretical background of their approach. In the following, I will demonstrate and investigate some aspects of this approach as far as it is concerned with ecology and has some significance for the question of unity.

The fundamental unit of “hierarchy theory” is the *holon*, a self-regulating open system. This term was introduced by Koestler (1969) for a level which is influenced by parts of lower levels and constrained by higher-level organization (cf. Webster 1979, 124). Holons function as autonomous units but are also parts of superior organizational units. They incorporate all inferior subsystems but are themselves parts of higher-level systems. Hierarchies are partly ordered sets, in which the subsystems interact through asymmetric relationships. There are also system constraints by which higher levels

¹¹⁵ “By a hierarchic system, or hierarchy, I mean a system that is composed of interrelated subsystems, each of the latter being in turn hierarchic in structure until we reach some lowest level of elementary subsystem.” (Simon 1969, 196)

¹¹⁶ Although I do not consider “hierarchy theory” to be a theory but several approaches to deal with hierarchical structures, in the following, I will use the term “hierarchy theory” for pragmatic reasons but I will always use quotation marks for it.

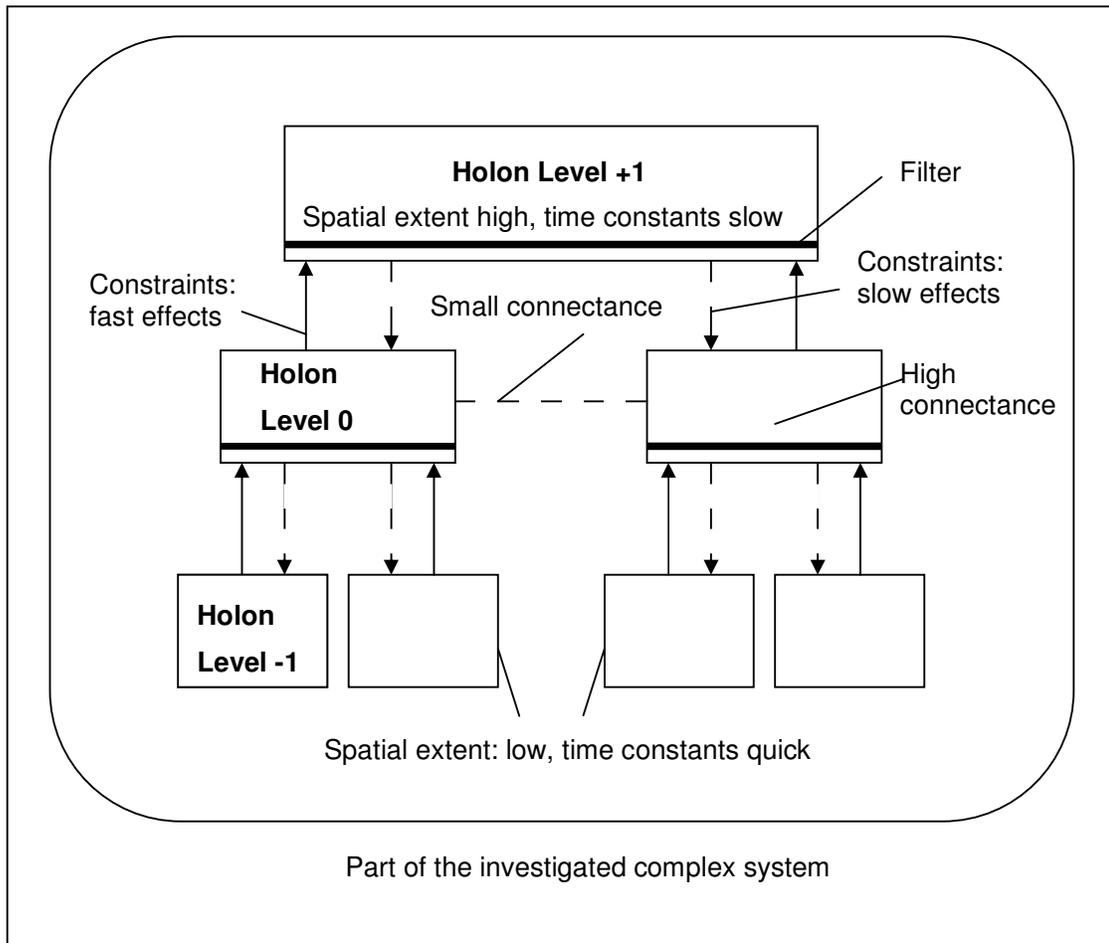
influence inferior subsystems (cf. pct. 6). One can distinguish between four criteria for the differentiation of the levels (Müller 1992, 221):

- a) The spatial extent of higher levels is broader than the extent of lower levels.
- b) Higher levels change more slowly than lower levels. The environment of a holon is the sum of outside influences with which it interacts and which behaves more slowly than the investigated holon itself.
- c) Higher levels control lower levels. They assert the physical, chemical and biological limits of the system of interest.¹¹⁷
- d) Higher levels can contain lower levels (nested hierarchy).

The status of a system at any level of resolution will be described by three different hierarchically ordered levels representing different forms of knowledge of the investigated system. There are processes at the level of observation (the focal level, the holon 0) which shall be explained. Ecologists often investigate the processes of underlying micro levels (holons of level -1) in order to understand the observation on the focal level. They also need a third level (holon +1) providing constraints for the integration of the other two levels (Tobias 1991). The higher levels define the overall envelope in which the ecological system may (re-) act e.g. the degree of nutrient recycling while the lower ones (e.g. the level of populations) represent the biological potential and exhibit much faster changes in space and time. This has been experimentally demonstrated (Gaedke et al. 1996).

Hierarchical systems can be described by means of structural or behavioral interconnections, wherein higher levels constrain lower ones and vice versa. The lower ones can be parts of the higher ones; in this case, one can talk of a nested hierarchy. One important feature of hierarchies is the fact that separate levels seem to have distinctive cycle times for the recurrence of events (e.g. nitrogen cycles). Cycle times are therefore a guide demonstrating how to separate levels in a hierarchy, measured in terms of direction and rate of information flow between the levels. The information flows are asymmetrically between higher and lower levels. Thus, higher levels of a system provide a relatively stable environment within which endogenous behavior of lower levels occur without destabilizing higher levels, but lower levels still exert important constraints on higher ones (Depew & Weber 1984, 234f.).

¹¹⁷ This need not to be understood in the sense of downward causation, but rather in a way that some constraints on a higher hierarchy impede some functions on a lower one. Thus, the growth of the population is influenced by the interactions of the whole community.



Picture 6: Some principles of hierarchical structures according to the "hierarchy theory" (after Müller 1992, 224). Level 0 is the level of observation which has to be explained. For further explanation see text.

"Hierarchy theory" is assumed to be the precondition for a new program of research that can lead to a unification of ecology and help to establish an ecological terminology that corresponds to the development of other natural sciences (Wiegand 1996, 20). "Hierarchy theory" wants to be neutral in relation to holism and reductionism. There is no basic level of research; ecological systems are rather investigated on very different levels. The focal level of investigation (Holon 0, cf. pct. 6) can be at any scale. Proponents do not talk of levels of integration or organization but only of levels of observation. Hierarchy theorists often reject the reductionistic program in favor of hierarchical ones. However, there is no contradiction. The preference of hierarchical

views does not deny the fact that higher levels depend on lower ones.¹¹⁸ From a pragmatic point of view, complex systems can be regarded as more than the sum of their parts. It is no trivial task to infer the properties of the whole from the properties of the parts and their laws of interaction. In face of complexity, an in-principle reductionistic may be at the same time a pragmatic holist (Simon 1969, 86).

The tasks of “hierarchy theory” are diverse. It seems to be a panacea for most of the problems in ecosystems ecology. Allegedly, it can be combined with cybernetics, thermodynamics, the concept of self-organization and emergence, it provides applications of chaos and catastrophe theory, it has been adapted to the concepts of evolution, trophic levels, and stability. “Hierarchy theory” also has the task to combine and integrate the top-down and the bottom-up- approach and as well holistic and reductionistic approaches. That is why it provides tools for integration and unification (Müller 1992).¹¹⁹ Several authors consider the application of “hierarchy theory” to be a means to come to a unified ecology (Wiegleb 1996, Müller 1992, Allen & Hoekstra 1992).

Proponents of “hierarchy theory” want to come to a unified approach of ecology by means of a common method (the investigation of holons on a variety of ecological levels). Although it has been claimed that population ecological and evolutionary approaches can be integrated into “hierarchy theory”, I do not think that this unifying program can be successful. It can only lead to a methodological unity in that every ecological level is considered under the aspect of the concept of the holon. In this case, there is nothing new in “hierarchy theory” compared to the traditional approach of systems ecology that wanted to model every system by means of energy and material cycles. “Hierarchy theory” seems to look for relationships of a functional sort and is interested in flows of matter and energy (cf. Allen & Hoekstra 1992, 10f.). Like systems ecology, “hierarchy theory” tries to come to a unity by means of analogical thinking. On the one hand, it is claimed that alleged ecosystem properties like stability and resiliency can be found in every ecosystem; on the other hand, it is assumed that every ecosystem can be described as construed by holons. Both forms aim at a

¹¹⁸ But the form of dependence is not obvious; often it is assumed that higher levels cannot be reduced to lower ones (e.g. Depew & Weber 1985, 234f.).

¹¹⁹ By this collection, one can see that the conception of “hierarchy theory” is sometimes very vague and that it is very difficult to find its theoretical core (in case there is any, probably there is none). I have the impression that everything in ecology that has to deal with hierarchies is integrated in “hierarchy theory”.

methodological unity but will not tell us too much about why nature is structured hierarchically.

In this rough characterization of the hierarchical approach to complex systems, many questions arise. It is claimed that “hierarchy theory” will lead to a new conception of ecological hierarchy, but it is difficult to find applications of hierarchy which will designate new concrete ecological levels. The hierarchical concept of ecosystems provides some similarities to the Odumian concept. It is applicable to systems of any size, but, in contrast, it pleads not to be interested in reductionism or holism. Here again, reductionism only refers to the level of investigation. Thus, “hierarchy theory” in ecology demands for a methodological pluralism in that one has to investigate several interdepending hierarchical levels in order to explain the level of observation. Probably, a form of ontological reductionism, pointing out that the behavior of complex systems can be explained by the properties of their components, will be accepted by proponents of this form of systems theory although proponents are not interested in this kind of question.

Thus, proponents of “hierarchy theory” may be as well proponents of an ontological reductionism, although most “hierarchy theorists” will not accept this. They are methodological reductionists because they want to explain every ecological system by as structured by holons. However, one can consider them as well as methodological antireductionists in that they want to investigate and explain on different levels. This is the interpretation ecologists would favor.

If one wants to arrive at a unity which is more interested in the ontological questions whether nature really provides the structures that are described by means of ecosystem models and hierarchical accounts, one has to take another approach. If one wants to understand why ecologists have to deal with hierarchical systems one has to consider evolutionary theory. The hierarchical structure of ecological systems can only be explained by means of an evolutionary and historical account which has to be integrated into ecology. That is why I want to investigate the relations between evolution and ecology by developing an evolutionary ecology which is able to unify the diversity of ecological objects and as well the different ecological approaches. This framework will be elaborated in the last sections of this book.

4.3 Evolutionary Theory and Ecology

I have demonstrated that the approach of population ecology tries to establish unifying explanations in ecology by reducing the existence of complex ecological entities and processes to the composing parts and their properties. Proponents of population ecology in general assume the possibility of an ontological reduction and try to explain complex systems by means of its composing parts. They also adopt a methodological pluralism in that they claim that, although everything can be explained reductionistically one can also find some useful and unifying explanations on higher levels. Systems ecology has wanted to be holistic and claimed that it was not possible to reduce the properties of complex systems to their parts and their properties. Proponents have been looking at ways to describe and analyze whole systems and regarded reductionistic ways of explaining as futile. Contemporary systems ecologists try to describe and explain ecosystems and their behavior by means of analogies and “hierarchy theory”. They use a methodological pluralism performing investigations and explanations on several levels. Nevertheless, this way of research does not contradict an ontological reductionism either.

Both forms will not come to a unified account of ecology although they are (more or less) successful with regard to a unification of their own approach. Systems ecology is able to show that many ecological systems can be only modeled and analyzed by systems analysis and investigating functions. Proponents try to understand ecosystems by means of analogies and by looking at the interactions of different hierarchical levels and their dependencies of quite different systems. By doing so, systems ecology can come to a unified way of description using structural generalizations. However, these explanations do not tell us too much about basic material parts and their mechanisms. Population ecology is not able to show that properties of complex systems can always be explained by the behavior of their parts and systems ecology cannot demonstrate that an ontological reductionism is unjustified. Since we have to deal with contingencies and changes of function in the course of evolution, it is impossible to find general fundamental laws and the population ecology approach cannot arrive at a unified explanation by means of fundamental ecological laws. Thus, both forms of unifying explanations will not arrive at a unity based on fundamental (material) ecological processes.

Now I want to investigate which form of unity can be provided by evolutionary ecology and I will discuss the relations between evolutionary ecology, systems ecology and

population ecology. If one wants to arrive at a unified ecology which does not only provide a unity by means of structural laws and unified methods of investigation and explanation but also by material units, one has to take evolutionary thinking into account. Ecological diversity and ecological relations will only be understood if one goes back in the history of nature and looks at contemporary complex systems, tracing their history. That means, evolutionary ecology cannot start with an explanation of the species or the genes, because it is impossible to go back in time as far that. It has to be concerned with co-evolutionary units, this means simple systems with co-evolving species. Without going too deeply into the debate on the unit of selection, it is obvious that there are evolutionary units like parasite-host or pollinator systems which evolve together. These are the objects which should be investigated by evolutionary ecology and which will show why systems ecology, population ecology and evolutionary ecology are necessary to arrive at a complete understanding of nature. In the following sections, I want to develop a framework for an evolutionary ecology which can establish this unity. I will first describe several approaches dealing with the close relationships of evolutionary and ecological problems before developing my own account in the last section.

4.3.1 The Role of Historical Thinking in Ecology

The discipline of evolutionary theory is central to all biological disciplines and can be considered the theoretical grist of biology. Even if we are unable to find lawlike statements in evolutionary theory, at least not according to the empiricist's notion, no biologist will deny the strong explanatory power of evolutionary theory (cf. Brandon 1996). Although there are limitations in the explanatory scope of evolutionary theory, the scope of natural selections applicability is not threatened (cf. Reed 1981, 67). Accordingly, it is obvious that the theory of evolution must also play an important part in ecological theory. The functional or proximate account of systems and population ecology cannot provide a general theory of ecology, they should be rather considered as research techniques than as unifying theories (cf. Orians 1962, 261). Ecologists have to apply the theory of natural selection, because it is a fundamental unifying theory of life and its diversity. A thorough knowledge of evolutionary theory is essential for an understanding of modern ecology (cf. Pianka 1978, 9).

Evolutionary ecology was self-consciously defined in the 1960s, largely by raising new questions. Williams (1966) wanted to understand ecological issues by means of a

genetic framework. This way of thinking was adopted by population ecologists and resulted in the emergence of evolutionary ecology as a new approach of population ecology which tried to explain ecological phenomena in terms of genetic changes and adaptations to the environment (cf. section 2.2.4). The strong emphasis on genetic explanations in evolutionary ecology has led to the still debated question, whether the field of evolutionary ecology is coincident with that of population genetics. This connection between evolutionary thinking, population genetics, ecology and the reductionistic form of explanation is one reason why ecosystems ecology has hardly been influenced by evolutionary thinking.

Evolutionary theory does not only investigate genetic mechanisms but also the genesis of the diversity of life as a historical process. Evolutionary ecology only seems to use the first strand of evolutionary theory. Proponents of evolutionary ecology tend to be as ahistorical as proponents of population or systems orientated approaches. Although they not only try to answer how-questions but as well why-questions, they do not take the historical aspect of evolution into account (cf. Futuyma 1986, 312). Thus, the occurrence of a species in a community will be explained by genetic mechanisms which will lead to specific adaptations. Evolutionary ecologists explain the reproduction cycles of a mouse, a bee and a bird as adaptations that helped the investigated organisms to better survive. The history of how specific traits have developed is not taken into consideration. Evolutionary ecology provides explanations for the fact that a specific trait which has been observed occurs by means of fitness advantages but they do not look at the history of this trait (e.g. by examining paleontological discoveries).

One could argue that it does not matter whether one uses proximate (functional causes explaining how specific processes run) or ultimate (evolutionary and historical causes explaining why specific processes occur the way they do) explanations in ecology. One can assume that the forces driving natural selection in evolutionary time (ultimate causes) are the same which have been responsible for demographic changes in ecological time (proximate ones) (e.g. Cooper 1993). If one accepts this, evolutionary ecology belongs to population ecology. It does not only try to explain the properties of complex systems by its individual parts (populations and individuals) but by their genetic components and molecular mechanisms. Thus, population genetics forms an integral part of evolutionary ecology and evolutionary ecology can be considered the most reductionistic form of explanation in ecology.

Evolutionary ecology would correspond to population genetics if proximate and ultimate causes were the same. Because of the contingent character of evolutionary results, this assumption is only partly true. Since evolution can change the ecological regularities so that contemporary patterns would not again evolve under the same initial conditions, it is not correct to consider ultimate and proximate causes to be the same. Contemporary ecological processes are in many ways very similar to evolutionary ones, but they are not the same. The existence of contingency stresses the importance of integrating historical aspects into evolutionary and ecological explanations.

Although the significance of history for evolutionary and ecological explanations seems to be obvious, the historical aspect is mostly neglected in ecology. The equilibrium theory of island biogeography is a typical form of an ahistorical ecological theory. Many difficulties in this theory arise, because it neglects history and contingency of evolutionary processes. One thread to this program is the sensitivity of community structure to small variations in the factors that impinge on it.¹²⁰ They may change the further process of colonization. An important historical factor is the order of the colonist's arrival. Thus, the Tasmanian fauna would have evolved differently if the order of colonization had been different. If a particular species composition is characteristic for an ecological community, then history will have to play a central part in the explanation of the structure and the development of the community (cf. Sterelny et al. 1999, 259f.). Here, one has to take as well geological constraints into account, e.g. the movement of continents and the distribution of marsupials.

All this demonstrates the importance of historical thinking for ecology. If evolutionary ecology adopts this way of thinking, it will not only be a part of population ecology but an approach of its own. This form of evolutionary ecology can bring a new form of unifying explanation into ecology. At first, this seems to be a little bit strange. History is normally combined with contingency and the investigation of single objects and thus, it contradicts the notion of general theories. Another aspect which makes unification even more difficult is that one cannot explain every trait produced by evolution by means of an adaptation but one has to consider specific constraints in evolution that may lead to traits which are not adaptations but occurred according to specific historical constraints (cf. Gould & Lewontin 1979). In spite of this, I want to demonstrate that historical

¹²⁰ One thus can imagine that an earthquake, a thunderstorm or other singular events will influence the order of colonization and thereby the composition of the community.

thinking in evolutionary ecology can lead to a unification of the entire field of ecology (cf. section 4.3.5). Before starting with this, I will have a closer look at the relations between ecology and evolution by examining the intersections of evolutionary hierarchies and the evolution of complex systems.

4.3.2 Ecological and Evolutionary Hierarchies

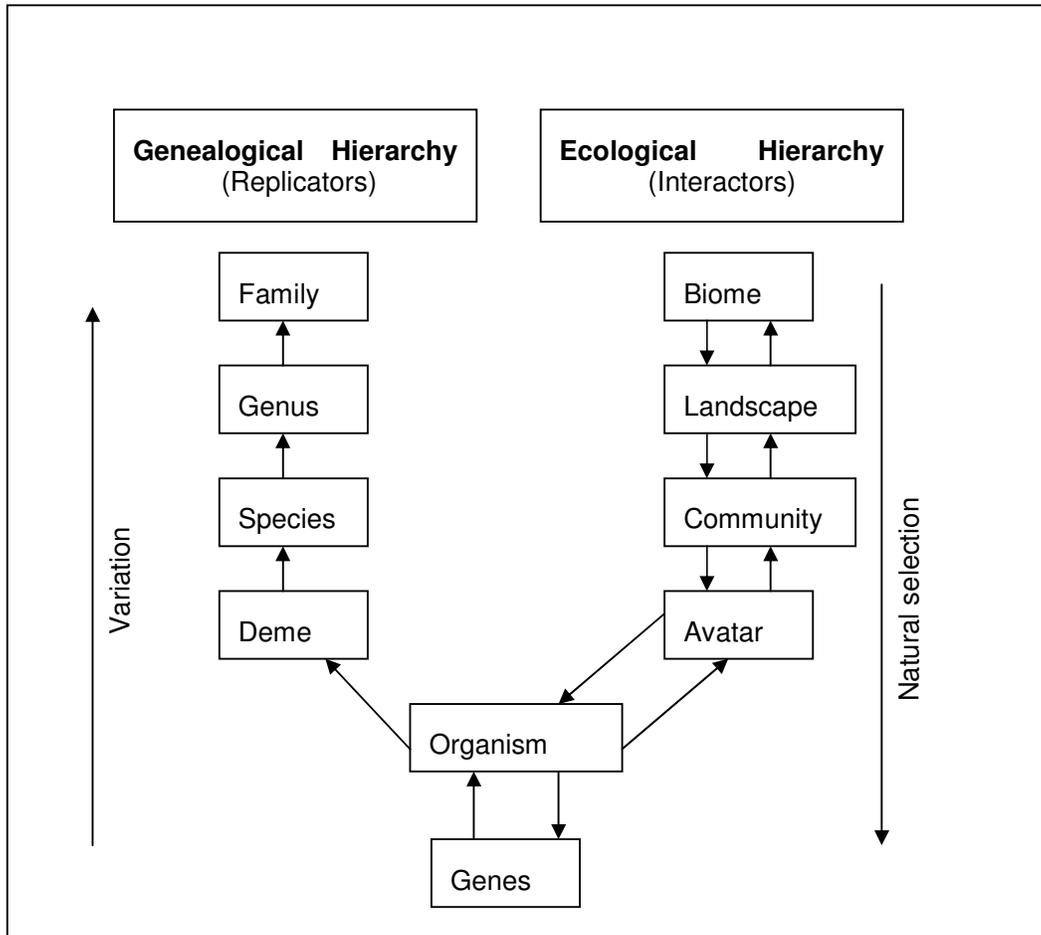
Hierarchies have always played an important role in biology. As already demonstrated, there are different conceptions of biological hierarchies. Most biologists will accept the levels of cell, tissue and organism but above the organism, one can distinguish between several different hierarchical orders. There is the phylogenetic or evolutionary hierarchy (organism, population, species, genus, family, order etc, cf. footnote 90), an ecological hierarchy considering biotic interactions (population, community) and an ecological hierarchy considering abiotic interactions (ecosystem, biosphere) (Mac Mahon et al. 1978). Other conceptions of supra-individual hierarchies distinguish between biotic and abiotic ecological hierarchies that can be unified to a single hierarchy by "hierarchy theory" or between evolutionary and ecological hierarchies (Eldredge et al. 1984). There have been attempts to arrive at a single hierarchy by combining the different notions (Cousins 1988).

In the previous chapter, I demonstrated that it is possible to develop a single ecological hierarchy by already integrating abiotic factors to the system of organism. The difference of biotic and abiotic hierarchical levels in ecology will thus vanish and the following hierarchical levels are the result: organism, population, community, landscape, biome, and biosphere. By now, one must distinguish between ecological and evolutionary hierarchies. One can thus talk of a genealogical (evolutionary) and an ecological hierarchy (cf. Eldredge & Salthe 1984; Salthe 1985, Eldredge 1998, 161f.). The first is composed of phylogenetically related entities. All the members of a family can be "reduced" by the genealogical strand their ancestral units. In this hierarchy, one has the genes, the individual, the population, the species, the genus etc. All the members of this hierarchy evolved from one basic unit. There has been a basic form of passerine bird and every member of this family can be "reduced" by evolutionary history to this basic form.

The ecological hierarchy is composed of levels characterized by interacting units which are not taxonomically related. In this hierarchy, we have individual organisms, the

population, the community¹²¹ etc. One should distinguish between the populations of the ecological and the genealogical hierarchy, because not every member of the ecological population is as well a member of the genealogical population. Every member of a local group of species has an ecological function (production and consumption of energy and matter, etc) but not every member of this group has a function of reproduction. Thus, one can distinguish between *avatars* as ecological populations and *demes*, the local breeding populations, being a unit of reproduction (Eldredge 1998, 163). Both forms of hierarchies are intersecting on the level of organism. Genetic mutations will cause changes in the phenotypic appearance of the organism and this will lead to a change of their ecological properties. Natural selection works via ecological relations in communities and populations, thus only specific organisms will survive. This form of selection will also result in a selection of genes. Thus, the ecological hierarchy is influenced by the genealogical and vice versa; as one can see in the following picture:

¹²¹ Actually, one should consider different levels of communities since this term designated a lot of different co-occurring and interacting species at any scale. A big community can thus encompass a small one (cf. section 3.2.1.1).



Picture 7: The ecological and the genealogical hierarchy (after Eldredge 1998, 166, strongly changed). The levels of different hierarchies above the population level have no direct connection and cannot be combined with each other.

Now, I want to have a somewhat closer look at evolutionary theory in order to get a clearer picture of the relations between ecological and evolutionary levels. In evolutionary theory, one distinguishes between replicators and interactors. Replicators are everything in the universe of which copies are made; interactors are entities interacting as a cohesive whole with its environment in a way that replication is differential. There are cases where replicators and interactors are the same objects (e.g. free RNA) but, in most cases, one can clearly distinguish between both of them (cf. Brandon 1990, 80f.).¹²²

The principle of natural selection can be expressed in various ways. Here, I will follow the suggestion of Brandon (1990, 97):

¹²² The distinction between replicator and interactor roughly corresponds to the known terms of genotype and phenotype. The new terms are better, because they can not only be applied to organisms, but to every form of life (e.g. bacteria, virus or even population and community in case on accepts group selection).

Natural Selection occurs at a given level iff

there is differential reproduction among the entities at that level, and
the interactors of the entities at that level screen off properties of entities
at every other level from reproductive values at the given level.

One can assume the existence of a hierarchy of interactors by presupposing this definition of natural selection. However, it is not obvious, whether there are levels of interactors above the level of the individual organism. There is the possibility of group selection, yet it is not clear on which levels it may occur.

Interactors correspond to the ecological hierarchy and replicators to the genealogical hierarchy. They must have some nodes of connection, because all biological and ecological entities are also a product of evolution. One can find various ways to connect ecological aspects directly with evolutionary ones. One is by means of ecological niches to which species are adapted by evolutionary processes, another connection can be found in the notion of co-evolution, where adaptive changes in one species influence evolutionary changes of other species. In this case, the link between ecology and evolution is obvious: most adaptations caused by genetic changes are not about reproduction, they are rather concerned with energetics by optimizing the ability to obtain food etc (Eldredge 1998, 145). The phenotypic properties which changed according to genetic variations will lead to a change of the ecological relations and an alteration in the ecological hierarchy may again have an effect on the replicators. Only those replicators which are selected by the various ecological interactions can reproduce. The selection of the replicator seems always to occur via an individual organism and not by means of group selection (cf. pct. 7).

In any case, the connection between ecology and evolution occurs at the level of the organism. Whether it can also occur on higher ecological levels remains to be investigated. However, probably it will not occur on higher genealogical levels than the deme (population) because these levels do not have any ecological meaning.¹²³ The levels of ecology and evolution are at least tightly connected up to the level of the population. Thus, genealogical levels above the population level do not seem to have

¹²³ Although ecologists often talk of species, it is not the species as species that has ecological significance but „species“ is used as a short form for individual members of the species and, in this case, the level of „species“ is below the level of population. If one conceives of species as all individual members belonging to one species, it encompasses several populations which may live in very different ecological surroundings. In this case, „species“ does not have any ecological significance. The principle of competitive exclusion is mostly valid for populations only and not for all the members of the species, because different populations of the same species may live in slightly different niches.

any ecological relevance. Individual organisms are obviously basic members of the two hierarchies.

4.3.3 Evolution and History of Complex Systems

There are obvious connections between the fields of evolution and ecology. On the one hand, ecological interactions lead to natural selection and adaptations; on the other hand, genetic variations influence ecological processes and form the precondition for adaptations. Thus, the theory of natural selection cannot be thought of without ecological processes which will lead to selection and ecological objects depend on genetic changes and adaptation. Evolutionary and ecological processes are so tightly interwoven that it is difficult to separate them. It is impossible to understand and explain natural diversity and ecological processes by considering one aspect only.¹²⁴

There are several suggestions of how ecological units could have been evolved, but only some which want to combine complex ecological systems with evolutionary theory. An early version was already provided by Lotka (1925). He wanted to understand all biological processes by means of reducing them to the exchanges of matter and energy. He regarded biological processes as governed by the laws of thermodynamics and considered evolution to be the overall accumulation and distribution of energy within a system. He had a strong influence on Odum, who tried to combine systems ecology with evolution (cf. Hagen 1992, 125f.).

Eugene Odum wrote a seminal paper, trying to combine ecosystems theory and evolution. In the "Strategy of Ecosystem Development" (1969), he wanted to demonstrate how ecosystems maximize their stability (Odum 1969). He conceived of ecosystem development as a mixture between group selection and co-evolution. The paper of Odum has been widely cited but it was not accepted by biologists thinking in terms of natural selection. In the beginning of the seventies, proponents of evolutionary theory believed natural selection to be operating upon individuals and not upon groups or even bigger unity like ecosystems. Ecosystems could not have strategies, not even metaphorically. These differences led to a splitting of approaches in ecology (cf. section 2.2). Although ecosystems obviously had something to do with evolution, it could not have been the way Odum suggested. Since it was possible to perform some interesting research on ecosystems without mentioning evolution, the topic of evolution

¹²⁴ There are good reasons to regard the theory of evolution by natural selection as an ecological theory based on ecological observations by Charles Darwin (cf. Harper 1967, 247).

was avoided by the majority of systems ecologists. Odum's hope that ecosystems ecology could become the unifying theory for all ecologists failed and the discipline was becoming increasingly divided (cf. Hagen 1992, 144f.). On the one hand, population ecologists have investigated the evolution of individuals; on the other hand, the proponents of systems ecology have been interested in the development of systems. Evolutionary thinking of the population ecologists became mainstream and the approach of evolutionary ecology became a new ecological field. Proponents of systems ecology emphasized the significance of contemporary functions by neglecting the question of evolution and history of ecosystems. They drew back from evolutionary explanations and wanted to explain ecosystem processes by means of proximate causes only. Thus, ecosystem ecology became explicitly non-evolutionary.

However, obviously the evolution of species cannot proceed in an ecological vacuum. It is not worth investigating e.g. the evolution of a specific flower without its pollinator or a parasite without its host. One actually should involve the evolution of an entire group of species forming a chain of interactions within its environmental context. Thus, the suggestion has been made that the ecosystem is not only the basic functional unit of ecology but also the basic unit of selection (Darnell 1970, 14). Sometimes it is even argued that ecological systems were prior to the development of species that evolve as parts of the systems. These conceptions show some similarities to the thermodynamical concept of Lotka (1925). Natural selection is considered an emergent property of chemically selecting, autocatalytic and entropy-dissipating systems. The entire evolution can be considered co-evolution and fitness has to be considered with reference to the role of every population by sustaining the maximum of energy flow through the whole system (Weber & Depew 1996). However, it is hardly imaginable that and how whole systems evolved. Ecosystem properties cannot be optimized by natural selection because it is not a superorganism (cf. Sommer 1996, 149). It seems much more probable that the individual selection of species has led to a stable system (e.g. a specific plant-pollinator-system) which has formed a new unit of selection. This unit can be regarded as a basic subsystem of contemporary ecosystems. This conception seems to be more convincing and in concordance with contemporary ideas of evolution than the assumption that there are large systems in which the evolution of species takes place.

At present, evolutionary theory is hardly an integral part of systems ecology or ecosystem modeling. Although systems ecologists assume that evolution will provide

mutual adaptation of species to form functionally integrated ecosystems and that ecosystems consist of historically developed individual parts (cf. Breckling & Müller 1996, 24), questions of evolution and history of ecosystems are not in the focus of interest. However, one can still find some ecologists interested in a connection between evolutionary theory and ecosystems research. They have assumed that evolution would provide a mutual adaptation of species to form whole ecosystems which will be organized and functionally integrated, if there is sufficient time (e.g. Patten & Odum 1981; Odum & Biever 1984). Although it is improbable that complex ecosystems evolve as units, the acceptance of group selection has again grown during the last few years. It is thus often assumed that there is no single level of selection but various. Selection will operate wherever the conditions of variation, heritability and fitness differences are satisfied. However, the constraints restricting the operation and power of selection above the level of the individual are not yet understood and have to be investigated (Cockburn 1991, 82f.).

The individual's fitness is determined largely by the interactions with other members of the population and the community. These interactions can be referred to as ecosystem functions in case one does not only consider biotic but also abiotic factors. Some of these functions may be explained by forms of group selection (cf. Wilson 1988). If there are cases, where group selection can be confirmed, an explanation of the evolution of ecosystems by means of group selection might reconcile evolutionary ecology and systems ecology. However, at present, this goal is a distant prospect (cf. Hagen 1992, 196), and there are only few cases, in which group selection seems to be probable.

I think that the investigation of group selection is a good way to come to a unifying explanation in ecology which will help to explain the existence of complex ecological systems and their properties. But I do not want to talk of *group selection* because this term has so many meanings, I will rather have a look at some forms of co-evolution which may lead to the same effects as group selection but which is undoubtedly in accordance with the theory of individual selection. Co-evolution, as will be outlined in the following section, sometimes takes the form of a very close evolution of species which can be considered to be a unit of selection.

4.3.4 The Role of Co-Evolution

Evolutionary consequences of species interaction are often referred to as *co-evolution*. There is a variety of forms of co-evolution. *Diffuse* co-evolution occurs due to weak

interactions of species. It has much in common with adaptations to the abiotic environment (Fenchel 1987, 107f.). Diffuse co-evolution typically takes place in guilds whose members use the same or similar resources. One can find many examples for this form of co-evolution, e.g. pollinator systems: plants depend on animals that distribute their pollen and the animals depend on the plants as feeding resources. In most cases, the pollinators (e.g. insects, bats) not need to be very specialized, many species of insects can pollinate the same plant species and many different plant species can be pollinated by the same insect. In this case, the bonds between the species are not very strong and if one pollinator becomes extinct, there will be enough other species which can take over its role.

One assumes an “arms race” between herbivorous insects and plants that has resulted in co-evolution. Nearly all plants are preyed by insects which led to adaptations in plants to reduce herbivory. Thus, plants grew thorns or hair but as well toxic compounds which impede insects to feed on them. Insects, however, developed traits by the help of which they were able to cope with thorns, hair and poison. Some species of insects are better adapted to thorns others to poison. Sometimes this arms race did not only lead to diffuse co-evolution but also to host specificity. Thus, the members of the plant family *Apiaceae* produce furanocumarins which are toxic for most insects. Nevertheless, the caterpillars of the family of *Papilionidae* can live on *Apiaceae*. Apparently, this family of butterflies has developed some mechanism with which it is able to cope with the toxic furanocumarins of the *Apiaceae*. Sometimes the butterflies are not only tolerant but they use the toxic substances as protection against predators. In this case, there is a specific bond between host and predator. One can also find similar examples in other families (cf. Fenchel 1987, 109).

Apparently, one can distinguish between ecological relations with relatively loose bonds like guilds of birds using the same resource and specific pollinator systems. In the case of a guild, one can remove one of these species and the others will broaden their niches. The guild will change but this change can be explained very well by means of individual selection and competitive interaction. A good example is the evolution of the Darwin’s Finches. These finches are endemic species of the Galapagos Isles that means that they do not occur on any other place of the world. It is assumed that the ancestor of these forms came to these islands from South America. The finches have occupied a variety of different ecological niches due to *character*

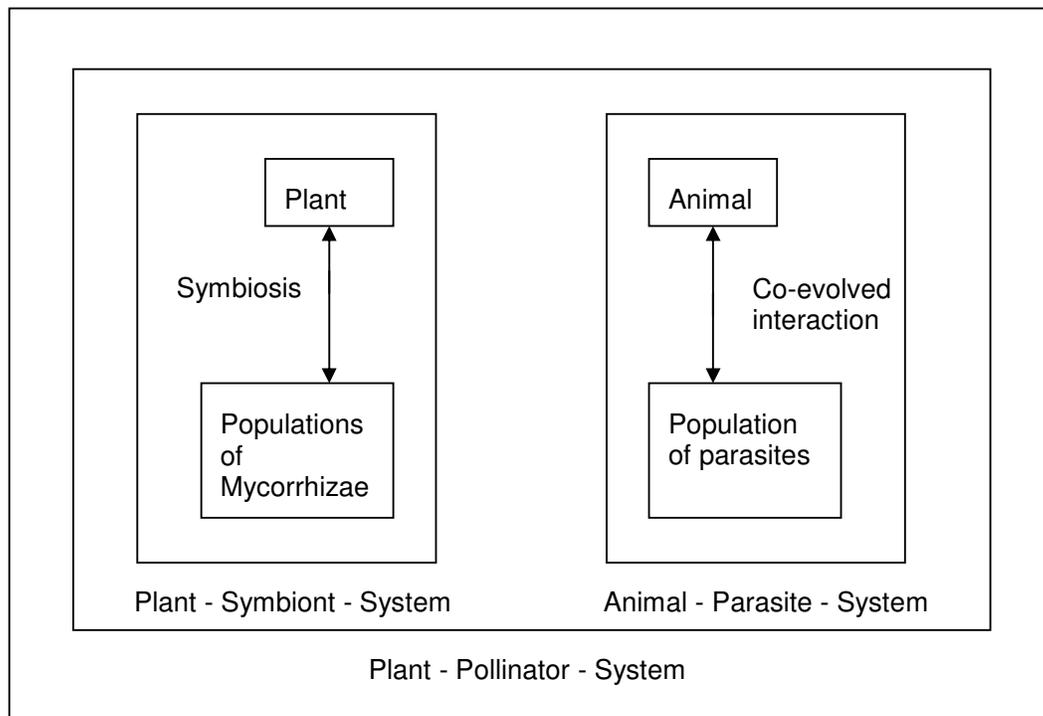
*displacement*¹²⁵ in the form of their beaks. It is difficult to imagine that the ecological and morphological divergences did not result from co-evolution of competing species. The Darwin's Finches represent the best thoroughly studied and best documented example of co-evolution by means of exploitation competition (cf. Fenchel 1987, 115f.). In accurate studies, it could be demonstrated that the genetically determined beak dimensions correlate with the type of food (Grant 1986) and that interspecific competition has forced the birds to use new resources of food.

However, other forms of co-evolution are more interesting for the question of unity in ecology. One can find strong bonds between one species of plant and one species of pollinator. This form of co-evolution is characterized by a specific reciprocal dependency and by permanent interactions. The dependency of these two species from each other can be so strong that the absence of one species will result in the death of the other and vice versa. These species can only occur and evolve together. In this case, the ecological unit characterized by its functional relationship will become as well an evolutionary unit and will be dealt with by selection like an organism. This unit may remain stable and behave like an organism in the proceeding evolutionary process. There is a quite well known example for this form of co-evolution which was already discovered by Darwin. From the extraordinarily long (30cm) tube of an orchid (*Angraecum sesquipedale*) in Madagascar, he concluded that there must be a hawk moth pollinator with a very long tongue and, after a while, this insect was indeed found. He proposed that orchids which compelled moths to probe the base of the tube would set more seed than those which were fertilized by moths with shorter tongues. Orchids with longer tubes will be selected by natural selection. This, in turn leads to a selection for longer tongues because the moths will only come to the plant if they reach the nectar. This Darwinian hypothesis could only recently be confirmed (cf. Cockburn 1991, 122f.).

There have only been few accurate investigations into the question of how evolutionary mechanisms and basic units might have come to build complex ecological systems. Evolutionary criteria have been used to determine groups of species showing stronger internal than external interactions to define hierarchies and aggregations. Groups of strong interactive, co-evolved species can be considered hierarchically organized

¹²⁵ In a guild there is a strong interspecific competition for similar resources. Thus, small differences in the form of the beak that allow the use of a slightly different food resource (e.g. long grain instead of short one) are selected by evolution. This selection for small differences of a specific trait will lead to *character displacement*.

subsystems within bigger ecological systems with weaker interactions. The following diagram demonstrates how strong systems of co-evolutionary relations can compose a bigger system with weaker bonds. Populations of mycorrhizae are in symbiosis with specific plants and form a plant-symbiosis system. This system will evolve as a unit and will interact with an animal-parasite system. Later in evolution, both forms were able to build a plant-pollinator system which includes the plant-symbiosis and the animal-parasite system. Evolutionary theory can thus help to establish a better understanding for the existence of ecological systems (cf. Loehle & Pechmann 1988).



Picture 8: Suggestion of how a complex Plant-Pollinator-System could have been developed from co-evolutionary systems (according to Loehle & Pechmann 1988, 893).

The diagram shows that strong co-evolutionary systems like the plant symbiont system may remain stable, can evolve as a unit and end as a subsystem of a contemporary ecosystem. Although one cannot decompose a complex contemporary system to its contemporary subsystems, it is highly probable that the complex system evolved from earlier stable subsystems by the historical process of evolution. These historical and evolutionary processes are to be investigated and explained by the evolutionary ecology I am suggesting. Now, I want to outline how this form of evolutionary ecology

can produce unifying explanations for the entire field of ecology and how it is possible to arrive at a unity of the discipline of ecology.

4.3.5 Evolutionary Ecology as a Tool for Unification

In this section, I want to outline a framework in order to arrive at unifying explanations in ecology. I will develop an evolutionary ecology that stresses the historical character of evolution and that has the possibility to establish unifying explanations by “reducing” the ecological diversity to basic material units. It has as well the possibility to combine the different approaches of ecology and thus to come to a unity of the discipline of ecology because it can show that the scientific results of the other approaches are necessary preconditions to establish the evolutionary explanations. In the following, I want to develop first the way of unification that can be provided by evolutionary ecology and then I will look at the status of the provided unity among the conceptions of unity in the philosophy of science.

4.3.5.1 Unification by Evolutionary Ecology

I demonstrated that the approaches of systems ecology and of evolutionary ecology are clearly separated and that there are only few attempts to reconcile them. The proximate explanations of systems ecology and population ecology are important and necessary starting points for the unifying explanations that can be provided by evolutionary ecology. Systems ecology and population ecology investigate the strength of ecological interactions. Since the ecological bonds of elements in a system show differences in their strength, one system may be much more stable than another. Strong reciprocal interactions of system components in most cases are a result of co-evolutionary processes and this co-evolution has led to the strong interactions of the contemporary system. Thus, one would come to a big achievement on the way to a more unified ecology if evolutionary and population ecologists showed more interest in systems ecology.

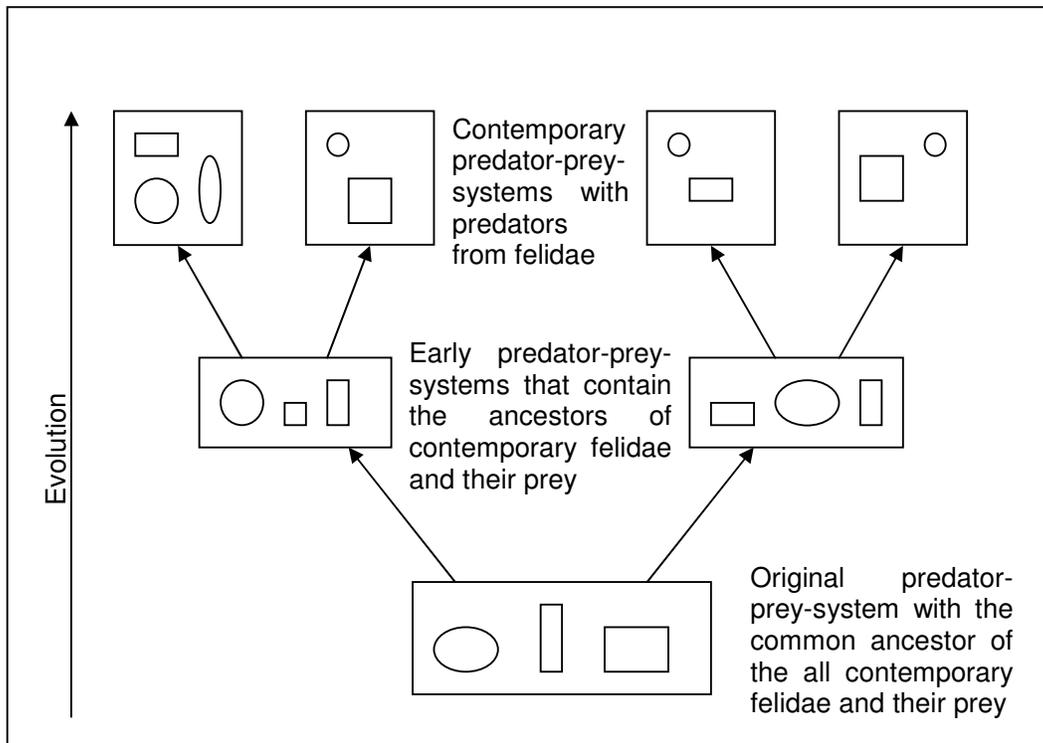
Proponents of systems ecology and population ecology are working with proximate explanations and they will not be able to explain *why* some ecological systems demonstrate strong reciprocal interdependencies whereas other ones just show weak interactions. Only evolutionary ecology can provide a why-explanation for this fact by investigating basic mechanisms and the evolutionary history of the systems involved. The usual form of evolutionary ecology can explain the interdependencies by means of advantageous adaptations of species. However, this is not sufficient. Not every

biological trait can be explained in terms of adaptation but as well by contingent historical conditions (Gould & Lewontin 1979), thus the historical process of evolution has to be investigated too. An explanation of why there are specific interrelations between system components is only possible by the investigation of the history of nature. Stable ecological systems (e.g. strong reciprocal pollinator systems) have evolved by co-evolutionary processes. In case the interactions are very strong, the participating elements may form a system so stable that it serves as a unit of selection and will continue to evolve as a unit. Thus, one can explain the existence of stable ecological systems by means of their co-evolutionary history.

This form of unifying explanation of evolutionary ecology faces the same problems as explanations in population ecology that try to reduce population phenomena to basic material units, their properties and interactions. It is only possible to provide accurate explanations for a specific population of community. One will not come to explanations of general population phenomena but to specific only. If one wants to explain general population or community phenomena, one has to use structural generalizations like the ones used in the equilibrium theory of island biogeography (cf. section 4.1.2). Evolutionary ecology can try to “reduce” contemporary ecological systems or parts of them to earlier forms of this system. Predator-prey-systems of a specific range (e.g. in the family of cats, see below) may have had a common ancestor in the history of evolution. Perhaps there have been co-evolutionary units from which the contemporary system evolved. The “ancestor systems” may be traced back to former ancestor systems. By this form of historical reconstruction, one may come to a basic system for a variety of contemporary similar ecological systems that evolved from this original unit. By means of paleontological, historical and genetic investigations, evolutionary ecology may show that contemporary population phenomena evolved from earlier ones and thus can be unified by means of basic material units and their properties.

One can arrive at unification by the historical method by both the diffuse and the strong form of co-evolution. At first, I want to give an example of diffuse co-evolution. The family of *felidae* (cats) belongs to the order of carnivora and they are considered a monophyletic group that means that all species of this family have one common ancestor. This ancestor probably was carnivorous and thus dependent on some prey species. There must have been an originally predator-prey system for all species of the family *felidae*. Although contemporary *felidae* live on a variety of prey (from mice to zebra), the different predator-prey interrelations in the family of *felidae* can be traced

back to an original system of the ancestor of *felidae* and some prey. In this case, one can talk of the evolution of a predator-prey system that proceeds along the evolution of the genealogical hierarchy of the family of *felidae*. Although the evolution of these co-evolutionary systems will lead to contingent results it is possible to come to a material (ontological) unity of population phenomena in the *felidae* by “reducing” them to original systems composed by the common ancestor of *felidae* and its prey. By a more accurate investigation of the evolutionary history of specific predator-prey systems one can reconstruct the genesis of diversity in contemporary ecological systems (e.g. all systems where species of the family of *felidae* are the predators). I want to demonstrate this suggestion by the following diagram:



Picture 9: Hypothetical and schematic evolution of predator-prey systems in the family of *felidae*. The rectangles represent members of the *felidae*, whereas the other forms represent their prey. Since these systems correspond to a weak form of co-evolution there are several possibilities which and how many species are preyed by species of *felidae*.

By looking at strong co-evolutionary processes this form of unification will be more successful. Candidates for strong co-evolution are specific plant-pollinator systems. A lot of empirical research is necessary to decide in which cases one can talk of strong

co-evolution and in which cases it is just an adaptation to specific resources like it is the case in the example of the *felidae*. The majority of ant-plant mutualisms evolve in response to selection, especially stress selection, on plants. The participating ant species respond to plant rewards on a facultative basis. Although strong co-evolution is reciprocal selection involving heritable traits it is remarkably difficult to demonstrate co-evolution as pattern in the evolution of ant-plant-mutualisms, this appears to be more the exception than the rule (Beattie 1985, 145). It seems that there is a gradual transition between diffuse and strong co-evolution and one needs extended research in this area to determine the degree of co-evolution.

A better example for the way of unification by means of strong co-evolution can be found in lichens. Lichens can be considered to be small ecosystems, associations with two or more components: an algal producer and a fungal consumer. From a taxonomist's point of view, lichens are a specialized form of fungi, like the ones that are forming mycorrhiza. The lichenization of fungi has evidently evolved independently in various non-related groups (Tehler 1996, 217). Thus lichens do not correspond to a monophyletic group of fungi. Fungus and algae live in such a close symbiosis that they were considered to be organisms for a long time by biologists. Neither the algae nor the fungus is able to live on their own. There is much speculation on the origin of lichens because there is a lack of fossils. Probably lichens were formed after a long development of their component parts, fungi and algae. Lichens are designed to live under harsh condition of sun, wind, snow and ice and the evolution of them started on places where only few other forms of life could survive. The most important factor enforcing the lichenization of fungal-algal organizations has probably been dryness (Ahmadjian 1967, 64). In this case, the ecological causes for evolutionary history become obvious.

Lichens correspond to a form of ecological system that evolved as a unit. One can consider them co-evolutionary units that will serve as a unit of selection as well. They are paradigmatic examples of how ecological systems can be unified by means of their basic parts.¹²⁶ Although they are the best example of an ecological system that can be considered a unit, it is no question that they developed via historical processes of evolution from its parts fungus and algae. Thus, they can be reduced to its elementary parts via tracing back evolutionary history.

¹²⁶ This is a form of unity because we do not need three different groups (fungus, algae and lichens) to deal with a specific part of nature but only two (fungus and lichen). This unity helps us to better understand the ecological diversity.

In case of diffuse co-evolution, one can replace species by other ones because the interactions are not very specific (for a lion it does not matter whether it will prey on a zebra or an antelope). This is different in case of strong co-evolution. A species only can be replaced by another one if some mechanisms of the bondage are changed too. Since this evolutionary change normally takes much more time than the time ecologists have to investigate their objects, it is surely justified to consider these entities to be more than just the sum of their parts. Although it is not possible to explain the complex system by their contemporary parts and their properties, one can establish reductionistic explanations of these complexes by considering the historical process of evolution which has begun by elementary parts and their properties. Complex and tightly interwoven systems evolved from distinct elementary units. We can understand contemporary system as composed by these elementary units via a long evolutionary process. It is not possible to separate fungus and algae of contemporary lichens, they are obligatorily bound and a reduction to its composing parts is not possible. One has to take the historical process of evolution into account and by tracing back the evolutionary history, one will be able to arrive at a form of "historical reduction" of complex systems to its basic parts.

Sometimes it is assumed that functional organizations at a given level can only be produced by natural selection operating at that level. If this is true, the adaptationist program cannot only be used for individuals but it can be applied as well to certain multi-species communities (cf. Wilson 1988). I do not think that this is true for every functional organization, but in the case of lichens one can accept strong co-evolution that has led to new units of selection and can be considered to be a form of group selection. The views of Clements and Odum that regarded communities (ecosystems) as forms of superorganism are not wrong but vastly overextended. The adaptationist program in some cases can be used as well for multi-species communities. For this, lichens are the best example.¹²⁷ The investigation of contemporary lichens has to be performed at the level of the lichen organization; otherwise, one will not understand its properties. This ecological system cannot be explained by the properties of its parts. It

¹²⁷ In a case like this the ecological interrelationship is in some way similar to the interactions of cells in an organism. They are not able to survive alone or to survive with other partners. That is why we can say that such strong ecological bonds can be considered to be a form of material unit. It would not be possible to survive for the individual species without the other one although these complexes are compositions from single species. One can imagine that the interactions of fungus and algae in the lichen organization will become even stronger and that lichens will become real organisms. One can find similar examples in the history of evolution. Thus one assumes that every cell evolved from former independent species of bacteria and protozoa that have evolved into a new unit.

has to be regarded as a unit. A reductionistic explanation by their parts and their properties can only be performed by tracing back the history of evolution and by reconstructing how and why the evolution of the co-occurring system components has proceeded.

The outlined framework is the form of unity that can be provided by my conception of evolutionary ecology. It can show why in some cases a reductionist population account is justified. In cases of communities with loose interactions e.g. the distribution of seeds by mammals feeding on plants one can explain the properties of the community (species number and distribution) and the seed distributing process by the properties of its participating species. In other cases, the account of systems ecology is justified and even required. Evolutionary ecology has the ability to combine both approaches and thus it will provide as well a unity of the discipline of ecology. It can explain how contemporary ecological systems developed from initial conditions and thus unify them by means of a “historical reduction” to their original parts. Nevertheless, this form of unification does not replace other approaches. Systems ecology and population ecology remain important approaches for general ecology. The results of their research are necessary preconditions for the account of explanation of evolutionary ecology.

This is only a rough characterization of the way how unifying explanations in ecology may be possible. I just provided a framework with which one may arrive at unity in ecology by means of basic material entities. The actual task has to be worked out by scientists, including behavioral biologists, paleontologists, molecular biologists, population and systems ecologists. The synthesis of these different methods will lead to explanations of evolutionary ecology and provide as well a synthesis of evolutionary theory and ecology.

4.3.5.2 *Philosophical Status of the Unity in Ecology*

The unification provided by evolutionary ecology cannot be regarded as a unified theory of ecology. There is no unique theory of evolutionary ecology that can explain every ecological phenomenon. Rather it is a family of reconstructions of evolutionary and ecological processes that can be traced back to the same origin. Thus, the unifying power of evolutionary ecology is not provided by its theories and accurate explanations but rather by theories and hypotheses that are not deductively closed and explanations that are often not very accurate but they increase our understanding. Since evolutionary ecology has to deal with historical processes, it can only provide how-possibly explanations and no how-actual ones.

This form of unification can be considered a mixture of the account of Friedman (1974) and a form of micro-reduction by including historical processes. Friedman's account requires that an explanation has to be sufficiently general, relatively objective and that it should somehow connect explanation and understanding. According to Friedman, the reduction of a multitude of unexplained phenomena to one or several other phenomena is the crucial characterization of scientific explanation. The increase in understanding of the world is given by the reduction of the total number of independent phenomena to simpler phenomena. A world containing fewer independent phenomena is more comprehensible than one with more. This form of explanation does not simply replace one phenomenon with another. The phenomenon will be replaced by a more comprehensive phenomenon and by this way, our understanding of the world increases (cf. Friedman 1974, 198).

This is the way of unification evolutionary ecology can provide. It explains contemporary ecological processes and their diversity by a "reduction" to earlier forms of the participating elements and their processes of interaction. It increases our understanding because we have to consider fewer elements (in case we go back far enough in the history, there will be no lichens but just fungi and algae) and our contemporary complexity can be explained by an earlier simplicity.

This form of explanation may be also considered a form of micro-reduction. This account of micro-reduction is quite different than the one constructed by Oppenheim & Putnam (1958). It is not interested in the reduction of theories and disciplines but rather in the historical reconstruction of complex systems and their properties. It is a reduction of contemporary systems to former systems and these former systems can be micro-reduced to an even earlier and simpler system. Although these former systems are not part of the contemporary existing ecosystem, they help to explain and to unify the diversity of contemporary systems. By tracing back the origins of complex contemporary systems to simpler systems of a time long ago, our understanding of ecological diversity will increase.

4.4 Conclusions

In this chapter, I have dealt with unifying concepts in ecology. I began by investigating forms of explanation in population ecology. In most cases, population ecologists provide proximate and structural explanations. This was demonstrated by the case studies of the Lotka-Volterra equations and the equilibrium theory of island

biogeography. Systems ecology is interested in functional generalizations and analogies. It also provides structural generalizations. Both approaches are unable to establish a way to unify ecology by means of generalizations and explanations that are based on basic ecological units. This form of unity can only be provided by considering evolutionary thinking.

That is why I examined the relationships between ecology and evolution. The role of historical thinking in evolution has been investigated and as well the nodes between evolutionary and ecological hierarchies. By this, it could be demonstrated that there are strong connections between ecological and evolutionary objects. Ecological interactions select the objects of evolution. The evolution of complex systems probably evolved via different forms of co-evolution. In case of strong co-evolution, ecological and evolutionary units can hardly be distinguished and they evolve as units. By this, it could be demonstrated that evolutionary ecology is able to arrive at a unity in and of ecology and makes natural diversity understandable. It is also able to unify the discipline of ecology because it needs the scientific results of other ecological approaches. Thus, I claim that ecology can be unified by means of evolutionary ecology via a specific form of ontological reductionism that takes the historical process of evolution into account.

5 Epilogue – Ecology as a Paradigmatic Scientific Discipline

In this epilogue, I want to characterize the status of ecology as a scientific discipline and compare it with other sciences. The previous chapters described many particular forms of theories and explanations in ecology. There are many differences to classical physics.¹²⁸ Although these differences are sometimes very distinct (e.g. the scope of application of material generalizations) the differences are only in degree and not absolute. The (material) generalizations of physics and even of genetics are much better applicable than the generalizations of ecology. The objects of research in physics and genetics are not as diverse and complex as the ecological ones. Both, physics and ecology use *ceteris paribus* clauses but they can be much better applied in physics. In ecology, the condition of all else being equal is only rarely realized. For this reasons it is hardly possible to compare a general principle of ecology with a law in physics.

Physics is often considered the paradigmatic scientific discipline. The differences in theory in ecology and physics are regarded as deficiencies of ecology. Thus, ecology is viewed as an immature or even anomalous science (Hagen 1989, Peters 1991). For this reason, the aim of many ecologists has been to make ecology a hard science, and „physics envy“ seemed to be a strong motivation for ecologists to mathematize and idealize ecological theories. However, the differences between physics and ecology (or biology in general) should not be embarrassing but interesting. A positive acceptance of the differences may give new insights in the different disciplines and their research objects (cf. Beatty 1980, 413). They may also lead to new insight in the structure of science.

We have seen that there are no material laws in ecology. This is due to the contingent results of evolution and to the fact that evolution selects for functions. Thus, one can only find structural laws in ecology. That is why the “immaturity” of ecology is not a problem of this scientific discipline but it has to appear according to the structure of biological nature. Therefore, *immaturity* and *anomaly* are the wrong terms to describe

¹²⁸ I am thinking of classical physical disciplines like mechanics and electrodynamics. As will be demonstrated in the following, there are some modern disciplines of physics that show much more similarities to ecology.

the differences between ecology and physics. If we accept this, then there are several possible relations between ecology and physics.

One assumption is that ecological explanations and generalizations have different structures than physical ones. Ecological objects consist of a diversity of forms and processes that cannot be reduced to physical elements and their properties and ecological models and theories are not reducible to physical laws and theories. In this case, we have a pluralist picture of sciences and special sciences like biology and its discipline ecology are autonomous disciplines.

Another possibility would include the following: Ecological explanations and generalizations have different structures than physical ones. Yet one can talk of a unity of science because the fundamental laws of physics are valid for ecology too. However, these laws do not say anything about specific ecological complexes and processes. This means that biology and the sub-discipline of ecology can be reduced to physics in principle (ontological reductionism) but that nobody will be interested in explaining ecological phenomena by means of basic physical units and the laws describing their behavior. From an ontological point of view, the unity of science could be reached by means of fundamental (material) laws of physics. Nevertheless, these laws do not have any special meaning for specific biological questions.

Both possibilities do not correspond very well to the outlined framework of unified explanation in ecology. How is it possible to integrate the developed framework for the unity of ecology into a broad concept of science? In physics, this form of explanation does not play an important role, because physical disciplines usually do not care about evolution and history. In ecology, we only have the possibility to trace back specific traits to a former state of evolution and trace back this state to its origin. However, this way will often stop at a certain level because it will become more and more difficult to reconstruct earlier steps. One could imagine that the biological evolution can be explained by means of (yet not found) fundamental physical laws but I do not think that this will work. Far more interesting is the idea that the mentioned way of explaining and unifying in ecology can be transferred to physics. The physical world is also in a process of history (cosmogony) that can be explained by causal mechanisms and steps of evolution. Now one can assume that there are no fundamental (material) laws of nature at all and that the generalizations commonly referred to as fundamental laws of nature have only validity for a special period in space and time. This means that the evolution of the cosmos is based on contingent processes as well.

By assuming that there are no fundamental laws in physics, the differences between the structure of physical and ecological theories will decrease. The contingency of biological phenomena and the non-applicability of universal generalizations in ecology is much more striking than the contingency of abiotic phenomena in physics, because the evolution of the cosmos and the physical world proceeds much slower than the biological evolution. According to this concept, ecology and physics describe similar structures and processes of reality, but the contingency and dynamics of evolution in nature is much more remarkable in ecological objects than in physical. In physics the assumption of the existence of laws and *ceteris paribus* clauses more often corresponds to the empirical facts than in ecology because the evolution of the cosmos proceeds much slower than the biological. Thus, the physical world seems to be much more stable than the biological one.

The difference between ecological and physical explanations seems to be just a gradual and not a principal one. I think that the outlined method of evolutionary ecology more adequately describes the structures of nature than traditional theories of physics. Contemporary physics has to understand that the single, historical elements play a much more important part in the abiotic nature than physicists had assumed. Thus, the individual - historical aspect of ecology (biology) will become an important part of physics too. For this reason, one should consider ecology to be a discipline that is nearer to natural processes (as we perceive it now) than physics and for this reason, ecology should replace physics as the paradigmatic scientific discipline for the philosophy of science.

This similarity of structures provides a hint for the unity of science. There are good reasons to assume that it is possible to arrive at a unity of ecology by means of explanations that increase our understanding of diverse ecological phenomena, and by deriving their contemporary existence from simpler states of a past long ago. By this method, one will never come to a universal statement for all ecological objects but to unifying statements that are valid for a group whose properties can be "reduced" to a former ecological - evolutionary state. This form of unifying explanation does not need fundamental laws. One just needs general causal mechanisms of change like mutation and selection and some starting point from which all the investigated phenomena evolved (the common ancestor). In the far future, perhaps it will be possible to construct a unified science with this concept. However, first it should be better to search for a unity in one discipline like ecology or cosmology and try to better

understand and explain the mechanisms and basic elements before constructing a fundamental science explaining nature from the big bang (cosmology) until the contemporary glass house effect (ecology).

Supposing this understanding of science, the discipline of ecology and especially the approach of evolutionary ecology will be in the center and the leading discipline for other scientific disciplines. Thus, I will conclude with a statement originally developed for biology but fitting very well also for evolutionary ecology:

“[Evolutionary ecology], then, is the science that stands at the center of all science. It is the science most directly aimed at sciences major goal and most definitive of that goal. And it is here, in the field where all the principles of all the sciences are embodied, that science can truly become unified.” (Simpson 1964, 107)

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