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Holism and reductionism in biology and ecology

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PART 1

HOLISM AND REDUCTIONISM IN BIOLOGY

CHAPTER 1 GENERAL INTRODUCTION

1.1 The holism-reductionism dispute

"The earth is a living organism", says Rolling Thunder¹ (Boyd 1974, p. 51), "the body of a higher individual who has a will and wants to be to well". In the view of Rolling Thunder, every living being is a cell or an organ in the body earth. And as an organism cannot live without organs and as an organ cannot live without an organism, so can the earth not live without the organisms inhabiting her and so can the organisms inhabiting her not live without the body of Mother Earth. "I can tell you that understanding begins with love and respect. It begins with respect for the Great Spirit, and the Great Spirit is the life that is in all things - all the creatures and the plants and even the rocks and the minerals. All things (..) have their own will and their own way and their own purpose; this is what is to be respected. Such respect is not a feeling or an attitude only. It's a way of life. Such respect means that we never stop realizing and never neglect to carry out our obligation to ourselves and our environment (..): to work together to make life good for all of us, all who live upon this Mother Earth" (Boyd 1974, p. 52, 260).

This is holism in *optima forma*. This holism is very comprehensive. It is an ontology, it contains aspects of an epistemology, and, associated to this, it is an ethics. It is a way of life. And it is, most of all, an ideology. This ideology is especially popular in circles of the New Age Movement (for example Capra 1975, 1984; Zukav 1979; Bohm 1980; Ferguson 1980, Sheldrake 1981, 1988, 1990; Davies 1983, 1992; Davies & Griblon 1991; Waldrop 1993).

When we put against this the following statement, which seems characteristic of (radical) reductionism, "an organism is essentially nothing but a collection of atoms and molecules" (Crick 1966)², reductionism contrasts glaringly and meagrely with holism. Yet reductionism too is a comprehensive doctrine, and in a certain sense we can say of reductionism too that it is a way of life and that it is an ideology. This applies at least to the modern scientist. For scientific practice can be said to be almost by definition a matter of reduction (Kuipers 1990, p. 241). Thus, in so far as reduction is coupled to reductionism and in so far as a scientist practices science, a scientist is almost by definition a reductionist. And as the average scientist devotes the larger part of his life to science, reductionism can be said to make up the larger part of a scientists' way of life. Considering the prominent role of science in society we might even say that reductionism is the dominant ideology of our society. And reductionism is, like holism, comprehensive in the sense that it is an ontology (materialism, causal determinism), an epistemology (unity of science through theory reduction) and a methodology (causal analysis, mechanicism). It also involves a certain ethics (control, experimentation, manipulation). In all these respects, there appears to be a contradistinction between holism and reductionism.

This book deals with this alleged contradistinction between holism and reductionism. Its

¹At the time Boyd (1974) wrote his book, Rolling Thunder was a spiritual leader and spokesman for the Shoshone and Cherokee Indian nations in North America.

²This is not just anybody speaking here. Francis Crick discovered, together with James Watson, the structure of DNA, for which they were rewarded the Nobel prize.

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purpose is to make an end to the contradistinction. I have only raised it in the above, caricatural way for the following three reasons. Firstly, because in a way it exists. It exists within our society in the way of, roughly, the 'holism' of the New Age Movement versus the 'reductionism' of (modern) science, and it exists within most scientific disciplines in the way of so-called reduction disputes, holism-reductionism disputes or autonomism-provincialism disputes (Rosenberg 1985; Kuipers *et al.* 1986). Secondly, the contradistinction regularly leads to extraordinary fierce and rethorical polemics and controversies, both in society and within scientific disciplines, for reasons which are to be found especially in the ontological aspects (differences in world view, conceptions of nature) and ethical aspects (respect versus manipulation) of both ideologies. Thirdly, and most importantly, I have raised the contradistinction in the above way to show that in most respects it doesn't hold wood. For example, the fact that there are holism-reductionism disputes within most scientific disciplines gives reason to doubt the contradistinction between 'the' holism of the New Age Movement and 'the' reductionism of science. For example, the fact that holistic systems ecology is particularly suited for, and used to the purpose of, control and manipulation of natural resources and nature reserves (see chapter 8) gives reason to doubt the contradistinction between 'holistic' respect and 'reductionistic' manipulation. For example, before we can arrive at a synthesis (holism), we shall first have to make an analysis (reductionism). For example, the average ethologist or behavioral ecologists spends more than sixty hours a week at observing animals without ever hurting or injuring them in any way, which gives reason to doubt etcetera. I can go on like this for a long time, which is exactly what I shall do in this book.

I will restrict myself, however, to a considerable extent. This book deals with the alleged contradistinction between holism and reductionism in biology (part 1) and in particular ecology (part 2). The reasons for this restriction are threefold. In the first place it is impossible in one book with any depth to delve into the several holism-reductionism disputes within the various sciences and within society. In the second place I am a biologist and ecologist myself and thus somewhat qualified in that field. And in the third place, because of the large number of levels of organization it deals with and because of its position in the hierarchy of sciences (see figure 1 in chapter 2), biology is particularly well suited as an arena for holism-reductionism disputes, and resolutions of these disputes will be relevant to other sciences as well. For in the end these disputes involve such diverse questions as: "Is a living organism (for example, a human being) 'essentially' nothing but a collection of atoms and molecules or is it 'more than the sum' of these physico-chemical parts?" "What is 'essentially'?" "What is 'more than the sum of'?" "Are diverse organisms functionally related in ecological communities and should the latter therefore be regarded as some sort of 'superorganisms'?" "Is there a balance of nature?" "Or are ecological communities 'nothing but' accidental associations of organisms in space and time, which are, moreover, ever changing in species composition?" Answers to these questions are of interest not only to biologists and ecologists, but also to many other scientists as well as to society as a whole.

The restriction to biology does not mean, therefore, that what will appear in this book will not be relevant to other areas of inquiry. On the contrary. I will develop the general thesis that, instead of conflicting views of nature or of relations between sciences, holism and reductionism should rather be seen as *co-operating and mutually dependent research*

*programmes*³. This thesis applies not only to biology but to all sciences and to all disciplines within sciences, whether 'natural' or 'social'.

1.2 Division of the book

This book consists of two parts. Part 1 deals with the holism-reductionism dispute in biology general (chapters 2 to 7), part 2 concentrates on ecology (chapters 8 to 13).

In chapter 2 I will provide an overview of holism and reductionism in biology and of the problems to which they relate. These are so-called reduction problems, which have in common that they pertain to part-whole relationships. It is important, however, to distinguish between ontological, epistemological and methodological aspects of these problems. Ontological aspects have to do with the things we assume reality (nature) to be made up of, the attributes we assign to them, and, in particular, the (hierarchical) relations between them. Epistemological aspects concern our knowledge of reality, the way this knowledge is laid down in (among other things) theories, and, in particular, the relations between different theories (research programmes, scientific disciplines) developed for different levels of organization. Methodological aspects concern the ways of acquiring knowledge of reality and the strategies thereby used.

From this overview it appears that there are three major 'contradistinctions' between holism and reductionism in biology. The first one is an alleged contradistinction between the (holistic) doctrine of emergence and the (reductionistic) reduction-thesis, the second is an alleged contradistinction between the need for functional explanations in biology (holism, organicism)⁴ versus the requirement of causal explanations (reductionism), and the third is an alleged contradistinction between phenomenology ('holistic', descriptive research at the level of the whole) and mechanicism ('reductionistic', mechanistic research at the level of the parts). The first contradistinction will be dealt with, and resolved, in chapter 5, the second in chapter 7. In almost all chapters, but especially chapter 6, I will deal with, and resolve, the third contradistinction. It is especially to this latter contradistinction that my thesis about the co-operation of holistic and reductionistic research programmes applies. Chapter 2 ends with a characterization of radical, moderate and anti-reductionistic research strategies in biology.

In chapters 3 and 4 I will discuss the meaning of the terms 'to reduce' and 'reduction' in science. Chapter 3 deals with the reduction of laws and theories, chapter 4 with the reduction of concepts.

In chapter 3 I will first discuss Nagel's (1961/82) classical model of law and theory reduction and then Kuipers's (1990) more recent and comprehensive model. This model

³Here and in the rest of this book I will use the term 'research programme' in the original sense of Lakatos (1978), that is, for a certain theory (or leading idea or concept; the hard core of the programme) and its positive and negative heuristics. However, I will often use the terms 'research programme' and 'theory' (or 'model') more or less interchangeably, treating them as more or less equivalent.

⁴As far as I know, no one before has ever linked functional explanations explicitly with holism, even though the link appears obvious and plausible. I will justify it in chapters 2 and 7.

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shows that there are many different types of reduction in science, depending on what sort of auxiliary hypotheses and bridge principles are being used in a reduction in addition to the reducing theory: approximation rules, aggregation rules, and transformation rules in the form of correlations (causal relations) or so-called ontological identity relations. I will discuss each of these types of reduction and the various steps of which they are composed. The type of reduction most relevant to reduction problems in biology is 'heterogeneous micro-reduction', so-called because it involves (1) part-whole relationships (micro-reduction) and, therefore, an aggregation step in which relations between parts in a whole are being aggregated, and (2) a 'heterogeneous' jump of language and, therefore, one or more bridge principles (or transformation rules) to connect terms that occur in the (macro-)law or theory to be reduced, but not in the reducing theory, with terms that do occur in the reducing (micro-)theory. These bridge principles may be correlation hypotheses, expressing causal relations between a term in the law or theory to be reduced and a term in the reducing theory, or ontological identity hypotheses, expressing that some term in the law or theory to be reduced is identical to a term in the reducing theory (for example, the term 'temperature' in the ideal gas law is supposed to be identical to the term 'mean kinetic energy' in the kinetic theory of gases). This distinction will reappear in chapter 4, as it is of importance in the reduction of concepts.

A major conclusion of chapter 3 will be that all types of reduction are kinds of explanations. Reduction, in this sense, is an *epistemological* issue: it involves *logical relations* between statements or systems of statements (theories). It should not be confused, therefore, with ontological reduction in any of the 'ordinary' senses of the word: decreasing, diminishing, devaluating or the like.⁵

In chapter 4 I will show that, contrary to the claim of many philosophers, the same holds for reductions of concepts. Concept reductions may stand on themselves but they may also play a role in one particular type of law or theory reduction, namely identificatory reduction or reduction with an identification step. In this step an *ontological identity* hypothesis is being used stating that some term (concept) occurring in the law or theory to be reduced, but not employed by the reducing theory, is identical to some term (concept) in the reducing theory (see the above example). The status of ontological identity relations, and hence of concept reductions, is highly controversial, however. In particular, it is unclear whether and in what sense they are different from causal relations. Also, because they involve *ontological* identity relations, several writers have claimed that concept reductions imply some form of ontological reduction. Some have even claimed that they make for cases of micro-reduction, that is, involve part-whole relationships or relations between a macro-level and a micro-level. My chief purpose in chapter 4 will be to show that these are grave misunderstandings. I will argue that concept reductions cannot be micro-reductions if they are to involve ontological identity relations, and I will argue that reduction of concepts is, like law or theory reduction, an epistemological issue, not an ontological one: it does not mean or imply in any sense that ontologies (objects or attributes of objects) are being reduced.

⁵A classical complaint from holistic side is: "You cannot just simply reduce an organism to a sack of molecules!". The moral indignation expressed in this complaint seems to stem from the fact that one thinks reduction in science means ontological reduction in one of these ordinary senses of the term 'reduction' (such as in sales reductions), where whatever is reduced is made less or less worth.

In chapter 5 I will discuss the first of the alleged contradistinctions between holism and reductionism in biology, to wit the one between the doctrine of emergence and the reduction thesis. As is well known, the central claim of holism is the thesis that 'the whole is more than the sum of its parts'. In the particular form of emergentism, this means that a whole has so-called 'emergent' properties which the component parts do not possess (neither separately nor in sum) and which, therefore (supposedly), cannot be reduced to properties of these parts. This claim is vague and open to several different interpretations (see Nagel 1961/82, pp. 366-397), but I will show that if interpreted in a certain plausible way, it can be seen as a valid ontological thesis. In that sense, however, the thesis applies not only to biological wholes, but to any wholes, biological as well as physico-chemical ones. Also, I will show that in this sense the thesis in no way contradicts the reduction thesis. For many properties of wholes, which on the grounds of this thesis may be called emergent, have proved to be explainable in terms of micro-theories about the component parts and appropriate bridge principles. Again, however, it is important to realize that reduction is an epistemological issue, whereas emergence is an ontological one. Reduction is a kind of explanation and as such has nothing to do with in any way ontologically reducing 'wholes' or 'emergent properties' of wholes. The conclusion following from this discussion is that, though a valid ontological thesis, the (epistemological) irreducibility claim attached to the emergence thesis must be abandoned. Next, using Kuipers's (1990) reduction model, I will show that it depends on the type of reduction whether we can speak of emergent properties at the level of a whole, and I will develop a new definition which expresses emergence in terms of the reduction-steps that may occur in actual reductions. This will lead to two remarkable conclusions: firstly, 'emergence' may be seen as the opposite of 'ontological identity', and, secondly, there would be no reason for us to even think of reduction if there were no emergence (that is, emergent properties or emergent entities). Finally, using both Kuipers's (1990) reduction model and Zandvoort's (1986) model of co-operating research programmes, I will develop my thesis that holism and reductionism should rather be seen as mutually dependent and co-operating research programmes than as contradictory views of nature or of relations between sciences. As mentioned, the type of reduction most relevant to reduction problems in biology is heterogeneous micro-reduction. This type of reduction requires three ingredients: (1) a macro-law or theory (at the level of the whole); (2) a micro-theory (about the component parts); and (3) aggregation hypotheses and bridge principles connecting the two. Thus, it requires both holistic research at the level of the whole and reductionistic research at the level of the parts, as well as what we might call a mixed strategy directed at the relations between the two levels. In terms of Zandvoort's model, this means that holistic research programmes may be seen as *guide programmes* and reductionistic programmes as *supply programmes*. Holistic programmes play an important role in science as guide programmes for reductionistic programmes, because they provide macro-laws or theories at the level of the whole, which, however, for lack of the appropriate means, they themselves cannot explain. For these explanations, they depend on the fruits of reductionistic programmes. If these latter programmes succeed in providing the explanations (reducing the macro-laws or theories), they act as *supply programmes* for the holistic guide programmes. Reductionistic programmes depend on holistic programmes, however, for providing the macro-laws or theories to be reduced.

In chapter 6 I will illustrate my thesis with an example from animal physiology (a discipline which is eminently involved with the 'essence' of life). The example concerns the reduction

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of the so-called Bohr-effect, a law about the rate at which oxygen is taken up and released by the blood. I will show that this law has been reduced to the theory of allostery (a theory of molecular biology), applied to hemoglobin molecules in red blood cells, and that this particular application of the theory of allostery has been reduced to the theory of chemical bonding (a theory of physical chemistry). This reduction, which involves four levels of organization, was accomplished through the co-operation of at least six research programmes and the relations between these programmes can all be characterized in terms of the mutual dependence of holistic guide programmes and reductionistic supply programmes. Also, it is possible to specify exactly, in terms of the reduction steps occurring in the example, at which level of organization emergent properties or emergent phenomena occur. Finally, however, the example also makes clear that a certain research programme can act both as a 'reductionistic' supply programme for a 'higher' guide programme and as a 'holistic' guide programme for a 'lower' supply programme. This means that the terms 'holistic' and 'reductionistic' are extremely relative and should always be related to a certain level of organization.

In chapter 7 I will discuss the structure and status of functional explanations in biology. Functional explanations are the prototype of the holistic claim that in order to understand a given level of organization one should not (only) study the lower levels but (also) that level itself as well as its relations with higher levels. That is, one should study the roles or functions of parts in wholes. Functional explanations abound and appear to be indispensable in biology. Because of their aberrant (supposedly non-causal) structure, they provide holists with a strong argument in favour of biology's autonomy with respect to physics and chemistry. Reductionists, on the other hand, argue that functional explanations are illegitimate pseudo-explanations and that they should be replaced by causal explanations, thus allowing biology to be reduced to physico-chemistry. I will argue, firstly, that functional explanations are perfectly legitimate explanations and that in a certain way they can be reconstrued as 'standard' causal, deductive-nomological explanations. Secondly, I will argue that functional explanations are indeed indispensable in biology, because they are necessary components of more comprehensive causal-evolutionary explanations. For precisely that reason, however, they are not in contradiction with causal explanations (or with the principle of causal determinism) and therefore do not provide any obstacle to reduction of higher to lower level theories. On the contrary, they contribute to such reductions. I will show that in the context of functional explanations too, we can speak of the co-operation and mutual dependence of 'holistic' guide programmes and 'reductionistic' supply programmes.

In part 2 I will apply my thesis to the reduction problem and the associated holism-reductionism dispute in ecology. Ecology spans at least four levels of organization, namely individual organisms, populations, communities and ecosystems, and between each of these levels reduction problems occur. I will show that here too, the solution to these problems lies with the co-operation of 'holistic' and 'reductionistic' research programmes.

In chapter 8 I will provide an overview of the issues and positions at stake. As in the rest of biology, in ecology there also appear to be several different positions or approaches, which can be characterized as more or less radically holistic or reductionistic. In the radically holistic approach, communities and ecosystems are regarded as a kind of 'superorganisms' exhibiting all sorts of properties of 'real' organisms, such as the capacity for self-regulation by means of various feedback mechanisms, analogous to the physiological mechanisms that maintain homeostasis in organisms, and the development (succession) from a young to an old

or mature, stable end-phase, called the climax, analogous to the ontogenetic development of organisms. In the radically reductionistic approach, all this is being denied and even the existence of communities and ecosystems as distinctive ontological entities is being disputed. In this approach, communities and ecosystems are seen as nothing but accidental and, moreover, ever changing collections of species, which can be fully explained in terms of individual species' adaptations to local environmental conditions. A common moderate approach is that communities and ecosystems do exist as 'real' entities having their own, emergent properties (such as diversity, productivity and a certain stability or resilience), which can be explained, however, through interactions between species, such as competition and predation.⁶

Thus, the ontological status of communities and ecosystems is highly controversial and it is understandable that discussions on the subject are heated and full of polemics. However, concrete solutions to reduction problems are very much frustrated thereby. For as it happens, not a single general law or theory about communities and ecosystems has yet been developed, on which even the slightest degree of agreement exists, and even adequate, well articulated conceptual theories appear to be lacking.⁷ In this connection, there is even talk of the 'intellectual immaturity' (Fretwell 1981; MacIntosh 1985) or the 'anomalous status' (Hagen 1989) of ecology. Though this is going a bit too far in my view, because ecology actually happens to be very rich (maybe even a bit too rich) in concepts, hypotheses, models and theories, it does seem a fact that general, well corroborated laws and theories about higher levels of organization are still lacking, while on lower levels (individuals, populations, species) they remain scarce (see chapters 10 and 11).

Of a number of possible causes I will lift out two, which appear most conspicuous, and which lend themselves to philosophical (conceptual) analysis and clarification. The first one is the ambiguity of many terms which are central to ecology. It appears that such core terms as environment, habitat, niche, diversity and stability, and also community and ecosystem, are being used in multiple and often disparate and incompatible ways, that is, for various different concepts. This ambiguity alone seems to be sufficient for the lack of 'general' laws and theories. This is the subject of chapters 9 and 10.

The second factor is the holism-reductionism dispute. I will argue that the dispute has a strong inhibitory effect on the growth of knowledge (theory development and maturation, among other things), because it regularly leads to fruitless yet time consuming polemics and controversies (see also Hagen 1989). This is the subject of chapter 13, where I will discuss one such fruitless controversy concerning the role of interspecific competition versus 'chance' in structuring ecological communities (see below).

In chapter 9 I will discuss the ambiguity of the term '(ecological) community'. I will show that this term is being used for a large number of different concepts, for different entities at various levels of organisation. After a conceptual analysis and clarification of these concepts, I will develop a new definition of the term which, contrary to former definitions, seems

⁶Similar positions exist (or existed) with respect to populations, leading to similar controversies (see chapter 8).

⁷As a result, of course, neither are there reductions of laws or theories about communities and ecosystems.

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theoretically adequate and is at least unambiguous. The crucial difference is that according to former definitions, communities are to be regarded as groups of *populations* of different species, whereas in my view they should be defined as groups of *individuals* of different species. As it happens, my definition will prove to have two extremely interesting and positive 'side-effects'. For it appears to provide (theoretical) solutions to two of the most notorious problems in community ecology, to wit the *boundary problem* and the *problem of heterogeneity*. The former problem consists of the fact that populations of different species rarely if ever occupy exactly the same area in a landscape, but mostly occur in different, more or less strongly overlapping areas. As a result, different communities, defined as groups of populations, gradually flow into one another, whence the boundaries between them are vague. This is a problem, of course, because it hampers adequate descriptions of the structure (species number and composition) of communities. The problem of heterogeneity originates from the same cause: because different populations generally occupy different areas in a landscape, the species composition in different sub-areas of the total area occupied by a community, again defined as a group of populations, generally differs, whence communities are (spatially) heterogeneous in species composition. This is a problem, because the occurrence of general laws appears to be related to homogeneous entities. I will show that both problems can be resolved by defining communities as particular sets of individuals of different species.

In chapter 10 I will analyze and clarify two other major ecological concepts, namely 'habitat' and 'niche'. The term 'habitat' plays a major role in ecology through the 'theory' of habitat selection and the 'principle' of habitat differentiation. Both relate to spatial separation of species resulting from differences in resource requirements and/or environmental tolerances. The term 'niche' plays an important role through modern niche theory (a theory about resource exploitation by species; see chapter 11) and through the 'principle' of niche differentiation (leading to differences in resource exploitation between competing species). While habitat differentiation leads to spatial separation (non-coexistence) of species, niche differentiation is considered to be a mechanism of coexistence. Both 'principles' play an important role in explanations of the structure (species number and composition) of communities.

However, there is considerable confusion about habitat and niche differentiation and this confusion results from confusion about the meanings of the terms 'habitat' and 'niche'. Conceptual analysis of the ecological literature reveals that there are at least four different habitat concepts and as many niche concepts, the additional complication being that two of these habitat concepts correspond to two of these niche concepts, whence the distinction between habitat and niche is blurred. Several of these concepts appear to correspond, moreover, to different concepts of environment, as well as to different concepts of biotope. Needless to say that this confusion is devastating to theory maturation, and especially modern niche theory is seriously suffering from it (even to the point where many have come to reject the term niche as useless). My purpose in chapter 10 is to disentangle all these different concepts and to supply each of them (in so far as I see fit) with a suitable term. In doing so, I will keep a close eye to commonly accepted opinions about habitat and niche differentiation.

After all this preparatory work I will finally be able to apply my thesis about the mutual dependence of holistic and reductionistic research programmes to ecology. In chapter 11 I will do so by discussing a concrete, though not yet fully recognized, example of successful reduction in ecology: the reduction of the Lotka/Volterra competition model to modern niche

theory (Glasser & Price 1982; Tilman 1982). The Lotka/Volterra model is a phenomenological (holistic) model: it describes the possible effects of competition between species (in terms of coexistence or local extinction). In being a phenomenological model, the Lotka/Volterra model calls for a deeper explanation of its assumptions and predictions, and, hence, plays the role of a holistic guide programme. The deeper explanation is provided by modern niche theory. This is a mechanistic theory: it specifies both the objects of competition (resources) and a mechanism (exploitation of resources by different species). Because modern niche theory reduces the Lotka/Volterra competition model, it plays the role of a reductionistic (reductive) supply programme. Incidentally, the type of reduction shows that one cannot speak of emergence at the level of the Lotka/Volterra model.

In chapter 12 I will discuss another example of co-operation of holistic and reductionistic research programmes in ecology, involving a case of idealization and concretization and, hence, approximative reduction (see chapter 3). The example comes from island biogeography, a branch of ecology directed at the distribution and abundance of species on islands. This branch went through a phase of rapid development in the nineteen sixties and seventies, after MacArthur and Wilson (1963, 1967) had published their equilibrium theory of island biogeography. Before that time, island biogeography consisted mainly of a large collection of facts (records) which were largely unrelated to one another and in which only a few regularities were observed. MacArthur and Wilson presented a simple, holistic model which not only explained these regularities but also lead to a number of new predictions. After a phase in which the model was tested, it appeared to be a bit too simple, however, and research shifted to analyses of the causal factors that might underlie (the parameters of) the model. I will show that these developments can be described very well in terms of the model of idealization and concretization (Krajewski 1977; Nowak 1980), where MacArthur and Wilson's theory appears as an idealization which subsequent research programmes have concretized (see also Haila & Jarvinen 1980). Because these concretizations have a reductive (be it approximative, that is, non-deductive) character, we can see in this structure of idealization and concretization also a form of co-operation of holistic and reductionistic research programmes. The example is interesting not only from the point of view of ecology but also from the point of view of philosophy, because it shows that the model of idealization and concretization applies not only to developments within research programmes, as has been thought so far, but also to developments between research programmes.

In chapter 13, finally, I will provide an example of the inhibitory effect which holism-reductionism disputes may have on the growth of knowledge. The example concerns a controversy in island biogeography between two of the research programmes that are involved in concretizations of MacArthur and Wilson's equilibrium theory. The one programme is moderately reductionistic, but also has a few holistic characteristics: it assumes that communities are stable, integrated entities whose structure results from strictly deterministic 'assembly rules', but it takes the integrating factor underlying these rules to be interspecific competition. The other programme is radically reductionistic: it assumes that so-called communities are nothing but random associations of species, which can be explained fully in terms of random colonization of islands by species, given some characteristics of individual species and islands. The controversy has lasted for about ten years (a long time considering ecology's existence as a science), appears to have bled to death rather than to have been resolved, and has produced nothing new. The major 'result' of the controversy seems to be that the radical elements of both programmes have been eliminated. This, and what is left

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over, is in complete agreement with my thesis about the co-operation of holistic and reductionistic research programmes: the structure of the investigated communities appears to be significantly non-random (implicating a role for holistic programmes in studying them), but it can be largely explained reductively in terms of autecological relations between species and environmental conditions (the radical reductionistic approach) while a small part of it could be the result of interspecific competition (the moderate approach).