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The hierarchy and spatial characteristics of ecosystems: A reconsideration of the ecosystem concept (II)

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Abstract — This paper, based on the autonomy concept, continues to investigate hierarchical forms and spatial structure of ecosystems. The former can lead to limits for the selection of the component parts of an ecosystem and a distinction between its endogenous and exogenous variables; and the latter can be lead to a hypothesis of the space of an ecosystem: the space of an ecosystem = its habitat area + supporting area + impact area, and two characteristics of ecosystems, space-overlapping and the area of ecosystem space, have been further studied referring to human activities.

Keywords: ecosystem; autonomy; hierarchy; spatial characteristics.

INTRODUCTION

The study of functions and structures of ecosystems have been maintaining the center of ecosystem theories. Several approaches have been developed, which include the highly complicated Energy-Circuit Diagrams by H. T. Odum (Odum, 1971), an Environs concept by Patten (Patten, 1982), an "IE + S + OE" structure by E. P. Odum (Odum, 1983), and "Dual Hierarchies" by O'Neill *et al.* (O'Neill, 1986). We have redefined the ecosystem using the concept of autonomy (Xu, 1991). Now we continue to investigate further the interrelationships within ecosystems which, we presume, have a degree of a autonomy and show hierarchical forms and spatial characteristics, whilst a comment will be given to E. P. Odum's concept mentioned above.

AUTONOMY AND THE HIERARCHY OF INTERRELATIONSHIPS WITHIN ECOSYSTEMS

We have re-defined the ecosystem using the concept of autonomy. Now we will discuss further the interrelationships within ecosystems in which we presume that there is a degree of autonomy. Ecologists seek to recognize and identify the nature of these interrelationships.

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Tansley pointed out that the ecosystems "are of various kinds and sizes" (1935), while Lindeman stated that the ecosystem is "a unit of any magnitude" (1942). Odum has further discussed the connections between ecosystems, biomes and the biosphere or ecosphere (1983). In general, the interrelationships within ecosystems are hierarchical in form. These hierarchies essentially come from the open and closed aspects of ecosystems.

It is obvious that ecosystems are open systems(Young, 1974; Odum, 1983). This is because:

1. All ecosystems are open to the sun, on which they depend for their survival.

2. Because of the mobility of materials and energy, all ecosystems must be open to the atmosphere and climate. This means that ecosystems are connected with each other through those flows.

3. Because of the migration of biological organisms. This is "the species channels through which matter and energy move" (Elton, 1949). The biotic connections (including edge effects) between ecosystems are strengthened. This means that ecosystems are open to others.

4. As human beings develop, utilize and reconstruct natural ecosystems, all ecosystems are forced to be open to human beings. The reason that these open aspects lead all ecosystems to become the same is that all ecosystems also have closed aspects, and the nature of an ecosystem is determined by both its open and closed aspects.

The closed aspects of ecosystems result from the fact the influences of their component parts are region-limited. Thus, the open aspects emanate from interaction with external systems, while the closed aspects are derived from internal factors which depend on the special nature of an ecosystem. They are both necessary elements for the ecosystem hierarchies which exist not only within ecosystems, but between them.

From this, we can see that there cannot be completely closed ecosystems, as all of them are open to some extent. This means that strictly speaking no ecosystem can be completely autonomic. Theoretically the whole world is much more autonomic than its parts. But SST community systems can be considered as the autonomic for practical purposes for the reasons given early. As ecosystems always exhibit closed aspects manifested in, a degree of autonomy can exist even in non-autonomic systems. Now, we will discuss the autonomy of ecosystems by means of the concept of hierarchy. Some studies on the hierarchy of biosystems (including ecosystems) have been made by Allen and Starr (1982), and O'neill, DeAngelis, Waide and Allen (1986). But we can carry out the analysis in another way.

The autonomic interrelationships of an ecosystem are shown in Fig.1. In this, a hierarchy of interacting community systems are depicted, without any indication as to what constitutes an ecosystem.

In Fig.1, community system 1 (CS1) is an IOT. It, as the study object, is at the primary level of the hierarchy. Community system 2 and community system 3 (CS2 and CS3) have direct effects on CS1, and are thus at the second level of the hierarchy. Community systems

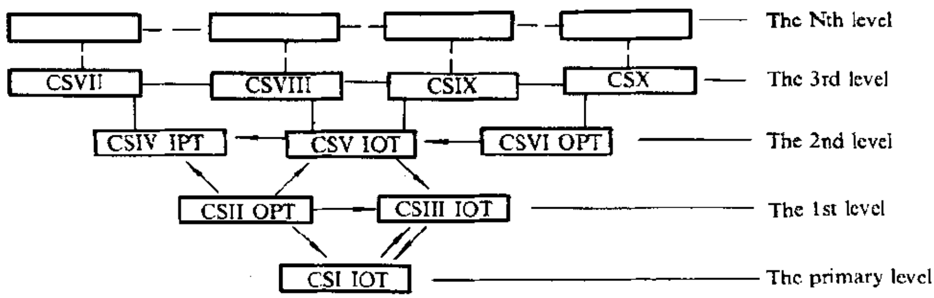


Fig. 1 The hierarchical structure for the study of CS1

4, 5 and 6 (CS4, CS5 and CS6) have the first-order indirect effects on CS1, and are thus the second level of the hierarchy. Similarly, CS7, CS8, CS9 and CS10 have the second-order indirect effects on CS1, and are thus at the third level of the hierarchy and so on. Thus a hierarchical structure exists between the primary level and the nth level. What, then, in this hierarchy constitutes an ecosystem? If we assume that CS1 is the core part of an ecosystem, according to Fig. 1 there are both direct and indirect effects upon it. Sometimes, some indirect effects may be of importance as much as direct effects, so that they cannot be ignored (Patten, 1982). Thus the community systems which have important indirect effects should also be considered parts of the ecosystem for the study of CS1. However the formulation of the study object mentioned early, includes the direct effects only, but not the indirect effects. It means that the formulation implies autonomy only in form, and not in essence. Thus, formulation is only the first the step in determining an ecosystem. The second step is the inclusion of some necessarily indirect effects.

We will now consider the problem of determining which indirect effects are to be included in an ecosystem. From Fig.1, we can see that the higher the level of the hierarchy, the smaller its indirect effect are on the study object CS1. This means that there is a certain level above which the indirect effects are so small as to be ignored, and where there is autonomy in the study of CS1.

It is obvious that the choice of the level of hierarchy is direct related to the level of precision that the study needs to attain, and the complexity of ecosystem. In general, the higher the demand for precision, the higher the level of the hierarchy of the ecosystem, and the more complex the ecosystem that will result. In a hierarchical system, the relationship between the precision and complexity of the system is not proportional, but comprises an "S" as shown in Fig.2.

In Fig.2, below A there is little complexity or autonomy for the study object, and the ecosystem so defined does not satisfactorily met the need for precision. Thus A can be termed the lower limit in ecosystem definition. And above B, the complexity added raises the level of precision slightly, but is expensive in terms of the cost of research. Thus B can be termed the upper limit in ecosystem definition. In summary, then, an ecosystem should be chosen between the lower limit, A, and the upper limit, B, according to the demands of precision and cost. This seems to be the reason that the boundaries of ecosystems are sometimes obscure (Van, 1966).

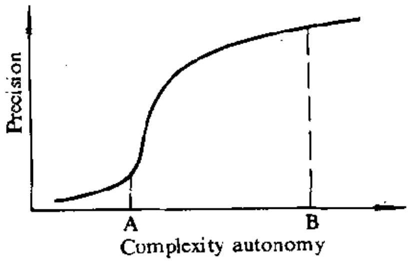


Fig. 2 The precision-to-complexity curve

The definition of an ecosystem is also related to concepts of endogenous and exogenous variables. In systems analysis, endogenous variables and exogenous variables have different characters and functions. Exogenous variables are usually used to present the interactions between the system and extra-systems. The effects of such extra-systems on the system are pre-set. Endogenous variables are used to present the interaction of components of the system. They are constrained by both external and internal effects. And exogenous variables cannot present the reactions of extra-systems on the system after they have been affected by the system. This is the main difference between endogenous and exogenous variables in systems analysis.

The choice and determination of endogenous and exogenous variables are very important in ecosystems analysis. Ecosystems can be viewed as being cybernetic in nature (Patten, 1981; McNaughton, 1981), because they exhibit feedback effects (Wiener, 1948) The feedback effects in ecosystems are basically of three kinds, as shown in Fig.3.

In Fig.3, A is the study object, such as a population, a community or a community system, and B is a component part which interacts with A. In this case, Type 1 feedback is that directly occurring between A and B with the form A, B; Type 2 is that which takes the form A, B, C, indicating that the feedback from B to A is through C; and Type 3 is that which takes the form A, B, D, E, indicating that the feedback from B to A contains the influence of D and E. Similar analyses also apply to other component parts.

Thus, if ecosystem research is focused on A, some of the associated factors, such as B, C, D and E, which together with A exhibit feedback effects, should be considered as endogenous variables, since exogenous variables cannot exhibit feedback effects.

Whether or not a component part is treated as an endogenous variable depends not only on whether it exhibits feedback effects, but also on what its role is in feedback is. If its role in feedback is too insignificant, the relevant elements can, for practical purpose, be considered as exogenous variables.

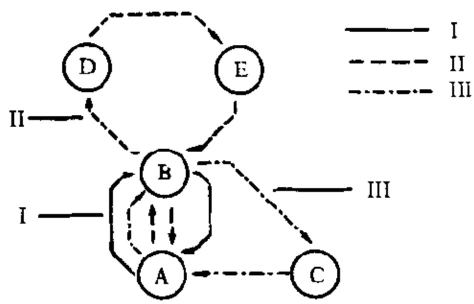


Fig.3 Three kinds of feedback between A and B

We are now in a position to summarize the discussion in this section. Because of the open and closed aspects of ecosystems, the interrelationships within ecosystems have a hierarchical structure. An ecosystem which has a degree of autonomy can be defined within this hierarchical structure, based on upper limit and lower limit of precision and complexity. Finally, the choice and determination of endogenous and exogenous variables in ecosystems can be made on the absis of feedback relationships.

THE SPATIAL CHARACTERISTICS OF ECOSYSTEMS

Spatial analysis is crucial in ecology. The spatial elements in ecology include for aspects: "distribution, `natural area', location, and interractional field "(Young, 1974). Some attention has been paid to spatial characteristics in recent thinking about the ecosystem, but not enough.

Margalef (1968), in discussing the divisibility of ecosystems, suggested the concept of spatial distance for the interaction between two elements. He argued that the interactions will be stronger the closer together are the elements. This can be viewed as micro-analysis of the spatial concept of ecosystems.

As to the macro-aspect of the spatial concept, Elton (1949), in a discussion of the methodology of ecosystem research, suggested that one should choose an area which is small enough to make detailed investigation feasible and which is sufficiently representative to enable comparisons to be made with the system as a whole. Elton and Miller (1954) made a further point arguing that an ecosystem is "composed of comparatively limited minor centers of action, each having certain distinctive characteristics as habitat, that are reflected in their communities, and which have a considerable amount of interchange by lateral and vertical movements". It is also interesting to note that Elton proposes a multi-community view of the ecosystem, which is put forward in the present paper. Major(1969) has pointed out that we must consider the spatial nature of ecosystems, which "will be add to what should be a continuing examination of our assumptions and logical position"

There are, however, several conceptual problems concerned with the spatial concept of ecosystems. We therefore analyze firstly the contradictions that result from different understandings of ecosystem space. From this, a new concept of ecosystem space is suggested. Finally, the significance of the concept of ecosystem space is examined.

In ecology, one of the prevailing conceptions is that there are two sorts of ecosystems: the autotrophic and the heterotrophic. This distinction is invalid, and stems from a misunderstanding of ecosystem space.

In Odum's works (1971, 1975, 1983), pond and lake ecosystems are considered to be examples of a autotrophic ecosystems, and oyster reefs are considered to be heterotrophic. For a detailed explanation see Odum (1975).

Fig.4 shows a lake.

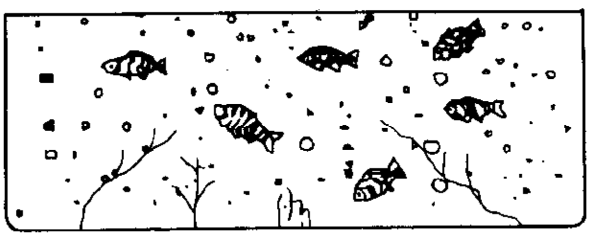


Fig.4 The view of a lake (after Odum, 1975)

Odum defines the lake itself as an ecosystem, and the boundaries of this ecosystem are delimited by the banks and the bottom of the lake. It means that the space of the lake ecosystem is that the lake itself. Thus Odum calls the lake an "• autotrophic ecosystem", because the food of fishes (the consumers in the lake ecosystem) can be provided by the lake ecosystem itself (namely, by the producers in the ecosystem). Fig. 5 represents an oyster reef.

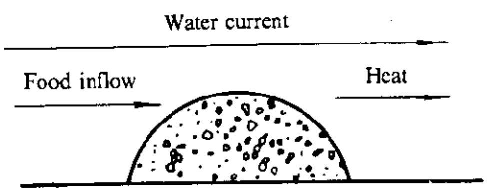


Fig.5 The view of an oyster reef (after Odum, 1975)

Odum similarly defines the oyster reef as an ecosystem. The boundaries of the oyster reef is also the boundaries of the ecosystem. It means that the space of this ecosystem is the oyster reef itself. Odum calls the oyster reef ecosystem a "heterotrophic ecosystem", because the food of oysters can only be provided from the outside of the ecosystem, since the oyster reef itself lacks the producers and the nutrient environment necessary to support the oysters.

However, the behaviors of both oysters an fishes are very similar: they are both heterotrophic species, their food must both be provided from their surroundings, and their wastes and heat must both be dispersed to and decomposed in their surroundings. Why is the lake called "an autotrophic ecosystem" but the oyster reef "a heterotrophic ecosystem"? What is interesting is that we can obtain another conclusion on the lake and the oyster reef, which is completely different from those mentioned-above, if we use different logic.

Firstly, suppose that the lake is divided into several layers by food webs, with different species of fish living on the different layers. This is shown in Fig.6.

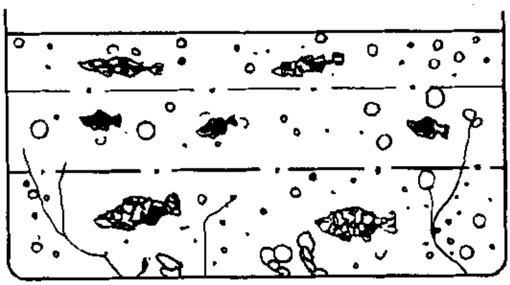


Fig.6 Another understanding of the lake

In this case, each layer of the lake can be taken as an ecosystem, and they all are heterotrophic, because the food of fishes in a given layer must be provided from outside of that layer.

Secondly, suppose that the oyster reef ecosystem contains not only the oyster reef itself, but also its surrounding area which extends sufficiently to provide enough food for the oysters. This is shown in Fig.7.

In this case, the oyster reef ecosystem is not heterotrophic but autotrophic, becuase the ecosystem has enough producers to provide food for the oysters.

In the above discussion, we can see that the key lies in an understanding of the space of ecosystems. Differents concepts of ecosystem space can lead to diametrically opposed conclusions for the same ecological object. These different concepts of ecosystem space arise from different definitions of the ecosystem concept.

Most ecologists agree that an ecosystem should contain the non-living environment, producers, consumers and decomposers. Thus every ecosystem always has its own autotrophic component parts (producers) and its own heterotrophic component parts (consumers and decomposers). As previously pointed out, an ecosystem must exhibit a degree of autonomy in relation to the study object, so that its two component parts, the autotrophic and the "heterotrophic" are in equilibrium. Thus it is clear that the "autotrophic" and the "heterotrophic" are not different types of ecosystem, but describe the trophic characteristics of species, populations and communities. The so-called "atrophic" ecosystems are SST community systems, while the so-called: heterotrophic" ecosystems are IPTs and IOTs. We have already demonstrated that the IPTs and IOTs cannot be regarded as ecosystems if the study objects are the IPT and IOT themselves or their component parts which suffer the external effects seriously. The oyster reef can be taken as an example. If the study object is the oysters or the oyster reef, Fig.7 rather than Fig.5 must be taken as the ecosystem. It means the oyster reef ecosystem should contain not only the oyster reef but its immediate surrounding area. Here we can also see that the difference in spatial character between ecosystems and community systems. In general, the size of a community system is fixed, but the size of an ecosystem may change depending on the nature of study objects.

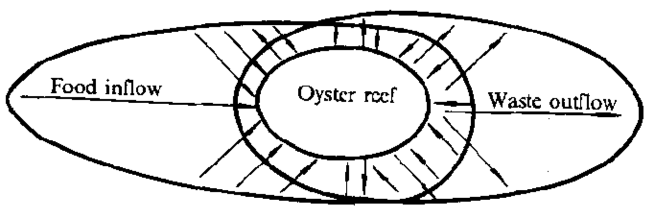


Fig. 7 Another understanding of the oyster reef

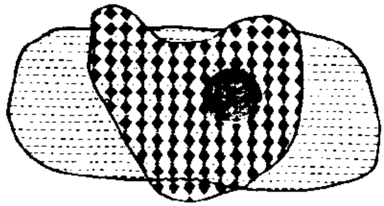
Thus, according to the discussion of the ecosystem concept in previous sections, the correct definition of lake ecosystems and oyster reef ecosystems are Fig.4 and Fig.7 respectively. The real difference between them does not lie in their trophic behaviors but in their spatial structure.

Fig.5 is acceptable according to Odum's Definition 1 and 2, but Fig.7 is valid according to Odum's Definition 3. This illustrates the difference between these three definitions.

Ecosystem space can be determined by combining our new definition of an ecosystem. The whole space of an ecosystem can be considered to include three parts: a. the habitat area (HA), where the studied object is located; b. the support area (SA), where functional inputs to HA take place; and c. the impact area (IA), where the functional outputs from HA manifest themselves. The spatial structure of an ecosystem can be shown in Fig.8.

In Fig.8, HA, SA and IA are always located in relation to community systems, their areas partly overlap, and their boundaries can be determined by the previously discussed limits.

In order to illustrate the concepts of HA, SA and IA, several kinds of ecosystem space



● Habitat area ◐ Supporting area ○ Impact area

Fig. 8 The space of an ecosystem: HA, SA and IA

are shown as follows:

1. A lake (Fig.9).

As the lake is SST, the HA, SA and IA of the lake ecosystem overlap each other. The SA and IA may contain the ecotones of the lake.

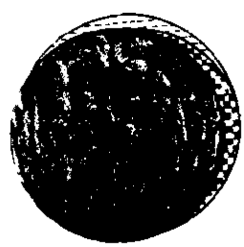
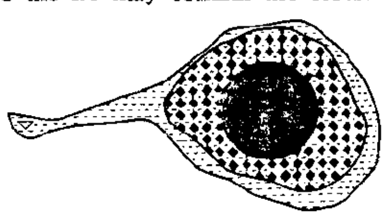


Fig. 9 The space of a dosed lake ecosystem

2. A woodland (Fig.10)

This woodland is IPT, so that the SA of the woodland ecosystem must at least include the terrestrial water source, and the IA may contain the ecotone of the woodland.



▽ Water-source site

Fig.10 The space of a woodland ecosystem

3. An oyster reef (Fig.11)

As the oyster reef is IOT, the SA of the oyster reef ecosystem must contain the area from which the food of oysters is provided, and the IA must contain the area where the detritus (heat or materials) of the reef is sent to.

To sum up, the spatial structures of the ecosystems associated with different types of

Table 1 The spatial structures of the ecosystems (associated with different types of community system. IPTs, OPTs and IOTs denote those community systems which the ecological study does not focus on, see text)

Type of community system	Support area	Habitat area	Impact area
SST	Ecotone + HA	SST	Ecotone+HA
OPT	Ecotone + HA	OPT	IPTs / IOTs+HA
IPT	OPTs / IOTs+HA	IPT	Ecotone+HA
IOT	OPTs / IOTs+HA	IOT	IPTs / IOTs+HA

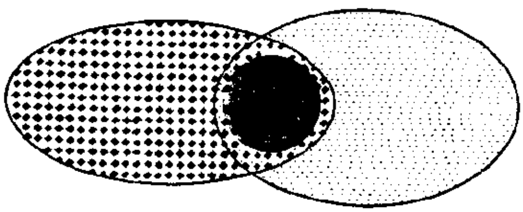


Fig. 11 The space of an oyster reef ecosystem

community system can be summarized in Table 1.

From this discussion of the spatial structure of ecosystems, some new ecological characters and behavior patterns are revealed, both which may be of value in understanding the ecosystem concept.

Space-overlapping in ecosystems

There are two sorts of space-overlapping of ecosystems:

1. Within an ecosystem

This means that the SA and IA may overlap partly or completely with each other. Space-overlapping between the SA and the IA can be shown in Fig.8 (shaded). The shaded area shows the influences on and from the HA.

2. Among ecosystems

This can be shown in Fig.12.

The shaded parts in Fig.12 express the interactions of the ecosystems. These interactions may include competition for nutrients or the processes involved in the decomposition of detritus. In general, the larger the overlap between ecosystems, the wider the interaction field and the stronger the interactions. The degree of interaction in Part 1 is obviously stronger than that in part 2 and part 3. Fig.12, however, just shows the space-overlapping of SAs among ecosystems. A more general consideration must include the space-overlapping of IAS. It is clear that the spatial patterns of ecosystems may be helpful when analyzing complicated

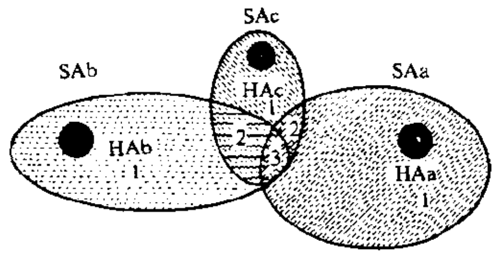


Fig. 12 The space-overlapping of different ecosystem

ecosystems like urban ecosystems (Xu, 1989).

Aerial characters of ecosystems

By comparing the areas of HA, SA and IA, we can find that there are two sorts of distribution patterns of ecosystems.

1. Well-distribution patterns

In this situation, the areas of HA, SA and IA overlap with each other. It means that the producers, consumers, decomposers and the non-living environment are distributed in the ecosystem in equilibrium. This pattern can be termed "area-nutrition, area-production, area-consumption and area-decomposition" . Most natural ecosystems, namely SST community systems, have this sort of pattern.

2. Non-well-distributions pattern (area-point patterns)

In this situation, since HA, SA and IA do not overlap with each other, the aerial characteristics of an ecosystem is SA > HA, or IA > HA, or both. Stressed ecosystems and some man-made ecosystems have this pattern. If SA > > HA, or IA > > HA, the aerial characteristic of the ecosystem can be regarded as point for HA, and area for SA or IA. In this case, the non-well-distribution pattern can be regarded as "point-area patterns", shown in Fig.13.

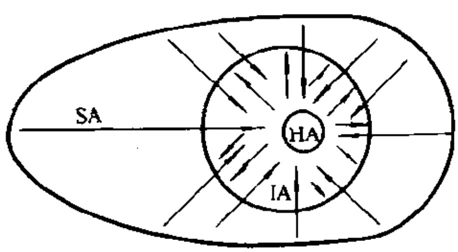


Fig.13 The "point-area" pattern of ecosystems

The point-area pattern is very important in ecological studies. A typical case can be shown in Fig. 13. The pattern in Fig. 13 can be termed "area-nutrition, area-production, point-consumption and area-decomposition" . Since SA > > HA, namely "area-nutrition, area-production and point-consumption", it implies a high rate of material accumulation and consumption in HA. The larger the ratio of SA/HA, the higher the rate of material accumulation and consumption. Since IA > > HA, namely "point-consumption and area-decomposition", it implies the heavy discharge of detritus from HA. The larger the ratio of IA/HA, the heavier the discharge is.

We can also discuss this pattern from another view. Suppose that the ratios of SA/HA and IA/HA is definite, if the rate of material accumulation in HA exceeds the support ability of SA, a nutrient crisis will arise, and if the rate of detritus discharge from HA exceeds the capacity of decomposition in IA, a decomposition crisis will arise. Both imply ecological crisis. This analysis can be applicable to urbanization, environmental quality, resource shortage and other human problems (Xu, 1989).

CONCLUSIONS

This paper reviews the development of the ecosystem concept. Tansley's thinking about the ecosystem is summarized as four aspects: autonomy of ecosystems, component parts or attributes, material basis of interchange, and spatial characteristics. Advances in understanding the ecosystem have been greatest in the second and third aspects. Less progress has been made in the remaining aspects. This has led some deficiencies in previous definitions of the ecosystem.

By means of a transitive concept, the community system, the autonomy of ecosystems can be discussed. The main difference between ecosystems and community systems is that the former are functional systems, which must exhibits a degree of autonomy in relation to the study object, whereas the latter are habitat or biogeographical systems, which need not necessarily exhibit autonomy. Thus, any definition of the ecosystem must refer to autonomy and a study object.

Based on autonomy, the interrelationships of community systems can be examined in a hierarchical form. Limits can be determined to guide the selection of the component parts of the ecosystem. A distinction between endogenous and exogenous variables can be made.

Based on autonomy, the ecological space of an ecosystem must contain three kinds of area: habitat area (HA). support area(SA) and impact area(IA). The space of an ecosystem = HA+SA+IA. This leads to two spatial characteristics of ecosystems: space-overlapping and the area of ecosystem space. Both are valuable for the study of complicated ecosystems.

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