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Holism and reductionism in biology and ecology

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PART 2

HOLISM AND REDUCTIONISM IN ECOLOGY

CHAPTER 8 THE REDUCTION PROBLEM IN ECOLOGY

8.1 Introduction

In the now following second part of this book I will discuss the reduction problem and the associated holism-reductionism dispute in ecology. Ecology is sometimes seen as the only truly holistic science, because it deals with relations between organisms mutually and with the environment, with interrelationships and connections in nature. On the one hand, given the definition of holism, there seems to be some truth in this. On the other hand, one of the main conclusions of part 1 was that the terms 'holistic' and 'reductionistic' are extremely relative and should always be related to some given level of organization. A theory (research programme, science) may be holistic with respect to some lower level of organization but at the same time reductionistic with respect to some higher level. Ecology as a whole may be holistic with respect to, for instance, physiology or molecular biology. However, within ecology several levels of organization are being distinguished, to wit the levels of organisms, populations, communities and ecosystems, and with respect to each of these levels ecological sub-disciplines have developed. The relations between individual organisms and the environment are the domain of autecology. Population ecology deals with groups of organisms of the same (or at most two or a few interacting) species, community ecology with the interrelationships between groups of organisms of different species of plants, animals and/or micro-organisms. And systems ecology deals with the complex of relations between various groups of plants, animals and micro-organism and the abiotic environment, which together make up an ecosystem. Apart from these, there is also landscape ecology, which studies the influences of structures and processes in landscapes on the distribution and abundance of species and communities, and global ecology which studies the flow of energy and matter through the various compartments of the biosphere as a whole. Autecology may be holistic with respect to for instance physiology, it is certainly reductionistic with respect to the other ecological disciplines.

Thus, ecology spans several levels of organization and between each of these levels reduction problems occur. For this reason there is also a holism-reductionism dispute within ecology. Usually this dispute is seen as a conflict between a holistic school of (functional) systems ecologists and a reductionistic school of (evolutionary) population ecologists (Hutchinson 1978; Simberloff 1980; McIntosh 1985; Hagen 1989), but I will show that, as in the rest of biology, there is a variety of positions which can be characterized as more or less moderately or radically holistic or reductionistic.

In the larger part of this chapter I will provide an overview of the nature of the reduction problems in ecology and of the various positions taken with respect to these problems. After that I will attempt to shed some light on solutions to these problems by applying the models of reduction and of co-operating research programmes discussed in part 1. In doing so, I will hit upon a special problem, which more or less frustrates concrete solutions to reduction problems, namely the almost complete lack of general laws and theories in ecology. This problem has been referred to as the 'intellectual immaturity' of ecology (Fretwell 1981; Strong et al. 1984; McIntosh 1985; Hagen 1989). I will point to two particular 'causes' of this problem, viz. the ambiguity of the ecological vocabulary and the inhibitory effect of the holism-reductionism dispute on the growth of knowledge. These 'causes' will be discussed at length in later chapters.

8.2 Holism and reductionism

As argued in part 1, in dealing with reduction problems it is extremely important to distinguish between ontological, epistemological and methodological aspects of these problems. On the epistemological level the reduction problem in ecology may be formulated as the question whether laws and theories about communities and ecosystems can be reduced to theories about populations or individual organisms. Also, the question may be put whether ecology as a whole can be reduced to some lower level biological theory, for which the modern theories of natural selection and population genetics are of course the most likely candidates. As mentioned, however, ecology suffers from a lack of general laws and theories, at least at the level of communities and ecosystems (see below). Therefore, there is little or no use in racking one's brain about the former question, let alone the latter. Also, I am not aware of any successful reduction of concepts in ecology (except the reduction of the concept 'carrying capacity', K , by Leslie (1926); see chapter 11).

For this reason, holism-reductionism disputes in ecology are primarily concerned with ontological and methodological issues. Ecologists are constantly discussing what should be the 'fundamental' unit of ecological research and what research strategy should therefore be followed. This is mostly described as a dispute between a holistic school of primarily systems ecologists and a reductionistic school of primarily population ecologists (Hutchinson 1978; Simberloff 1980; McIntosh 1985; Hagen 1989). The former argue that the 'functional' level of organization in ecology is formed by ecosystems and that research should therefore be directed at these systems. The latter, who take modern evolutionary theory as a starting point, argue that populations should be the fundamental units of ecological research. The question thereby is not so much whether systems ecology can be reduced to population ecology, but rather whether there is any use at all in doing systems ecology (and community ecology) besides population ecology (and autecology). This has everything to do with the ontological status of communities and ecosystems, which is actually the core of the reduction problem in ecology: are communities and ecosystems 'real', discrete ontological entities with emergent properties (such as biomass, productivity, diversity, stability), which are largely independent of the component species, or are they nothing but accidental assemblages of species which just happen to share the same space and time? Of course, the answers to this question largely determine the methodological positions taken. Those who assume that communities and ecosystems are 'real' ontological entities argue that research should be directed at these higher levels of organization, whereas those who deny their existence (for that is what their position actually boils down to) naturally argue that research at these levels is pointless. Incidentally, within the former position a distinction can be made between those who do see a certain relevance of lower level research for the understanding of higher level phenomena (that is, of population research for the understanding of the structure and dynamics of communities and ecosystems) and those who don't. The latter may justly be called radical holists or anti-reductionists, the former moderate holists. A common position, which may be called moderately reductionistic, but just as well moderately holistic (thus, above all things, moderate), is that on the one hand one recognizes that communities and ecosystems are real ontological entities while on the other hand it is assumed that their structure and dynamics are being determined primarily by interactions between species. Logically, in this latter view research should be directed at both higher and lower levels. In the following sections I will enter in more detail into these various, more or less radical, holistic and reductionistic

positions.

8.2.1 Radical holism

The radical holistic view in ecology is that the entities of higher levels of organization - communities and ecosystems, but the approach has also been applied to populations - are discrete integrated wholes with their own emergent structure and dynamics which cannot be derived from properties of the component species, populations or individual organisms. Characteristic of this view is that it is primarily *organismal* or *physiological*. That is to say, populations, communities and ecosystems are regarded as analogues to organisms, their main characteristic being the capacity for *self-regulation*. This would be achieved through various feedback mechanisms and an information network similar to the physiological mechanisms that maintain homeostasis in organisms. Also, communities and ecosystems would show a development from a young to a mature stage, comparable to the ontogenetic development of organisms.

a) communities

The standard example of this is the view of the American plant ecologist Clements (1916, 1936; Clements et al. 1929), who described plant communities as *superorganisms* which, analogous to real organisms, have a certain physiological integrity and which come into existence, grow and ripe to a stable 'mature' stage which Clements called the *climax*. His theory was primarily meant to explain a phenomenon which is known as (primary) *succession*. This is the development of a plant community which starts with the first plant growth on a formerly bare soil and which runs in the direction of a more or less stable end phase, the climax. Depending upon the biogeographic region, this is mostly some sort of wood or forest. According to Clements, this succession cannot be explained in terms of adaptations of individual species to local environmental conditions, but is mainly the result of interactions between species, in particular competition: in a succession species are constantly being out-competed (competitively displaced) by other species until in the end only a few dominants survive. Similar views were held by Forbes (1883, 1887), Adams (1913), Thieneman (1918) and Lindeman (1942) with respect to aquatic communities or animal communities.

In Europe, where most ecologists did not at all agree with Clements' view, one finds its counterpart in various plant-sociological approaches, such as the Scandinavian 'school' of Raunkiaer (1934) and the French-Swiss 'school' of Braun-Blanquet (1928). Characteristic of these approaches is that concrete plant communities as they are found in nature (so-called phytocoenosa) are instantiations or tokens of certain types (phytocoena) and that therefore it is possible, for each biogeographic region, to set up a typology or classification scheme of communities (see chapter 9). A major difference with the Clementsian approach is that in Europe one has assumed that properties of plant communities (species composition and abundance) are primarily determined by the type of environment occurring in a certain area and that to each type of environment a specific type of plant community belongs. Perhaps these European, plant sociological approaches should therefore be characterized as essentialistic rather than holistic: the community regarded as a natural kind. On the other hand, viewing communities as natural kinds is in itself not essentialistic. It becomes essentialistic, however, when these kinds are seen as ideal types (so-called 'typological')

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thinking) of which the concrete tokens found in nature are 'imperfect reflections' (see also chapter 9 and 13.6.3).

b) ecosystems

As argued by Simberloff (1980), the (radical) holistic Clementsian approach at the level of communities has been abandoned in favour of reductionistic approaches (see below) but it remains alive with regard to ecosystems. Around the beginning of the sixties a strong movement in ecology arose which came to apply the holistic approach to ecosystems (McIntosh 1980; 1985). The vision of these systems ecologists shows a great resemblance to the Clementsian view of plant communities. According to its best known representative, Eugene Odum (1969), ecosystems would have a 'strategy', show a development (succession) from a young to a ripe or mature end phase. As in Clements' theory this end phase is called the climax and is considered to be stable. A major difference between Clements and later systems ecologists is, however, that while Clements vision was primarily physiological and can therefore rightly be called superorganismal, the vision of later (modern) systems ecologists should rather be called mechanistic (see Kwa 1984; but also Hagen 1989). A characteristic feature of holistic systems ecology is the application of thermodynamics, information theory and general systems theory, in particular cybernetics, to ecosystems (Margalef 1958; Patten 1959, 1975; von Bertalanffy 1968; Odum 1959, 1969, 1971, 1977, 1983; Odum & Patten 1981). Ecosystems are considered to be cybernetic systems with the capacity of self-regulation, analogous to homeostasis in organisms and self-adjustment in some machines. According to Odum (1959, 1983), homeostasis is a general trait of biological systems, ranging from cells to ecosystems. The norm of the system, 'stability', would be achieved and maintained in ecosystems through various feedback mechanisms and an information network in the form of food webs and nutrient cycles, which integrate and coordinate the workings of their components (species, amongst others). It is thereby assumed (but see below) that there is a relation between the diversity of a system (its number of species) and its stability: the more diverse an ecosystem, the more stable it is. Supposedly, this relation can be explained very well in terms of cybernetics: the more species there are, the more interactions there are, hence the more feedback mechanisms and the tighter the information network, and therefore the better the integration of the parts and the more stable the whole.

Patten (1975) calls ecosystems the units of co-evolution. According to him, evolution is being directed by interactions between species in the ecosystem, such as predation and competition. In suitable environments co-evolution would thus lead to the highest possible species diversity (richness).

Odum (1959, p. vi) argues that ecosystem studies should be based on a 'whole-before-the-parts' approach. "The concept of the ecosystem is and should be a broad one, its main function in ecological thought being to emphasize obligatory relationships, interdependence and causal relationships" (p.11). This emphasis on interdependences and relationships, and the associated ideas about stability and self-regulation, can be seen as modern expressions of a much older concept: the *balance of nature* (Egerton 1973; see also Pimm 1991). They form the core of (radical) holism in ecology. Parts, whether they be organs in organisms, individuals in populations or populations in communities and ecosystems, are seen as *functionally* related in the whole. Holistic systems ecology is generally equated, by both

proponents and opponents, with 'functional ecology' (Mayr 1961; Hutchinson 1978; Odum 1959, 1983). "It is evident that as long as a purely descriptive viewpoint is maintained there is very little in common between such structurally diverse organisms as spermatophytes, vertebrates and bacteria. In real life, however, all these are intimately linked functionally in ecological systems, according to well defined laws. Thus, the only kind of general ecology is that which I call "functional ecology"" (Odum 1959, p. ix).

Yet it is not the organisms or populations as parts of the whole that form the units of ecosystems research. The units of this research are so-called *trophic levels* (or food levels): primary producers (green plants), first order consumers (plant eaters), second order consumers (meat eaters) and reducers (fungi and the like). These are conceptual black boxes, theoretical compartments through which energy and matter flow on their way through the system. The information for the contents of these boxes does come from metabolic studies of individual organisms and populations, but these are no objects of study in themselves. Ecosystems research is particularly directed at measuring or estimating the amounts of energy and matter which enter into each trophic level and the efficiencies with which they are used. Often, applications of this are found in agriculture and nature conservation, for instance by way of yield measurements in grasslands or forests or of carrying capacity estimates of the number of cattle that can graze a certain area. The purpose of cybernetics, moreover, is to find general models and concepts that can be applied to both machines, organisms, ecosystems and human societies (Odum & Pinkerton 1955; Odum 1971).

c) populations

The holistic perspective has also been applied to populations. From this perspective, populations are seen as self-regulating entities which occur in equilibrium with their environment. Thus, Allee et al. (1949) asserted that populations exhibit homeostasis and other organismal properties. Cole (1957) spoke of autoregulatory mechanisms which would work as mechanical 'governors' to control the growth of populations. This approach has become known as the *self-regulatory school*, particularly through the works of Chitty (1960) and Wynne-Edwards (1962). This was one of four schools which were involved, and partly still are involved (see de Boer & Reddingius 1996), in a controversy over the regulation of population numbers. Beside the self-regulatory school, there is a biotic school, a climate school and a comprehensive school (see for example Krebs 1994). The *biotic school* takes as a starting point the *stability* of populations and stresses the importance of *density dependent, biotic* factors (competitors, predators, parasites) in the regulation of populations (Nicholson 1933, 1954; Lack 1954). The *climate school*, on the other hand, stresses *fluctuations* in the size of populations and assigns a major role thereby to *density independent, physical* factors, such as weather and climate (Bodenheimer 1928; Uvarov 1931; Andrewartha & Birch 1954, 1984). The *comprehensive school*, finally, argues that both physical and biotic factors play a role (Thompson 1929; Schwerdtfeger 1941).

Contrary to the other schools, who seek to explain population numbers in terms of extrinsic factors, the self-regulatory school concentrates on *intrinsic* factors within populations, on individual differences in behaviour and physiology (Chitty 1960; Pimentel 1961; Wynne-Edwards 1962). The general assumption of this school is that the abundance of species can change as a results of changes in the qualities of individuals (through genetic changes in the population). The unlimited increase of populations can be prevented by intraspecific

competition leading to a decrease in the quality of individuals at increasing density, without any changes in external (physical or biotic) environmental factors.

An outspoken representative of this school was Wynne-Edwards (1962) who became particularly famous for his ideas on group selection. Wynne-Edwards argued that populations are homeostatic systems which are capable of regulating their own size by means of complex, negative feedback mechanisms analogous to the physiological mechanisms that maintain stability (homeostasis) in individual organisms. According to Wynne-Edwards, information about population size would be spread in a population through behavioral signals which he called 'epideictic displays'. On the grounds of this information, individuals would regulate their own reproduction in order to optimize the size of the population as a whole. Because this sometimes meant that individuals would sacrifice their own reproductive success in favour of the population, Wynne-Edwards believed that these homeostatic mechanisms had evolved by group selection. His view was so devastatingly criticized, however, by Williams (1966) that the idea of group selection has been eliminated from the mainstream of (evolutionary) biology. As far as I know, the ideas of the self-regulatory school about homeostasis and self-regulation of populations have also been worsted and only intraspecific competition remains a major factor in models of population regulation today (but see Seeley 1989; Moritz & Southwick 1992; and also Wilson & Sober 1989).

8.2.2 Radical reductionism

Radical reductionism was introduced in ecology as a critique of Clements' superorganism theory by another American plant ecologist, Gleason (1939, 1962). Gleason formulated an '*individualistic*' concept of the (plant) community; individualistic, because it went out from individual species' adaptations to local environmental conditions. Later, it became known as the individualistic hypothesis (McIntosh 1985, 1995).

Gleason argued that the distribution and abundance of species is first of all determined by two factors: immigration and environmental conditions. Both have an element of randomness. Environmental conditions are rarely if ever discretely distributed but vary continuously, both in space and in time. Since the environmental tolerances of different species are not the same, moreover, one cannot expect different species to occupy exactly the same area. Therefore, communities are rarely if ever clearly delineated entities but rather assemblages of species that gradually flow into one another. And since environmental conditions vary continuously also in time, neither can there be a deterministic succession towards one stable end phase. According to Gleason, succession is not an orderly and predictable process and can be explained only through the dynamics of individual species. This view has been taken over and extended upon by many later (plant) ecologists (for example Whittaker 1948, 1972; Drury & Nisbet 1973; Pickett 1976, 1982; Bazzaz 1979, 1982, 1986). Much plant ecological research consists of so-called gradient analyses and is directed at individual species' responses to environmental gradients (Whittaker 1975).

Because of the mobility of most animal species, it is to be expected that animal communities are even less spatially discrete than are plant communities. In the radical reductionistic view, this applies even stronger to ecosystems. For an ecosystem is generally defined as the whole of a biotic community, or *biocoenosis*, of plants, animals and micro-organisms and its abiotic environment. But if biotic communities, or their sub-communities of plants, animals and micro-organisms, are not discrete entities, then neither can be

ecosystems. Holistic systems ecology has been heavily criticized, therefore, especially the idea that ecosystems are stable, self-regulating systems. Engelberg and Boyarsky (1979) have questioned the cybernetic nature of ecosystems, because in their view there is no information network, with the required characteristics such as low energy input and high output, in ecosystems. Many ecologists have also disputed the alleged relation between the diversity and the stability of ecosystems, both on empirical grounds and on the basis of theoretical models (Holling 1973; May 1975, 1979; Pimm 1984, 1991). These ecologists do not deny that there is something like ecosystem development, but they do deny that this development would run deterministically towards one possible stable end phase. Holling (1973) introduced the term 'persistence' in this connection, the capacity of an ecosystem to maintain itself in ever varying states. And Pimm (1984) argues that 'resilience' is a better criterion than 'stability' to describe the ever varying states of ecosystems. Incidentally, the position of ecologists like May, Holling and Pimm, who study communities and ecosystems from the point of view of interactions between populations, can better be characterized as moderately than as radically reductionistic (see 8.2.3).

The most outspoken radical reductionist in ecology today is Simberloff (1980, 1983, 1986), a population ecologist who actually argues that communities and ecosystems do not exist at all, at least not as discrete, structurally and/or spatially distinct entities. According to Simberloff, what are called communities and ecosystems are essentially nothing but accidental collections of species (populations), which can be fully explained in terms of on the one hand properties of species and on the other hand local environmental conditions. Simberloff and his colleagues of the Florida State University (Connor & Simberloff 1979; Strong 1980; Strong et al. 1984) have become particularly well-known for their view that explanations of the so-called 'structure' of communities should always be tested against the null hypothesis that this structure is completely 'random', given the properties of individual species and the environment. This strategy was first based on Popper's naive falsificationism and later, after it had been criticized, on Lakatos' refined falsificationism (Simberloff 1983). The general idea behind it is that in searching for explanations of community structure one should first assume that this is purely the result of chance processes before looking at deterministic, biological explanations. The strategy is more in particular directed against the, in the eyes of Simberloff c.s., premature and unjustified applications of competition theory to the structure of communities. I will return to this extensively in chapter 13.

8.2.3 The moderate position

As mentioned above, the Clementsian superorganismal approach of communities has been abandoned in favour of reductionistic approaches. Yet not all holistic elements of Clements' view have disappeared from community ecology. Many present-day ecologists, perhaps even the majority, take a moderate position in the sense that on the one hand they recognize that communities are 'real' entities with their own emergent properties (such as diversity and productivity), which are not completely determined by properties of individual species, while on the other hand they attempt to explain them reductively. The explanations are particularly sought in interactions between species, such as competition and predation. Almost every ecological handbook contains a part dealing with autecology and population ecology, and a part dealing with community ecology and involving interactions between species (for example Krebs 1994; Begon et al. 1996).

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This position can be called moderately holistic, but just as well moderately reductionistic, for two reasons. Firstly, because it recognizes communities as 'real' ontological entities with emergent properties (the holistic element), while on the other hand the aim is to explain them in terms of their component parts (the reductionistic element). And secondly, because the explanations are not being sought entirely in autecological adaptations of species (the radical reductionistic approach) but also and in particular in terms of interactions between species (another 'holistic' element). The latter point requires some explanation.

In ecology it is quite usual to characterize explanations of community structure and dynamics in terms of relations between species and (abiotic) environmental factors as reductionistic, and explanations in terms of (biotic) interactions between species as holistic (for example Simberloff 1980; Levins & Lewontin 1980; Gilbert 1982). This deviates from the use of these terms in other (natural) sciences and in philosophy, where explanations of wholes in terms of interactions between their parts are considered paradigms of reductionistic (reductive) explanations (see chapter 3). Still, there is something to be said in favour of the usage of these terms in ecology.

As I have argued in chapter 5, a property of some whole can be called emergent if and only if it (or its instantiation) is either (1) not reducible to a micro-theory about its component parts, or (2) reducible to a such a micro-theory in conjunction with either a correlation hypothesis (about interactions between the parts) and/or a non-trivial aggregation hypothesis. A property cannot be called emergent if it is reducible to some micro-theory in conjunction with a trivial aggregation hypothesis and an identification hypothesis, because then it would be exactly identical to the sum of its parts. In other cases either non-trivial aggregation or correlation guarantees that 'the whole is more than the sum of its parts', the usual interpretation of emergence. In other words, a property that can be explained reductively in terms of a micro-theory and an auxiliary correlation hypothesis can be called emergent. Therefore, given the link between emergence and holism, there is something to be said in favour of the view in ecology that explanations of wholes in terms of interactions between parts may be considered 'holistic'. Apart from this, this view is probably also related to the fact that holism in ecology is associated especially with the idea of connections and interrelationships in nature. Interactions between species, resulting in food webs and nutrient cycles, provide exactly the sort of connections between species in communities and ecosystems to which holists attach so much importance and which, in their view, make them into higher-level entities. Thus, I will go along with the ecological interpretation of the term 'holistic' and I will characterize the position that emergent properties of wholes can be explained in terms of interactions between their parts as moderately holistic (but at the same time as moderately reductionistic, and thus above all things *moderate*).

A great deal of ecological research may be considered to belong to this moderate approach. This applies for instance to analyses of food chains and food webs in ecosystems (Cohen 1978, 1989; Pimm 1982, 1984, 1991), analyses of the structure and assembly of communities (Diamond 1975; Diamond & Case 1986; Cody 1989; Roughgarden 1989), investigations into the mechanisms of coexistence of species (Armstrong & McGhee 1976, 1980; Braakhekke 1980; Aarssen 1983) and the mechanisms of succession (Connell & Slatyer 1977; Tilman 1985; Gray et al. 1987; Olff 1992; van Andel et al. 1993) and, of course, to all the theoretical and empirical research of interactions between species that play a role in these matters. In the theoretical field there is an overwhelming amount of literature in the tradition of the logistic model of population growth by Verhulst (1838) and the competition models of Lotka (1925)

and Volterra (1926) based on it. Today, there are various 'resource-consumer' models which can be applied to several types of interactions between species (competition, predation, parasitism) and which go together under the name of niche theory (MacArthur 1968; Vandermeer 1974; Pianka 1981; Glasser & Price 1982; Schoener 1989). The 'classical' problem of the (phenomenological) Lotka/Volterra models, that they bear little or no relation to actual empirical situations and pertain to only two species, seems to become ever better solved by the modern (mechanistic) multi-species models. Modern niche theory, or the set of resource-consumer models that belong to it, seems to be a very serious candidate for an empirically adequate and general ecological theory (Schoener 1989; see also chapter 11).

As mentioned in 8.2.1 there has been, and still is, a major controversy in population ecology over the factors regulating population numbers, where the (holistic) self-regulatory school is opposed by the biotic, climate and comprehensive schools. Although this point of view is seldom taken, it is interesting to find out whether the other schools can also be characterized in terms of holistic or reductionistic positions or approaches.

The climate school of Andrewartha and Birch (1954, 1984), who stress fluctuations in population size and seek the principal determinants of population numbers in physical factors, such as weather and climate, can be easily characterized as radically reductionistic. The biotic school (Lack 1954; Nicholson 1954), who has many recent representatives, is a lot more difficult to classify. Since the emphasis is laid by this school on interspecific interactions (competition, predation, parasitism), at first sight one would be inclined to characterize it as moderately reductionistic (or moderately holistic; that is, moderate). However, this runs counter to, firstly, the fact that this school stresses the stability of populations and, secondly, the fact that it seeks to explain this stability, not in terms of interactions between the component parts (individuals) and abiotic environmental factors (the radically reductionistic approach) nor in terms of mutual interactions between the parts (the moderately reductionistic approach), but in terms of interactions with other species, that is, on a higher level of organization. At second sight, therefore, and somewhat paradoxically, the approach of this school should be characterized as (radically) holistic. The mechanisms of population regulation assumed by this school would be typical examples of so-called 'downward causation' (Campbell 1974), a major claim of holism (see chapter 2). This is again a nice example of the relativity of the terms 'holistic' and 'reductionistic': theories about interactions between species are to be counted as holistic when applied to the lower level of populations, but at the same time as reductionistic when applied to the higher levels of communities or ecosystems.

Incidentally, a similar paradox occurs with respect to the self-regulatory school. For on the grounds of its main ideas, about homeostasis (stability) and self-regulation, it should be characterized as radically holistic. However, in so far as it stresses intrinsic factors within populations (individual differences in behaviour and physiology; intraspecific competition), it should rather be characterized as moderately reductionistic.

Finally, we could characterize the comprehensive school, which considers both physical (density independent) and biological (density dependent) factors of importance in regulating populations, as moderate or as mixed holistic-reductionistic, but comprehensive doesn't sound like a bad term either.

8.2.4 Summary of approaches

Summarizing, we can distinguish between three basic approaches in ecology; (1) a radically holistic approach in which communities and ecosystems are viewed as discrete higher-level entities with their own structure and dynamics, which are largely independent of individual species' adaptations to local environmental conditions and which therefore should be studied at their own level; (2) a radically reductionistic approach in which the existence of communities and ecosystems as discrete independent ontological entities is being denied and in which it is claimed that they are actually nothing but random collections of species, which can be explained fully in terms of individual, autecological adaptations of species; and (3) a moderate or mixed approach in which it is acknowledged that communities and ecosystems are discrete higher-level entities with their own emergent properties, but which seeks the explanation of these properties especially in interactions between the component species.

With regard to the study of populations we can also, albeit not without some paradox, distinguish between a radically holistic approach (the biotic school), a radically reductionistic approach (the climate school), and a moderate or mixed approach (the comprehensive school). The self-regulatory school should be characterized on the one hand as radically holistic (homeostasis, self-regulation) and on the other hand as moderately reductionistic (intraspecific competition).

8.3 The intellectual immaturity of ecology

8.3.1 Reduction and co-operation

When we would try to apply the models of reduction and of co-operating research programmes discussed in part 1 to the reduction problem in ecology, we could say that three ingredients are required in order to solve this problem. Firstly, there must be some macro-law or theory about a certain higher level or organization (for example communities). Secondly, there must be some micro-theory about a lower level (individual species). And thirdly, there must be auxiliary hypotheses (or theories) in the form of aggregation, identification and/or correlation hypotheses, the latter dealing with interactions between species.

Thus one would expect co-operation to occur between 'holistic' and 'reductionistic' research programmes, *in casu* between systems or community ecological programmes and population or autecological programmes. Now to a certain extent this is indeed the case. As I have mentioned before, probably the majority of ecologists today share the moderate, mixed holistic-reductionistic view, which can be traced in many ecological handbooks. In these books attempts are made to integrate (mostly)⁴⁶ community ecological knowledge on the one hand and population and autecological knowledge on the other, which are indeed attempts to explain phenomena at the level of communities in terms of on the one hand autecological adaptations of species and on the other hand interactions between species. It is very difficult, if not impossible, however, to find concrete examples of successful reductions in these books. This is being caused by another problem, which is the almost complete lack of (well confirmed or corroborated) general laws and theories, at least at the level of communities (and

⁴⁶The common trend of the last few decades is that separate books on systems ecology appear, though in so far as community ecology deals with biocoenoses (the biotic components of ecosystems; see chapter 9) some systems ecology is described also in the more general handbooks.

ecosystems) but with some exceptions (such as competition theory) also at the level of species (apart from the 'imported' theories of natural selection and population genetics, of course, which play a central role in autecology and population ecology). To be sure, there are all sorts of candidates, such as, at the higher level, hypotheses about the relation between the number of species and the area of some particular piece of land or island, and the alleged relation between the diversity and the stability of a community or ecosystem. Also, there are several, rival, succession theories, and various classification systems of communities. Examples at the level of species are 'habitat theory'⁴⁷, which pertains to autecological adaptations of species; 'niche theory'⁴⁸, which pertains to the exploitation of resources by species; and various competition models and predator-prey models, which are more or less explicitly related to niche theory. However, with the possible exception of some competition models, none of these candidates is generally accepted, neither within nor amongst disciplines, and each of them is more or less controversial. In general one can state that in ecology on the one hand an enormous amount of empirical data has been gathered while on the other hand for over seventy years one has worked on the development of mathematical models, but there is still a lack of the combination of both: empirically testable, quantitative theories with a large explanatory and predictive power (McIntosh 1985).

8.3.2 The anomalous status of ecology

The lack of general laws and theories has been referred to as the 'intellectual immaturity' of ecology (Fretwell 1981; Strong et al. 1984; McIntosh 1985). Hagen (1989) speaks of the 'anomalous status' of ecology in this connection, because the intellectual immaturity is hard to rhyme with the enormous institutional growth of ecology during this century (when looking at scientific departments, institutes, societies, journals, etcetera). Though in my view this verdict is going a bit too far, because ecology happens to be very rich (perhaps even a bit too rich) in theories, models, hypotheses, concepts, etcetera, it does seem a fact that general, well-corroborated laws and theories are still lacking, at least at the higher levels of organization.

The question is, of course: why? In principle, two kinds of factors could be responsible, namely factors that have to do with the objects of ecological study, and factors that have to do with ecology as a science. As to the former, the factors most commonly mentioned are the complexity, variability and idiosyncrasy of ecological systems. In this context the term 'ecological systems' refers to both individual organisms in relation to the environment and

⁴⁷One will not be able to find something like a general 'habitat theory' in ecological handbooks. There are ideas about habitat selection and habitat differentiation, which are based on a particular habitat concept, but to my knowledge a general habitat theory has never been formulated, and there are many different habitat concepts. I will discuss these concepts in chapter 10.

⁴⁸One will also not be able to find a general 'niche theory' in ecological handbooks, even though such a theory *has* been formulated (Glasser and Price 1982). The reason is that *this* niche theory is not (yet) generally recognized as a full-blown and promising theory, and that the niche concept of this theory is confused with several other niche concepts. See chapter 10.

populations and communities, as well as ecosystems proper. Of course, the degree of complexity increases with the level of organization. The term 'idiosyncrasy' indicates that every ecological system is supposed to be unique, is supposed to have its own structure and dynamics. I will leave aside whether this is indeed the case, but it seems beyond doubt that ecological systems are extremely complex and variable. However, since this applies to a certain extent also to physical, chemical and other (non-ecological) biological systems, I consider this an insufficient reason for the lack of general laws and theories in ecology. Underlying this there seem to be also factors relating to ecology as a science.

As to this second type of factors, two appear to be conspicuous. The first one is a certain inability on the part of ecologists to come to agree upon a common vocabulary, a common and unambiguous conceptual apparatus. As a result, even the development of adequate conceptual theories is being impeded. Every few years there is a conference on 'unifying concepts' (van Dobben et al. 1975) or 'conceptual issues' (Saarinen 1981; Strong et al. 1984; Cherrett 1991; Allen & Hoekstra 1992) in ecology, and the list of publications in which the meaning of key terms in ecology is discussed is almost innumerable (see chapters 9 and 10). Conceptual analysis of the ecological literature reveals that such terms as environment, habitat, niche, community, ecosystem, diversity, complexity and stability are being used in multiple different and sometimes incompatible ways (see also Pimm 1991; Allen & Hoekstra 1992; Shrader-Frechette & McCoy 1993). Naturally, this is not to say that an unambiguous vocabulary is a guarantee to the discovery of general laws and theories, but the prevailing ambiguities do seem to be sufficient for the lack of them.

8.3.3 The inhibitory effect of the holism-reductionism dispute

Hagen (1989) points to a second factor which, in his (and my) view, seems responsible for the anomalous status of ecology. This is the existence, apart and more or less separate from, but primarily opposite to each other, of two different approaches, or 'perspectives' as he calls them, analogous to visual perspectives. These are a '*merological*' and a '*holological*' perspective. Both terms are originally due to Hutchinson (1978). "According to Hutchinson (1978), the merological approach focuses upon populations of independent organisms and is based on the assumption that populational phenomena determine the properties of higher levels of ecological organization. The holological approach focuses upon the flow of materials and energy through ecosystems without considering the organisms that are the constituents of the system" (Hagen 1989, p. 434). Though Hagen himself does not wish to use the terms reductionistic and holistic, it will be clear that the indicated approaches are those of, respectively, reductionistic population ecology and holistic systems ecology.⁴⁹

According to Hagen, the two perspectives are in principle complementary, since they deal with different research areas (domains or levels of organization), but there are certain grey areas where it is unclear which perspective applies or where both could apply (and hence compete). (Hagen doesn't provide examples of such grey areas but one may think of, for instance, analyses of food webs, models of interspecific interactions and coexistence studies.)

⁴⁹According to Hagen, the chief difference between the two perspectives is that the merological perspective is primarily demographic, whereas the holological perspective is primarily physiological. This may be so.

Indeed, starting at the beginning of the sixties, the two approaches have more and more become opposites. This has led to many controversies and polemics which have contributed little or nothing to the clarification of ecological issues. As the best known example Hagen mentions the controversy over the (alleged) cybernetic nature of ecosystems (see 8.2.2). He also mentions the controversy over group selection between Wynne-Edwards (1962) and Williams (1966) (see 8.2.1) as a major cause of the divergence of the two perspectives.⁵⁰

I broadly agree with Hagen and in chapter 13 I will discuss another controversy which is characteristic of the inhibitory effect of the holism-reductionism dispute on the growth of ecological knowledge. Particularly this controversy shows, however, that matters are a bit more complicated than Hagen puts them. He writes that "The merological perspective is reflected in two quite different traditions in ecology. Although these two traditions share important characteristics, they have sometimes been at odds with one another (Strong et al., 1984; Diamond and Case, 1986). One tradition emphasizes the importance of stochastic processes, and stresses the independence of individual populations. The other considers populations to be part of tightly knit communities, and assumes that demographic changes are due primarily to deterministic interactions, such as competition and predation" (Hagen 1989, p. 439). These are the approaches which I have called the radically reductionistic and the moderate approach, respectively, and it is between these two approaches that the controversy occurred which I will discuss in chapter 13. It doesn't seem fit to me to unite two such different approaches under one (the merological) perspective. Hagen himself notes with respect to the moderate approach that "these ecologists have also incorporated part of the holological perspective into their thinking. Indeed, some members of this tradition have taken an intermediate position between the extreme merological and holological perspectives" (p. 442). It seems to me that this intermediate position had better be distinguished as such.

8.4 Remainder of the book

In the remaining chapters of this book I will first discuss some examples of the ambiguities within the ecological vocabulary, to wit the term 'community' (chapter 9) and the terms 'habitat' and 'niche' (chapter 10). However, rather than merely discussing their ambiguity, my aim will be provide conceptual clarifications of these terms and to define them unambiguously. The results of this will hopefully be of interest in themselves, but they are also necessary for my chief purpose in the next chapters. This purpose is to substantiate my claim that in ecology too, holism-reductionism disputes notwithstanding, holistic and reductionistic research programmes are mutually dependent. I will do so by providing two examples of reduction in ecology involving the co-operation of holistic and reductionistic

⁵⁰At this point I do not agree with Hagen. In the first place, the controversy between Wynne-Edwards and Williams was a controversy in evolutionary biology rather than in population ecology (though it was of course of interest to the latter). In the second place, the merological and holological perspectives already existed long before the controversy between Wynne-Edwards and Williams took place, as evidenced by the Clements-Gleason controversy. In the third place, the rise of holistic systems ecology in the sixties has been a much greater influence in the divergence of the two perspectives (Simberloff 1980; Kwa 1984; McIntosh 1985).

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research programmes. The first example (chapter 11) is the reduction of the classical Lotka/Volterra competition model to modern niche theory, where the latter employs, of course, one concept in particular of the various niche concepts discussed in chapter 10. The second example (chapter 12) concerns some developments in island biogeography which can be described very well in terms of the model of idealization and concretization discussed in chapter 3, and hence in terms of approximative reduction. It pertains to MacArthur and Wilson's (holistic) equilibrium theory of island biogeography and subsequent attempts of later (moderately and radically reductionistic) programmes to concretize (approximately reduce) this theory. As mentioned, in chapter 13, finally, I will discuss 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 programmes involved in the attempts to concretize the MacArthur-Wilson theory, where the one programme is radically reductionistic and where the other is moderately reductionistic but also has some radically holistic elements. The controversy has lasted for approximately ten years, appears to have died out rather than to have been resolved, and has produced no new insights. I will show, however, that ultimately the controversy can be settled, and in a way has been settled, in a way that corroborates my thesis.