Biol. Rev. (2008), **83**, pp. 71–78.
doi:10.1111/j.1469-185X.2007.00032.x

Levels of organization in biology: on the nature and nomenclature of ecology's fourth level

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(*Received* 30 *May* 2007; *revised* 15 *October* 2007; *accepted* 22 *October* 2007)

ABSTRACT

Viewing the universe as being composed of hierarchically arranged systems is widely accepted as a useful model of reality. In ecology, three levels of organization are generally recognized: organisms, populations, and communities (biocoenoses). For half a century increasing numbers of ecologists have concluded that recognition of a fourth level would facilitate increased understanding of ecological phenomena. Sometimes the word "ecosystem" is used for this level, but this is arguably inappropriate. Since 1986, I and others have argued that the term "landscape" would be a suitable term for a level of organization defined as an ecological system containing more than one community type. However, "landscape" and "landscape level" continue to be used extensively by ecologists in the popular sense of a large expanse of space. I therefore now propose that the term "ecoscape" be used instead for this fourth level of organization. A clearly defined fourth level for ecology would focus attention on the emergent properties of this level, and maintain the spatial and temporal scale-free nature inherent in this hierarchy of organizational levels for living entities.

Key words: ecoscape, landscape, ecosystem, ecological system, spatial ecology, hierarchy theory, community ecology, emergent properties, holism, spatial and temporal scales.

CONTENTS

I. INTRODUCTION

Hierarchical arrangements are increasingly being appreciated by ecologists as meaningful conceptual schemes, both for heuristic purposes and to guide research questions and protocols (Ahl & Allen, 1996; Allen & Hoekstra, 1992; Allen & Starr, 1982; Lidicker, 1988; McIntosh, 1963; Odum, 1953; O'Neill, DeAngelis, Waide *et al.*, 1986; Rowe, 1961; Urban, O'Neill & Shugart, 1987). In this essay, I focus on one particular hierarchy, namely, the conventional levels of organization of life. I review the current status of the ecologically relevant portion of this hierarchy and ask if a fourth level for ecology is warranted. If so, what should it be called? Sometimes hierarchies are nested, as in the one under scrutiny here, in that each level is composed of parts representing the next lower level. However, other hierarchies are not nested, the levels being recognized by the importance of differing constraints characteristic of each level (Ahl & Allen, 1996). Often these constraints are tied to varying spatial scales and temporal frequencies that

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characterize entities at each level. Examples of non-nested hierarchies of interest to ecologists are behavioural dominance, trophic levels, social groupings, military rankings, and business organizations. Recently, a provocative non-hierarchical approach to conceptualizing emergent properties of ecological systems has been proposed (Ponge, 2005).

The nested levels of organization hierarchy has been widely adopted by biologists, and in some form or other appears in many introductory texts. It is sometimes called the "pyramid of life" because, being nested, each successive level contains fewer and fewer instances. This widely appreciated hierarchy, applying to all of biology, is based on the holistic notion of systems. Each level in the hierarchy is represented by a system composed of interacting parts which are also in themselves systems (holons). As such, a given system provides the organizational framework for the functioning of the parts, as well as the context within which the focal system is itself a subsystem. As Ahl & Allen (1996) explain it: the parts determine what is possible in principle, and the context limits which of these possibilities can in fact be realized. An important feature of this hierarchy, which may be viewed as a disadvantage for some purposes, is that each level is arbitrarily defined in a way that is scale independent. The real world is of course much influenced by matters of spatial and temporal scale, and this is being increasingly appreciated (Peterson & Parker, 1998; Urban *et al.*, 1987; Wiens, 1989). Therefore there are limits on the extent to which the levels of organization concept can successfully model life's real organization. On the other hand, being liberated from complications of scale allows one to focus on the implications of the increasing complexity generated by successive levels in the hierarchy.

The fact that ecologists widely acknowledge the utility of viewing the universe as composed of hierarchically arranged systems, implies no less than that ecology as a discipline may be appropriately defined as "the study of ecologically relevant systems" (e.g. Evans, 1956; McIntosh, 1963; Tansley, 1935). Yet, incredibly there is no generally accepted definition of a level of complexity above that of the three traditional ones of organism, population, and community. This is the case even though the need for recognizing a fourth level has been felt for more than half a century.

It should be emphasized that assignment of a phenomenon of interest to a level of organization is only the starting point in our quest for understanding. Experience tells us, however, that it is an efficacious place to begin. The history of ecology (Golley, 1993; Lidicker, 1994*a*, 2002*a*; McIntosh, 1985) illustrates the increasing depth of understanding that has been achieved as successive levels of organization have been incorporated into disciplinary discourse (Table 1). This success alone is a signal that, imperfect as it is, the levels of organization approach provides a useful model for material reality. Once this level is determined in any real situation, the next imperative is to establish the spatial and temporal dimensions of the system of interest.

Before addressing the nature and nomenclature of a fourth level in the ecological hierarchy, I briefly review the relevance of general systems theory for ecology, as well as the current status of the three levels of organization generally recognized.

II. THE SYSTEMS CONCEPT

The essence of the systems concept (Bertalanffy, 1950; Friederichs, 1958; Koestler, 1969; Lindeman, 1942; Novikoff, 1945; Odum, 1953; Smuts, 1926; Tansley, 1935) is that a system consists of a three-dimensional portion of the universe over a specified time period. The boundaries of a system are arbitrary in principle but are most usefully matched to natural discontinuities of matter and energy such as the planet Earth or an individual human being. In addition to the boundary, a system contains parts which interact with each other, as well as inputs and outputs (fluxes). Aside from these five components, the most important property of a system is that as a whole it has features not possessed by its constituent components. These

Table 1. Ecologically relevant levels of biological organization. Those placed in square brackets are speculative, requiring further investigation

Level	Biotic parts	Subdiscipline
Organism (multi-cellular)	Organs	Physiological ecology
Population	Two or more individuals of one kind or species	Population ecology
Community (biocoenosis)	Populations of two or more kinds or species	Community ecology
ECOSCAPE	Two or more community types	Landscape ecology "Spatial ecology", "Ecosystem ecology"
[Biome]	[Ecoscapes]	[?]
[Physiographic (topographic) region; ecoregion]	[Biomes]	[?]
[Biotic province; bioregion]	[Physiographic units; ecoregions]	[?]
[Continents, ocean basins]	[Biotic provinces]	[?]
Biosphere (ecosphere)	Continental and ocean basin biotas	Global ecology

new properties arise as a consequence of the interactions among the parts as well as constraints that arise from the system's context, and are called 'emergent'. Water is a molecular system that has properties much different from those of its atomic parts, namely hydrogen and oxygen. The second most important property of systems is that their parts are themselves systems (or subsystems). These subsystems are in turn composed of even smaller systems, *etc*. It is this property that gives rise to the nested hierarchical nature of the universe's organization. Solar systems, for example, are parts (subsystems) of galaxies.

In biology, systems thinking and its hierarchical corollaries takes the form of a progression in levels of organization or of relative complexity. Biological systems (which are invariably open) all contain at least one living subsystem (part or holon), and so living systems have the additional attribute that they contain both biotic and abiotic components. Each level of the biological hierarchy of complexity from cellular organelles to the biosphere is characterized by a suite of emergent properties. Because these new features require scientific attention, the various levels are associated with recognizable subdisciplines (Table 1), for example, cell biology and population biology.

III. THE ECOLOGICAL LEVELS

The infiltration of systems thinking into ecology has been gradual and controversial, but its roots are deep (Allen & Hoekstra, 1992; Lidicker, 1978, 1994*a*, 2002*a*; Mares & Cameron, 1994; McIntosh, 1985; Odum, 1953). Ecologists are interested in levels of biological organization from the organism upwards. In other words, any system that contains at least one living organism is an ecological system. At the dawn of ecology as a discipline, most viewed it as a branch of physiology (Lidicker, 1994*a*, 1995). The primary focus was on individual organisms and their environmental relationships. Later this focus was labeled "physiological ecology" or "autecology." Attention to population processes was soon added to the discipline, although this move to a higher level of complexity was met with predictable resistance (Mason & Langenheim, 1957). Population systems are defined as ecological systems containing more than one individual of the same "kind" (usually species). The new component in these systems is the interactions among the individuals, and this is what generates the new suite of emergent features. As ecology progressed, the community (biocoenosis) level of organization was added. This time there was even more anxiety and trepidation, which generated controversy that continues even to the present. There are still ecologists who deny that communities constitute ecological systems, and view a community as merely a list of species that live in some particular place and are of special interest to the investigator. Some of this disagreement stems from confusion between community classification and the concept of community as particular living systems. In a systems context, communities are ecological systems composed of two or more species (kinds) of living organisms.

Thus it developed that ecology encompasses three levels of biological organization: organism, population, and community, and three subdisciplines exist in recognition of the unique attributes of each level (Table 1). These three levels represent ecological systems arranged hierarchically, albeit imperfectly nested. In 1935, Tansley coined the appropriate term 'ecosystem' as a short-hand jargon to incorporate this systems viewpoint (Evans, 1956; Golley, 1993; Lidicker, 1994*a*; Lindeman, 1942; Odum, 1953). Emergent properties that are associated with these three levels of ecological organization are listed in Table 2A-C. Some of the items listed may not at first seem to be emergent. For example, numbers, biomass, and density would appear to be simply summation properties of the relevant parts present in the system of interest, and therefore not new features. However, there is a sense in which these properties are also products of the interactions among the parts. Numbers of individuals may be a function of sexual reproduction, social behaviour, intraspecific competition, cooperation, *etc*., and in any case numbers are not predictable from a knowledge of individual organisms alone. The simple sum of parts in a system may obscure the complex interactions among those parts that generated that sum in the first place. It is for this reason that listing some descriptive summations as emergent properties is appropriate.

IV. WHAT ABOUT A FOURTH LEVEL?

For a long time ecologists have felt the need for recognition of levels of organization above that of the community. Some useful concepts of this type are 'biotic province' (Dice, 1943; Longhurst, 1998), 'ecoregion' (Ricketts *et al*., 1999), 'biome' (Clements & Shelford, 1939), and 'biosphere'. The last of course refers to the entire living realm on this planet, and is also called the 'ecosphere' (Cole, 1958). However, these postulated levels of organization leave a large gap between communities and biotic provinces. E. P. Odum, in his classic series of ecology texts, formalized the idea that a level above that of the community would be realistic and useful. Unfortunately, he used for this purpose the handy but inappropriate term 'ecosystem'. In 1983 (Odum, 1983), he retracted this arrangement and applied the term 'ecosystem' to the community level only. Subsequently, he went back to using ecosystem as a fourth level (Odum, 1989), although one can sense his uncertainty in doing this as he listed "community" in lower case letters, but "landscape", "ecosystem", "population", and "organism" in upper case.

The use of 'ecosystem' for this hypothesized fourth level of organization is inappropriate for two fundamental reasons: 1) definitions of ecosystem refer to the inclusion of abiotic and biotic factors together in a systems context. Therefore no new biological organization is added by simply recognizing that abiotic factors are appropriate components of the systems of interest. We must conclude that a new, higher level of biotic organization is not created simply by adding abiotic components to the system. Moreover, a systems view of biology puts biotic and abiotic

Table 2. Some emergent properties characterizing four levels of ecological complexity

A. Organism	B. Population	C. Community	D. Ecoscape
coordinated developmental trajectory	numbers, density, biomass	kinds of organisms present	community types present
division of functions among organs	growth rate (including vital rates: birth, death, immigration, emigration)	diversity (numbers and proportions of species)	diversity (numbers and proportions of community types)
growth rate, biomass	biotic potential	biomass	biomass
potential life span	dispersion	spatial distribution of populations vertical stratification	spatial configuration of patches (dispersion, sizes, shapes, juxtapositions)
coordinated metabolism	demographic behaviour (including equilibrium density, minimum threshold density, *etc.*)	dominance relations (numbers, biomass, keystone features)	ecotonal features (edge effects)
food acquisition and internal distribution	temporal patterns (seasonal, multiannual, stochastic, long-term trends)	coactions (+ +, +−, +0, − −, −0, 00)	connectedness (links among patches, corridors, barriers)
excretion (metabolic products, toxins)	metapopulation structure	connectedness (numbers and intensities of coactions)	interpatch fluxes (energy, nutrients, organisms, information)
elimination of undigested food	sex (mating types) ratio	stability (variability, resilience, predictability)	stability (resilience, constancy, predictabilty)
reproduction (including mate finding, courtship, mating)	age structure	long-term trends (succession, stability, degradation, exotic invasions, extinctions) energetic properties: trophic structure (food webs), productivity (gross, net), P/R ratios (P+I/ R+E)*, trophic efficiencies, transit (turnover) times	long-term trends (succession, stabilty, degradation, exotic invasions, extinctions)
defence against pathogens and parasites	genetic heterogeneity		energetic properties (productivities, *etc.*)
defence against predators	genetic structure (spatial, kinship, inbreeding)		
sex or mating type	social organization	historical context	historical context
social role	historical context		
activity patterns			

* P = production of organic matter; I = imports of organic matter; R = losses of organic matter through metabolic activity (respiration); E = losses through export.

factors together into living systems at all levels of organization: 2) using the term 'ecosystem' for a single level of organization, whether it be the third or fourth level, implies that other levels of organization are **not** ecological systems. Clearly, this is contradictory to a holistic view of the world and to the traditional view of what constitutes ecology. It is indeed ironic that Odum's influence through his books and teaching did so much to instill holistic philosophy into generations of ecology students while at the same time he promoted the widespread adoption of anti-holistic terminology. Personal discussions with Odum in the early 1990s revealed his recognition of this problem and its inherent logical contradictions. Nevertheless, he felt that he was too committed to using "ecosystem" as a fourth level to contradict himself at that stage in his career. Others have argued that ecosystem is not a single level of organization (Blew, 1996; Dale, 1970; Evans, 1956; Lidicker, 1988; Lindeman, 1942; McIntosh, 1963; O''Neill *et al.*, 1986; Pickett & Cadenasso, 2002; Tansley, 1935), and perhaps it is time to heed the advice of Kirby (2005), who complained about the widespread practice of using the term 'ecosystem' only for large-spatial-scale landscapes, and proclaimed that "we should start taking guerrilla action when we see ecobabble."

Meanwhile, the need for formal recognition of a fourth level of complexity in ecology has not disappeared. If communities are ecosystems containing two or more species of living organisms (populations), it would be logical to ask if ecological systems composed of two or more types of communities would generate the emergent properties that would signal a new and higher level of biological organization. A list of proposed emergent properties for this level is given in Table 2D; see also Lidicker (1995; table 1.2) and Wiens *et al.* (1993). The designation of community types as the subsystems of ecosystems at this level of organization presupposes the reality of being able to classify communities into types. Some ecologists believe this is not possible, because community systems are individually unique. However, uniqueness is a property of all living entities from organelles upwards. All living entities are unique in space and time, and usually in properties, and yet we readily classify them into groups that share specified properties. All classifications are abstractions of reality because they emphasize the shared, rather than unique properties of entities, and because they focus on the discontinuities in the distribution of matter and energy rather than the continuities. Moreover, the categories that we devise can vary depending on the properties of interest for the entities being classified. Moreover, there will always be exemplars that defy easy identification. Communities share these difficulties with all other classifications of biological entities. Nevertheless, there seems no doubt that they can be realistically and usefully classified.

V. WHAT ABOUT A NAME?

If 'ecosystem' is pre-occupied and in fact inappropriate to label this fourth level, what should we use for this purpose? A second term that appears frequently in the literature is "spatial ecology." This is a poor choice, because spatial (and temporal) issues occur at all levels of biological organization. The spatially explicit arrangement of parts is not unique to community types, and considerations of space alone add no new biological complexity to an ecological system. It is the juxtaposition and interactions among community types that produces emergent properties, not space considerations *per se*.

A third possibility is to use the widespread term 'landscape'. At the 4th International Ecological Congress (IEC) in 1986, I proposed that this fourth level in ecology be called the 'landscape' level (Lidicker, 1988). This was at a time when landscape ideas were spreading rapidly (Forman, 1983), and it seemed opportune to focus this new energy and excitement in a scientifically rigorous manner. The emergent properties of this fourth level were increasingly proclaimed to be landscape features (Forman & Godron, 1986), even though the roots of landscape ecology were largely independent of traditional ecology (Hansson, 1995; Lidicker, 1995; Turner, 1989; Wiens *et al.*, 2007). By adding landscape conceptually to the traditional three levels of organization studied by ecologists, I thought this would help connect landscape ecology to traditional ecology with all the anticipated synergistic benefits that would ensue. Others have also viewed "landscape" as a level but generally placed it above an "ecosystem level" (eg., Ahl & Allen, 1996; Allen, 1998).

Both at a symposium on landscape approaches in ecology at the 6th International Theriological Congress (Lidicker, 1993) and at the 6th IEC (symposium on landscape ecology; Lidicker, 1994*b*), I pursued this approach arguing for labeling this fourth level as 'landscape.' I now acknowledge that these efforts have not been and perhaps cannot be successful (see Lidicker, 2002b). The word 'landscape' continues to be used in its traditional and colloquial sense as meaning some large expanse, usually of land. Landscape ecologists sometimes even formalize landscapes as being 1 km or more in size. Frequently, one sees in the literature the expression "landscape scale" meaning a large expanse of land. Clearly, the term is used for a spatial scale that is large from a human perspective. There is no implication that a biological level of organization is connected to the expression, only large size. I now see no hope that this tidal wave of popular usage can be reversed or even modified to include a scientifically rigorous definition along with the colloquial usage. Chew & Laubichler (2003) warn us that using a common language word as a metaphor to express some rigorous scientific concept carries serious risks of perpetuating sloppy thinking and misunderstandings. Perhaps efforts to use 'landscape' as such a metaphor is a case in point. Allen (1998) also gives a thorough analysis of why the terms 'landscape' and 'landscape level' should be eliminated from ecology as technical terms.

The conclusion from this analysis is that we are still left without a satisfactory name for ecology's fourth level. I suggest that the word 'ecoscape' be used for this purpose. It combines the root for ecology as a prefix and the suffix "scape" as taken from "landscape" and "seascape." The ending "scape" has been attributed to the Dutch "schap" which comes from "scap" meaning ship. The notion of "land + ship" became modified in more recent Dutch to mean "tract of land" or "region". The image of a ship surrounded by a matrix of some other habitat seems particularly fitting for the juxtaposition of community types as proposed here. A further advantage is that "ecoscape" can easily be applied to aquatic systems whereas "landscape" is semantically awkward for this essential purpose. 'Ecoscapes' defined by the fourth level of ecosystems would be spatially and temporally scale-free as are the other three levels of organization in ecology. However, there is obviously a positive relationship between levels of organization and spatial/temporal scales (Fig. 1), but it is weak because there is a wide range of space and time that characterizes each organizational level in real systems. While it is unlikely that an individual organism could be as large as 1 km, a population might be. On the other hand, an ecoscape could be hundreds of kilometers in one dimension or merely be measured in meters.

The term 'ecoscape' is not original with me. In the INTECOL Newsletter (winter 2001/02) the 5th International Eco-city Conference held in Shenzhen, China, in August 2002 was titled "Ecoscape Eco-industry Eco-culture". W. D. Schmid used 'ecoscape' to refer to local biome patches, for example "a forest", at a conference on boreal ecology (Schmid, 2000), and I am sure there are other instances. As far as I know, however, this is the first attempt to define 'ecoscape' in a rigorous and conceptually meaningful way.

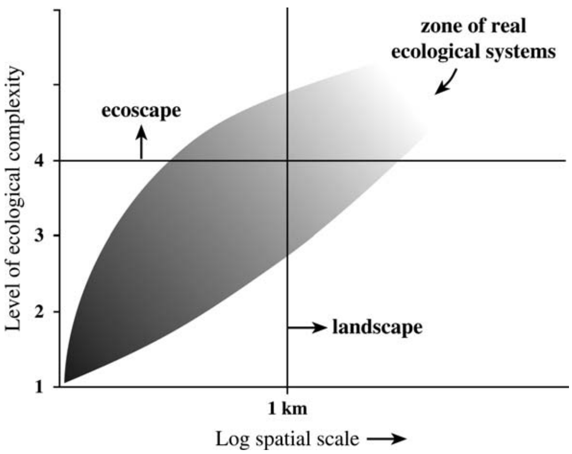

Fig. 1. Four levels of ecological organization, defined independently of spatial and temporal scales, shown as they relate to spatial scale (log scale) in real ecological systems. Relationships to temporal scale are not shown, but a similar diagram could be constructed for this purpose. Level 1 = organism, 2 = population, 3 = community, 4 = ecoscape. The 1 km spatial scale marker is the spatial dimension often arbitrarily used to define the minimum size of "landscapes." The shaded area approximates combinations of organizational level and spatial scale likely to be realistic. Note that for any given organizational level, systems can occur over a wide range of spatial dimensions.

By focusing attention on the emergent properties that are generated when different community types are juxtaposed, regardless of spatial (and temporal) scale, research can be directed to ecoscape-level processes that are relevant to organisms of varying sizes. Moreover, the ecoscape concept provides a conceptual bridge between traditional three-level ecology and investigations on more inclusive scales. It further avoids the tendency to assume that processes above the community level are exclusively human-oriented.

VI. DISCUSSION AND CONCLUSIONS

(1) General systems theory is a widely acknowledged unifying concept for science in general and biology in partcular (Bertalanffy, 1950; Feibleman, 1954; Koestler, 1969; Lotka, 1925; Smuts, 1926). Ecologists are especially aware of this perspective since they regularly study multiple levels of biological complexity. Throughout its history as a discipline, additional levels have been serially embraced with corresponding subdisciplines being spawned (Table 1; Lidicker, 1988, 1994*a*). Three levels are well established (Miller, 1957; Odum, 1953; Park, 1964), and the reality of a fourth level has been long suspected.

(2) Formal recognition of a fourth level of ecological organization requires that emergent properties be identified as characterizing systems at this level (Lidicker, 1988, 1995; Wiens *et al.*, 1993).

(3) The new level must be spatially and temporally scale-free as are all the levels in the natural hierarchy of science. Of course, all particular instances of natural systems at any level are identified by boundaries in space and time, but it is the emergent properties that define the level of organization (Table 2), not its dimensions in time and space.

(4) We need an appropriate name, and the concept 'ecoscape', as applied to ecological systems (ecosystems) that contain more than one community type, meets all of these requisites. 'Landscape', being spatially defined, is inappropriate to use for a level of biological organization. Nevertheless, what we construe as a landscape will generally also be an ecoscape because it will include multiple community types. However, the two concepts are not coincident (Fig. 1). Nevertheless, because there is substantial overlap in what could be classified as landscape and ecoscape, the latter will undoubtedly be studied mostly under the general rubric of landscape ecology. It is important, however, that it is the scale-free concept 'ecoscape', and not the scale-endowed 'landscape' that connects research on these more complexly organized systems to traditional ecology.

(5) Are there other, still more complex, levels of organization in the ecologists' future? Undoubtedly, this is true. Already we recognize the biosphere as the most complex, most inclusive, ecosystem that we know about. In between, however, there are likely several more levels that will turn out to be scientifically useful to recognize (Table 1). Possible candidates include biomes, ecoregions, major watersheds or ocean currents, biotic provinces, and continents or ocean basins. More understanding of possible

emergent properties associated with these postulated levels will be required before we can confidently add them to the ecological purview as distinct levels of organization.

VII. ACKNOWLEDGEMENTS

I thank E. P. Odum for useful discussions, and W. D. Schmid for providing impetus by independently using the word "ecoscape" in a different but related way. Tim Allen kindly directed me to some relevant literature, and two anonymous reviewers provided helpful commentary.

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