



Tansley review

Units of nature or processes across scales? The ecosystem concept at age 75

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Received: 30 August 2010

Accepted: 21 November 2010

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Summary

New Phytologist (2011) **190**: 21–34
doi: 10.1111/j.1469-8137.2011.03646.x

Key words: community, complexity, ecosystem and ecosystem services, energetics, global change, nutrient cycling and primary production, social–ecological systems, theoretical ecology.

The ecosystem has served as a central organizational concept in ecology for nearly a half century and continues to evolve. As a level in the biotic hierarchy, ecosystems are often viewed as ecological communities integrated with their abiotic environments. This has always been imperfect because of a mismatch of scales between communities and ecosystem processes as they are made operational for field study. Complexity theory has long been forecasted to provide a renewed foundation for ecosystem theory but has been slow to do so. Partly this has arisen from a difficulty in translating theoretical tenets into operational terms for testing in field studies. Ecosystem science has become an important applied science for studying global change and human environmental impacts. Vigorous and important directions in the study of ecosystems today include a growing focus on human-dominated landscapes and development of the concept of ecosystem services for human resource supply and well-being. Today, terrestrial ecosystems are viewed less as well-defined entities or as a level in the biotic hierarchy. Instead, ecosystem processes are being increasingly viewed as the elements in a hierarchy. These occur alongside landscape processes and socioeconomic processes, which combine to form coupled social–ecological systems across a range of scales.

I. An organizational concept

Ecologists study locales in which thousands of species co-exist with chaotic dynamics and natural disturbances reorganize patterns of production at irregular and unpredictable intervals. They study environments that range from having low to extreme human alteration. They consider scales from molecules to continents over time periods from seconds to thousands of years. At essentially any scale they observe a richness of information. In the face of this complexity, ecologists seek principles of underlying organization and causes of that organization (Gleason, 1926; Odum, 1953). The ecosystem as an organizational concept is particularly appropriate for a *Tansley review* because both the terminology and the central ideas most familiar today were introduced by Sir Arthur Tansley (1935), after whom these reviews are named.

One of the first things to understand about the ecosystem concept is that it is both useful and insufficiently resolved as a formal framework. In the 75 yr since its introduction, it has become a central theoretical and applied concept in the sciences of ecology, global change, and human environmental impacts (Odum, 1969; Aber *et al.*, 1989; Vitousek *et al.*, 1997). At the same time, its usage glosses over many critical issues that either remain unresolved or continue to be debated and reassessed. In common usage of the ecosystem concept, the dominant vegetation in a locale is presumed to be adapted to the climate, soils, and disturbance regime so that primary production exhibits some regularity and returns to regularity after disturbance. Vegetation, through primary production, provides energy and reduced carbon compounds to drive the life processes of all species in the food web. The vegetation and animal communities, considered together, are typically assumed to have some stability but also vulnerability in the face of change. Consider the usage of 'threatened (or endangered) ecosystem' which can be found in publications as diverse as an agricultural extension manual on native grasses (Harper *et al.*, 2004) and a *Science* news story on the forests of Madagascar (Bohannon, 2010). The vegetation is viewed as supporting dependent wildlife by providing both food and habitat. There is also a sense of long-term balance with climate and disturbance regimes (native prairie, for example, requires fire to be maintained) and a sense of regional identity or uniqueness (the particular vegetation–wildlife ensembles in Madagascan forests occur nowhere else).

Analysis of the ecosystem concept among specialists does not contradict the common usage but does continue to question many underlying assumptions. The specialist literature is rich with debate surrounding the topics of feedbacks and stability, biodiversity and stability, holism vs reductionism, and the importance of considering scale when studying ecological processes and interactions that regulate plant and animal populations (e.g. O'Neill *et al.*, 1986; Pomeroy *et al.*, 1988; Allen & Hoekstra, 1992; Golley, 1993;

Pickett & Cadenasso, 1995; Jørgensen, 1997; Ulanowicz, 1997; Bergandi, 2000; Mayer & Rietkerk, 2004).

This article continues that debate by proposing that an ecosystem is difficult to view rigorously as an entity in a locale, as common usage dictates, but instead should be viewed as a particular set of integrated processes in a re-conceived hierarchy of processes. I focus, as Tansley did, on terrestrial systems. (The concept is widely used in the study of aquatic systems, but there are key differences related to scale, boundaries, the spatial distributions of ecological communities and observational techniques.) My main themes are that the ecosystem concept has always been imperfect as a marriage of systems theory and community ecology; that, for scientific study, ecosystem concepts need to be made operational and testable, and while progress has advanced there remain key limitations; that complexity theory has the potential to rejuvenate ecosystem theory but has been slow to do so; that ecosystem services are an important applied area of research but should build more directly on our integrated understanding from ecosystem science; and that the biotic hierarchy should be re-conceived to focus on processes instead of entities, with landscape processes parallel to, and coupled social–ecological systems the next level above, ecosystem processes.

II. An imperfect marriage

1. Concepts derived from thermodynamics and systems theory

Since its inception, the ecosystem concept has represented a marriage of population–community ecology with energetics and systems theory. Many of the concepts related to energetics and systems theory derive ultimately from thermodynamics, an intellectual debt that has been reviewed by many writers (Golley, 1993; Jørgensen, 1997; Ulanowicz, 1997; O'Neill, 2001). In the mid to late 20th century, the ecosystem provided a framework for investigators to study and generalize the biological structure and function of nature, including metabolic functions, by focusing on rates and quantities at an aggregated scale without necessarily focusing on organisms and species (Lindeman, 1942; Odum, 1968; Hannon, 1973; Weigert, 1988). A key historical success was the organization of energy flows and trophic levels to explain the Eltonian pyramid (Hannon, 1973; Reiners, 1988). Fundamental to the ecosystem view has also been the idea that numerous processes such as photosynthesis and nutrient mineralization, among others, are not simply biological but result from intimately connected abiotic conditions and biotic function.

Ecosystems are thermodynamically open, meaning that they exchange matter and energy with their environment (Fig. 1). Consider processes that control the storage of carbon (C) in vegetation. In photosynthesis, energy enters

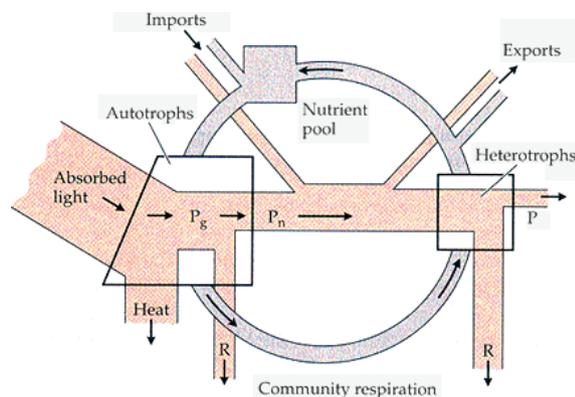


Fig. 1 Schematic diagram showing fluxes of energy (orange shading) and nutrients (gray) in an ecosystem. Because ecosystems are thermodynamically open, energy and nutrients flow in and out across system boundaries. Energy flows in only one direction because it is degraded as it passes through an ecosystem. Energy flow through autotrophic and heterotrophic compartments of organisms drives intrasystem nutrient fluxes, which in turn limit biotic energy flows. Limiting nutrients often recycle within the system at rates greater than their imports and exports. Reproduced, with permission, from Odum (1997).

the system in the form of sunlight and carbon enters as CO_2 . Respiration and decomposition follow production (Fig. 1), exporting carbon again as CO_2 and energy as sensible heat, latent heat, and longwave radiation, while increasing the entropy. The continual flow and degradation of energy through an ecosystem are critical not only because they are prerequisites for life itself (Schrodinger, 1944; Morowitz, 1979) but also because energy flow structures communities (Hannon, 1973). Tansley (1935) wrote that to the ecologist such integrated, aggregated, physical–biological systems are the ‘basic units of nature on the face of the earth.’

The systems perspective appealed widely to ecologists in the late 20th century. It lent itself to mathematical formalism (Shugart, 1998). It also provided a conceptual framework to connect the functions of components, or fine-scale variables, together in an effort to mechanistically understand the dynamics of aggregated, or coarser scale, system-level variables (Costanza *et al.*, 1993; Jørgensen, 1997; Bergandi, 2000). Component interactions could be weak or strong and direct or diffuse. They could be linear or non-linear, the latter including positive and negative feedbacks and lag times, providing a means with which to understand rich dynamics in system-level behavior (Gleick, 1987). It is important to note that ‘components’ could be viewed in a number of ways. Population–community ecologists could view ecosystem components as organisms, species, guilds or trophic levels. Others could consider system components to be tissues such as foliage, wood, litter, and so on, lumped across all organisms and species and referred to as homogeneous pools or stocks. The latter is an approach used in numerous ecosystem models to study ecosystem function

and responses to global change. While such choices in how to view components allowed a useful multiplicity of approaches, they also lead us to question how much the ecosystem concept has really achieved as a unified synthetic idea.

2. Ecosystems are an imperfect level in the biotic hierarchy

The biotic hierarchy was popularized by E. P. Odum (1953) as an organizing principle in ecology. It is usually presented as a hierarchy of entities, in which an entity at one level, called the focal level, both contains entities in the next level below and is itself a component of the level above (Koestler, 1967, 1978; Ulanowicz, 1997). The biotic hierarchy may be listed as cell, organism, population, community, ecosystem, landscape, and biome. The idea of a biotic hierarchy is generally insightful, but this view of the community and the ecosystem has serious limitations (Allen & Hoekstra, 1992). Different levels in the hierarchy show key differences in their degrees and types of organization. An organism is a highly integrated and organized entity. Its structure and function are strictly coded in its DNA. A population or metapopulation, likewise, is a highly integrated entity. It is made up of individuals of the same species; understanding how a population grows, declines, and persists over time is easy and unambiguous. It is a key unit in evolution because genes are selected and redistributed within a population or metapopulation. But any higher functional level of the biotic hierarchy shows much less organization and much more noise. For example, it has long been a debate in the study of vegetation whether plant communities are better conceived as plant associations or as combinations of species responding individually to environmental gradients (Gleason, 1926; Verhoef & Morin, 2010).

The ecosystem is often viewed as a biotic community plus its abiotic environment, including the suite of biotic–abiotic interactions that take place in a locale. This offers a great deal of insight because it integrates ecological phenomena at the community level in a fundamental way with abiotic processes and environmental drivers. Nutrient cycling offers an example. Nutrient uptake and mineralization depend not only on growth and biotic stoichiometries of organisms but also on temperature (itself regulated by radiation exchange and air temperature), moisture, soil texture and soil chemistry.

A difficulty with the hierarchy arises when we try to treat an ecosystem as a closed, or complete, biotic system. Plant populations interact with one another through shading and competition for nutrients, but each population is likely to reproduce over a different spatial range dictated by the movements of its pollen and seeds. Animal populations interact ecologically with plant populations (e.g. through herbivory) and with one another (as in predator–prey interactions) but do not necessarily share the same spatial ranges as either plant or other animal populations (Fig. 2).

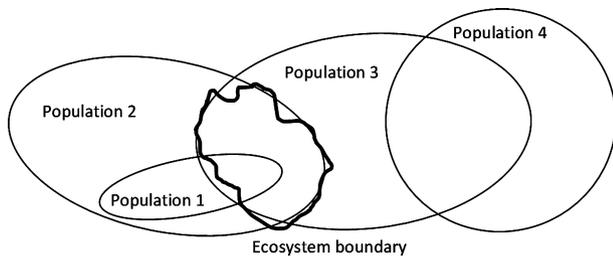


Fig. 2 The choice of a system boundary (thick line) is a key operational element in the study of an ecosystem, allowing energy, carbon, water, and nutrient cycling fluxes to be quantified. But it presents a mismatch with the theoretical notion of a complete ecological community that drives or responds to those fluxes. Here, populations 1 through 4 are different plant or animal species that interact ecologically across different areas (thin lines), for example through competitive, symbiotic, or predator–prey relationships. Populations 1, 2 and 3 occur in the ecosystem under study but may gain food, reproduce, and interact with other species outside of the boundary, including those such as species 4 that are absent from the ecosystem under study. Tracing all such interactions would extend an analysis to the biome scale or beyond.

Investigators often define a boundary around an area to delimit a locale in which to study an ecosystem. An early example is the small watershed ecosystem, created out of the need for a feasible approach to quantify inflows and outflows of water together with dissolved elements (Likens *et al.*, 1967). Today the horizontal boundary widely used in studies of energy and carbon budgets is the fetch of an eddy-flux tower (Wofsy *et al.*, 1993; Yuan *et al.*, 2009). Plant populations extend through these areas, while animal populations might forage in this locale but reproduce somewhere else, or vice versa. If we believe that flows of energy (e.g. in herbivory and predation) are key for organism growth and survival, that reproduction is key in regulating populations, and that ecological interactions among populations are key, then in the vast majority of cases it would be extremely difficult to study, or even to define, a complete ecosystem.

While this difficulty has long been recognized, it continues to militate against the definition of an ecosystem as a level of organization in a biotic hierarchy in a way that is both rigorous and observable. Tansley viewed the ecosystem as a useful ‘isolate’, which loosely corresponds to the current concept of a level of organization. But Tansley argued against the ecosystem conceived as a hierarchical level that subsumed a well-defined, complete biotic community at a locale. He wrote that he could not accept such an idea because ‘birds and mammals range freely not only through an entire plant community but far outside its limits’ (Tansley, 1935). I will refer to this as the ‘problem of partial communities’. A decade ago, O’Neill (2001) proposed that the ecosystem concept should be re-conceived to include the ranges of dispersal of all plant and animal populations in a community. But this is an incomplete solution to the problem. The issue is not only dispersal but also the acquisition of energy for reproduction and the ecological

interactions among populations. With the possible exception of small islands, some part of the energy acquisition and subset of ecological interactions would take place outside virtually any boundary we could define. On a continent, we would have to continually overlay all of the overlapping ranges of populations (Fig. 2) to the edges of biomes or beyond (neotropical migrant birds move regularly between temperate and tropical biomes). This carries the boundary so far geographically that we lose the concept of the ecosystem as a focal level and we certainly go beyond any locale that lends itself to concrete study in the field.

3. A new focus on ecosystem processes instead of ecosystems as entities

An early solution to the problem of partial communities was to group species into trophic levels to link community patterns with energy flows (Hannon, 1973). If individual organisms or even species come and go, perhaps the trophic level remains as a meaningful aggregation to study within a locale. This is, of course, a simplifying assumption but served a useful purpose for decades. In building a model of ecosystem structure and function based on observations, this approach assumes that trophic interactions observed in a study area are representative of the interactions that govern populations across their entire ranges. As ecology has focused more attention on spatial patchiness and heterogeneity in the past 25 yr (Pickett & White, 1985; Levin, 1992; Pacala & Levin, 1997; Maurer, 1999), the science has outgrown these assumptions.

The solution to the problem of partial communities that is in wide use today is to formulate variables that represent *ecosystem processes* and to conceive of these as distinct from (yet strongly connected to) population–community processes and landscape processes. Key ecosystem processes include primary production, evapotranspiration, respiration, decomposition, secondary production, soil formation and cation exchange, nutrient mineralization and immobilization, and many others. The primary focus of study among ecosystem scientists today is these processes and the causes and effects of their dynamics, not the study of ecosystems as entities.

The current focus on processes can still suffer from spatial oversimplification if processes quantified in an experimental area (for example in the fetch of an eddy-flux tower) are assumed to represent a much larger, heterogeneous area. But investigators conceptually and experimentally consider ‘spatial variability in ecosystem processes.’ Linking ecosystem process models to a geographic information system (GIS) to model such spatial heterogeneity has been a standard technique for over a decade (Burke *et al.*, 1991; Currie & Aber, 1997; Fan *et al.*, 1998; Jenkins *et al.*, 1999). Spatial variability in driving variables or relevant parameters, created through either spatial statistical modeling from ground-based observations (e.g. Ollinger *et al.*, 1993) or directly

from satellite observations (e.g. Asner *et al.*, 1998) are used to produce maps of spatial heterogeneity in production or nutrient cycling (Rastetter *et al.*, 2003). Thus, ecosystem processes can be considered at a variety of scales and can accommodate spatial heterogeneity. This is quite different from viewing an ecosystem as an entity that subsumes a discrete community. It illustrates a dramatic conceptual shift.

With the rise of landscape ecology as a distinct field, investigators now consider phenomena directly related to landscape position, spatial heterogeneity, and patch geometries and adjacencies (e.g. Robinson *et al.*, 2009) to be *landscape processes*, allowing a key conceptual separation that has advanced our ability to confront issues of scale (Pickett & Cadenasso, 1995). Rather than viewing an ecosystem as an entity at a finer scale than a landscape, we can view ecosystem processes and landscape processes as strongly interacting sets of distinct phenomena that can each occur across a range of scales (O'Neill *et al.*, 1986). For example, in Arctic tundra, topological sequences of different plant communities and soils can occur in only tens to hundreds of meters from ridges to streams. Researchers have found that patch adjacency is key in controlling ecosystem processes such as nutrient cycling because flowpaths connect the patches in sequence (Shaver *et al.*, 1991). This is an example of a landscape process (the spatial relationship among heterogeneous patches of soil and vegetation) linking closely to ecosystem processes at the 100-m scale. A similar example is the 'hot spots' concept. An ecosystem process such as denitrification can be considered at any scale at which an observer draws a boundary (from 10 m to hundreds of kilometers), yet within any such boundary denitrification is controlled by patch adjacency and landscape position at a finer scale (McClain *et al.*, 2003).

A process-oriented approach frames ecosystem processes as one integrated subset of processes operating across scales, but not necessarily *all* of the processes that operate within a boundary, to create an entity called the ecosystem. At the same time, investigators recognize that there are important causal linkages among ecosystem, community, and landscape processes (Turner, 1989; Levin, 1992; Pickett & Cadenasso, 1995; McGill, 2010). Of course this further diminishes the conception of ecosystems as entities in a hierarchy.

To build on the process-oriented approach in ecosystem science, a better way to conceive of multiple levels in the biotic hierarchy may thus be in terms of *processes* as opposed to entities. This would solve additional problems. For example, organisms exist at a lower level than ecosystems in the hierarchy of entities, so ecophysiological functions such as stomatal conductance should be defined at a scale finer than that of ecosystems. Yet present-day dynamic global vegetation models (DVGs), key tools in global change and earth systems science, employ ecophysiological functions and parameters at scales of tens to hundreds of kilometers. At the same time, these models do not necessar-

ily including processes such as nutrient cycling that are associated with the ecosystem level (Ostle *et al.*, 2009). The process-oriented approach provides a framework in which to consider whether a model applied at a particular scale includes ecophysiological processes, ecosystem processes, community processes, and so on – and whether it needs to include various subsets of processes depending on its purpose. In fact, this is the usage that dominates in ecosystem and global change science at present, even though introductory ecology textbooks present communities and ecosystems as entities in a hierarchy (e.g. Ricklefs, 2008).

Another important problem solved by a process-oriented approach is the problem of including human societies. Some scholars have argued that the complex interactions in human societies should be considered as elements of ecosystems (Kay & Schneider, 1994). This is a position we are forced to take if we conceive of the ecosystem as an entity made up of all of the relevant phenomena that occur within a delimited boundary. Of course, human alteration and impacts are pervasive in units of the landscape. But to say, for example, that new household creation through marriage (An *et al.*, 2005), or farmers' gaming-style decision-making (Becu *et al.*, 2003), or the effects of discount rates on a landowner's net utility function (Rodrigues *et al.*, 2009) are 'ecosystem processes' seems to cast the net much too wide. These would dilute the ecosystem concept beyond recognition. It requires us to address ill-formed questions such as 'is a human economic market part of an ecosystem?'

Alternatively, a process-oriented hierarchical approach allows us to study social or socioeconomic processes separately, while linking these to ecosystem processes at a higher level in the hierarchy. The level that combines these is coupled social–ecological systems. With this framework we can consider the effects of social dynamics and human decision-making on, for example, primary production, water runoff, and nutrient retention, together with the reciprocal effects these processes have on human societies. The complexities arising from such two-way interactions, and their importance, are ably described by Kay & Schneider (1994). Conceiving of a hierarchy of processes rather than entities allows us to ask interdisciplinary research questions in a more productive way. This view of ecosystem and landscape processes as part of social–ecological systems is one of the most significant and important developments in ecosystem science over the last 10 yr. I will return to this topic below (section IV).

III. A type of complex adaptive system?

1. Complexity theory as a conceptual framework for ecosystems

Complexity theory has the potential to provide renewed insight into many branches of ecology, including ecosystem

science (Green & Sadedin, 2005). This has long been forecasted. Simon's (1973) discussion of how components within one level of a functional hierarchy typically show loose horizontal coupling, permitting them to evolve independently of one another while continuing to fit functionally into a whole at the higher level, sounds very much as though it could be referring to species within an ecosystem. Bak *et al.* (1988) wrote that species in an ecosystem "support" each other in a way which cannot be understood by studying the individual constituents in isolation'. Even Tansley's treatment held the seeds of the study of complexity in richly prescient passages such as 'There is in fact a kind of natural selection of incipient systems, and those which can attain the most stable equilibrium survive the longest' (Tansley, 1935).

As a quantitative underpinning that directly supplies theoretical, organizational ideas, complexity theory has much in common with systems theory but offers some advantages. Both build up an aggregate from reductionist understanding and provide theory for understanding causes of the dynamics of the aggregate in terms of the causal connections among the components. Systems theory could be viewed as bringing the connotation of control with a set point in the sense of cybernetics (O'Neill *et al.*, 1986). Complexity theory, by contrast, emphasizes self-organization and embraces the idea that there is no central control or master plan; large-scale patterns arise from the multitudinous fine-scale interactions among components (Nicolis & Prigogine, 1989; Waldrop, 1992). Systems theory, by lumping large numbers of individuals and species into homogeneous, well-mixed pools, militates against an improved incorporation of population–community processes. Complexity theory emphasizes components (such as a species, or a trophic level) that are comprised of multiple, heterogeneous elements (Levin, 1998), providing a fresh and more sophisticated view of how aggregate-level phenomena can arise. Another key difference is that complexity theory emphasizes that the parts of a system are adaptive; some means of selection or adaptation takes place among elements, providing a directionality of change that affects whole-system structure and function (Holland, 1995). Scholars in complexity theory very often list ecosystems as examples of complex adaptive systems (Costanza *et al.*, 1993; Kauffman, 1993; Holland, 1995; Levin, 1998).

For terrestrial ecosystems, the idea of directional change calls to mind the widely used example of succession. Perhaps this offers a test of how well the complexity perspective could contribute to ecosystem theory. In a locale, shade-intolerant plant species dominate early in succession, while individuals from species that can reproduce and grow in the shade of both conspecific and heterospecific individuals will be differentially successful (or selected, in the language of complexity theory) as canopy biomass increases and persists. This is in fact a mechanism that produces

community-level succession from competitive interactions among individual trees in a widely used class of forest ecosystem models, gap replacement (or simply 'gap') models (Pastor & Post, 1986; Urban & Shugart, 1992). Gap models are a subset of individual-based models, a larger class that were viewed decades ago as having the potential to unify ecological theory (Huston *et al.*, 1988). Individual-based models are also key tools in complexity theory, where they are often called agent-based models. The stage would seem to have been set for decades for complexity theory to inform the theoretical foundation for the study of ecosystems.

Complexity theory has been embraced by key ecosystem scholars (Costanza *et al.*, 1993; Levin, 1998), but its embrace by ecosystem science as a field has been limited. (It has penetrated the fields of landscape ecology and the study of social–ecological systems, discussed below in section IV.2, much more fully.) One reason is that writers on complex adaptive systems, when mentioning ecosystems, often write about evolution and community assembly (e.g. Holland, 1995), without adequate consideration of what ecologists view as ecosystem processes – that is, production, respiration, decomposition, water use, nutrient cycling, and so on. The effects of evolutionary mechanisms on these processes would be an exciting area of research, but not one that has historically been a major topic in the study of ecosystems. Similarly, community assembly speaks to part of the ecosystem view, but stops far short of addressing the suite of processes that are central to specialists' views of ecosystem function. When writers on complexity mention ecosystems as examples of complex adaptive systems, typically the state variables they describe are populations of plants and animals. This misses the linkage of biotic with abiotic processes that is necessary to understand aggregated rates and quantities, which are central to ecosystem science. It also fails to address the central difficulties of boundaries and scale that arise either when ecosystems are thought to subsume complete communities or when ecosystems are studied empirically.

A philosophical issue in applying complexity theory to ecosystems has also slowed its adoption: the concept of emergence and its relationship to holism and reductionism (Pomeroy *et al.*, 1988). To understand emergence, consider a set of aggregated elements in which a dynamic property of the aggregate is shaped by nonlinear interactions among its elements. When multiple nonlinear interactions are present, complex patterns can arise, or emerge, from simple interactions. The cycling of nutrients in soil and vegetation is an example (Fig. 3). A nutrient cycle in a locale can arise as a system-level phenomenon that is shaped by numerous nonlinear interactions among individual processes (mineralization, uptake, etc.) and ecologically interacting populations. Emergence simply refers to system-level phenomena. The study of ecosystems is rich with such phenomena. Examples

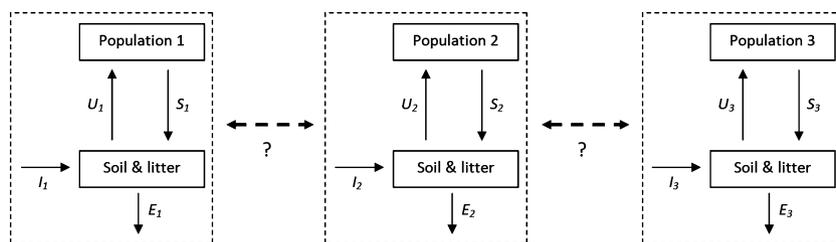


Fig. 3 Illustration of the concept of emergence in ecosystem function. Solid boxes represent nutrient pools in three plant populations and nutrients in the litter and soil that cycle with each population. Solid arrows represent nutrient fluxes (U , uptake; S , shedding of litter; I , inputs; E , export). Plant populations exist in a common locale and may or may not interact ecologically (denoted by dashed arrows with question marks). The question of emergence is not whether a total flux in this locale such as plant nutrient uptake U_e (for ecosystem uptake) is equal to the sum over the uptake in the component populations U_i . Whether interactions are present or not (dashed arrows), the total uptake is always precisely equal to the sum of the components: $U_e = \sum U_i$. Emergence would be a phenomenon in which U_i were altered in the presence of interactions among individuals or populations (dashed arrows), creating spatial patterns or temporal dynamics in U_i or U_e , or in the sum U_e , that differed significantly when interactions were present vs absent. GIS, geographic information system.

from nutrient cycling include the observations that a limiting nutrient tends to be retained in an ecosystem in the absence of disturbance, and that external inputs can lead to increased cycling over time (Magill *et al.*, 2004), that internal cycling of a limiting nutrient between producers and heterotrophs is often greater than inflows and outflows of the nutrient (Currie *et al.*, 1996; Odum, 1997; Fig. 1), and that a major disturbance can cause losses of nutrients from the system (Likens *et al.*, 1978).

Some ecosystem scientists may view the concept of emergence as being too close to holism, and holism as a rejection of reductionist understanding. While some investigators of ecosystems do equate complexity with holism (Jørgensen *et al.*, 1992), in my view this is incorrect. Far from a rejection of reductionism, complexity theory has the potential to offer significantly improved insights and explanations regarding how fine-scale or pairwise interactions, which need to be understood through reductionist research, combine to produce aggregate phenomena. This is not holism (Bergandi, 2000). In my view this could be seen as a facet of scaling. Instead of spatial scaling, perhaps it could be viewed as ‘interaction scaling’.

2. The need for theoretical and empirical work

Investigators can all agree that an ecosystem is a quasi-organized type of system; the Eltonian pyramid illustrates a type of organization. But to go beyond a certain point in explaining why any organization occurs brings us into debate. Is there self-generated internal selection and adaptation of components that gives rise to this quasi-organized nature? Such mechanisms are often assumed (Holland, 1995), an assumption with a long history dating back to Tansley (1935). To advance the science, concepts such as emergence, autocatalysis, and selection (not in the evolutionary sense, but in the sense of winners and losers of ecological competition) need to be made operational in field studies.

Observational and experimental work on whole ecosystems is difficult to conduct (Likens, 1985; Carpenter, 1998). Ecosystems are large and individualistic; the classically taught ‘scientific method’ does not apply well (Pomeroy *et al.*, 1988). Empirical research with the ecosystem as the experimental unit takes creativity, collaborative teams, and long periods of time, often including observations made for years before and after experiments are conducted (Likens, 1985). Over the coming decade, an increase in field-based cyberinfrastructure, or the collection of vast amounts of data at fine scales, will provide key new tools and a wealth of data (Green *et al.*, 2005). To facilitate the testing of theory, such increases in fine-scale observational data should be directly combined with ecosystem-level observations and experiments, such as field studies at the US LTER (Long-Term Ecological Research) sites and other sites with eddy-flux towers where energy, water, and carbon balances can be quantified. Ecologists need to work directly with complexity researchers to design experiments that can make use of combined observations from fine to aggregate scales. Individual-based models that allow heterogeneity among individuals and that represent numerous pairwise interactions among individuals, together with trophic interactions and energy flow, should be designed and used to link observations to theory in such cross-scale experiments. An example likely to contribute to new understanding would be to use individual-based models to represent element stoichiometries in trophic levels and their relation to individual growth and reproduction, energy flow, and nutrient flow through trophic webs (Peñuelas & Sardans, 2009).

The test of whether complexity theory will help to rejuvenate ecosystem theory will hinge on whether complexity concepts lead to any increase in our causal understanding of ecosystem processes (Fig. 4). This is a central point. Ecosystem science, as practiced today, does not address ecosystems as supposedly complete biotic entities. It addresses a particular set of integrated biotic and abiotic processes that

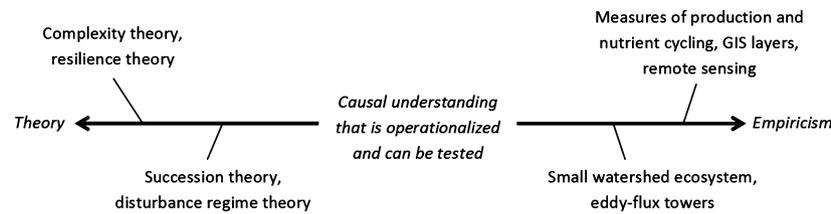


Fig. 4 A spectrum from theory to empiricism. Ecosystem science takes theory (from the left), and makes it operational to produce testable, causal understanding (in the middle) so that hypotheses can be tested using available approaches and data (from the right). Alternatively, empirical data from the right are interpreted in terms of theory from the left to improve causal understanding in the middle.

integrate energy flows and biogeochemical cycling and exchange across boundaries, production and decomposition, energy flow in trophic webs, and water budgets, among other processes, at an aggregate scale. For complexity concepts to contribute to ecosystem theory, analyses or models that address emergence, interaction scaling, self-organization, or adaptation need to include the aforementioned ecosystem processes. To date, inclusion of these processes has been largely undeveloped. Where it has been developed, it has contributed to an improved synthetic understanding. A major success for forest ‘gap’ models was their ability to produce succession as a population–community process arising from individual competition for light, but this was only the first step; the integration of water use and nitrogen cycling in the LINKAGES gap model (Pastor & Post, 1986) was a further success that stands as a landmark in the analysis of ecosystem processes.

Even with improvements in data and conceptual integration, complexity principles will be difficult to evaluate scientifically in ecosystems. For example, if we consider community self-organization as a selection (in the language of complexity theory) among populations, do we consider their entire ranges, and do we consider assembly-rule time scales or evolutionary time scales? To test hypotheses concerning energy, carbon, water, and nutrient flows, we require an operationally defined approach that refers to a specific unit of terrestrial surface – a watershed, a field plot, or the fetch of an eddy-flux tower. This limits the complexity and adaptiveness that can be studied for real systems because these units and boundaries are arbitrary, chosen for convenience and feasibility. We are also likely to miss cycles of disturbance and recovery, which are key in shaping ecosystem structure and function but can be observed only on very long time scales (Carpenter, 1998).

I believe that complexity theory and individual-based modeling do have the potential to address the problem of partial communities outlined above. A modeling framework could address energy flows, nutrient availability, and reproduction and mortality in large, overlapping ranges of populations, at the same time superimposing a small arbitrary boundary meant to delimit a study area within the larger sets of ranges (Fig. 2). Modeling analyses could examine how population–community processes occurring

across a range of scales and in a spatially distributed manner (Maurer, 1999; O’Neill, 2001) produce observed ecosystem processes within the smaller study area. Such work could help to rejuvenate the marriage of energetics and systems theory with population–community ecology. It could also help provide insight into questions of biodiversity and ecosystem function, including the biodiversity–stability debate (Ives & Carpenter, 2007). Such work could help to address, for example, the importance of biodiversity not only in an ecosystem study area but in the larger landscape, and the importance that overlapping population ranges at very large scales may have for promoting stability of ecosystem processes in a much smaller locale.

IV. A component of social–ecological systems

1. Human-dominated systems and ecosystem services

The plea that ecologists should study human-dominated systems, instead of focusing on only wildland systems, has been made repeatedly for decades (Odum, 1969; Pomeroy *et al.*, 1988; Costanza *et al.*, 1993; O’Neill, 2001). Human impacts and alteration of the landscape are not limited to densely populated settlements or agricultural fields, but are now nearly ubiquitous even at the continental scale (Cardille & Lambois, 2010). Some investigators claim that we have entered a new era, the Anthropocene, in which humans are altering the earth system on a geologic scale (Clark *et al.*, 2004; Steffen *et al.*, 2007). Vitousek *et al.* (1997) described how human activities fix more nitrogen than all of nature and appropriate more than half of the world’s freshwater. Hobbs & Fowler (2008) described how humans consume 50% of the Pacific pollock production, compared with a mean of 1.3% per predator species across all 20 species of pollock predators. Kareiva *et al.* (2007) suggested that there are few truly wild places left on earth.

In making observations and testing hypotheses, terrestrial investigators in ecosystem science historically emphasized wildland systems (Pickett & Cadenasso, 1995). On this point a significant change has occurred over the last 10–20 yr. It is now easy to thumb through (or scroll through) a current journal in the field and see substantial treatment of human-dominated systems (e.g. Kaye *et al.*, 2006; Pataki

et al., 2006; Pickett *et al.*, 2008; Robinson *et al.*, 2009; Churkina *et al.*, 2010). The US LTER network, with 24 sites focused mainly on wildland ecosystems, has always been a critical network of sites for the advancement of ecosystem science (Aber *et al.*, 1989; Burke & Lauenroth, 1993; Rastetter *et al.*, 2003; Harmon *et al.*, 2009). This network added two densely populated human landscapes, surrounding the cities of Baltimore and Phoenix, to its network within the last 10 yr. The planned National Environmental Observatory Network (NEON) infrastructure will provide a new set of tools. While its permanent eddy-flux towers will be placed in wildland systems, a number of re-locatable flux towers will be available (Pennisi, 2010). Investigators should place some of these in human-dominated areas and fragmented landscapes. The fact that they will be re-locatable would allow towers to be placed in areas expected to undergo human-driven alteration and then moved back for repeated measurements 10–20 yr later.

Now that ecology is more widely investigating human-dominated locales, how is this effort making use of the ecosystem concept? A framework that is growing rapidly at present is that of ecosystem services. The services framework addresses the supply of food and fiber for human societies and economies, the supply of water, and the regulation of environmental conditions for human well-being (Reid *et al.*, 2005; Carpenter *et al.*, 2009). The idea was present at least 40 yr ago in the writing of Odum (1969), but its development and application have surged only in the last decade. Since the publication of the Millennium Ecosystem Assessment report (Reid *et al.*, 2005), categories of ecosystem services have typically been outlined as provisioning, regulating, cultural, and supporting. Although it may seem obvious, a notable contribution has been the explicit recognition that there are desirable and less desirable sets of ecosystem states for humans (Elmqvist *et al.*, 2003).

Going forward, ecosystem scientists should become more engaged with the developing study of ecosystem services for three important reasons: (1) the services framework requires an improved scientific underpinning to represent ecosystem function at any point in time and space; (2) the issue of long-term ecosystem integrity needs greater attention; and (3) economists are developing the services framework for use in decision-making but with inadequate input from ecologists. I will briefly address each of these issues.

Investigators who study ecosystem services have noted that we need increased ecological understanding of how to connect multiple services (Bennett *et al.*, 2009). Recent methodological advances include the spatial mapping of services across heterogeneous landscapes (Anderson *et al.*, 2009; Eigenbrod *et al.*, 2010). Tradeoffs and overlaps in combinations services (termed 'bundles') are being assessed across heterogeneous landscapes (Raudsepp-Hearne *et al.*, 2010). It is easy to see this as related to the mapping of eco-

system processes linked to a GIS described above. At the same time, the linkage of these analyses to a deeper understanding of ecosystem function, drawing on the rich history of ecosystem science, is lacking. The mapping of services has emphasized statistical relationships among GIS data layers. While this is a useful first step, future research should incorporate greater causal understanding of functional relationships. For example, net primary production, water budgets, and nutrient retention are not simply disconnected observations that we should aim to correlate. Through ecosystem function, they are intimately connected in a way that we can understand. One means for incorporating better mechanistic understanding will be to make clearer, more well-defined translations from ecosystem *processes* to ecosystem *services* (Carpenter & Folke, 2006; Carpenter *et al.*, 2009). Future research should incorporate such translations into ecosystem process models. Models incorporate much of our synthetic understanding of the causal relationships among ecosystem processes; translating these into services will allow their extrapolation across heterogeneous landscapes and, equally importantly, an ability to forecast changes in services through time.

On the topic of long-term ecosystem integrity, Kareiva *et al.* (2007) suggested that we need to consider how the use of one ecosystem service could affect the resilience of an ecosystem and thus its ability to provide future flows of services. This is a critical area of research to which ecosystem science should contribute. In both its common usage and its usage among specialists, the ecosystem concept addresses the persistence of organization through time. If there is an ecosystem function that is vulnerable to loss or to a shift into a different set of dynamic states, this needs to be understood and incorporated into decision-making about resource use, land use change, and environmental management (Kay & Schneider, 1994; Heal *et al.*, 2004; Mayer & Rietkerk, 2004; Koch *et al.*, 2009; Norgaard, 2010). Ecosystem services are likely to be an important framework for such decision-making (e.g. Nyhus *et al.*, 2007; Raudsepp-Hearne *et al.*, 2010). Decisions need to consider not only the present state of ecosystem services, but alterations to the long-term future flows of services that are likely to result from human impacts such as land cover change, climate change, fragmentation, invasive species, and harvesting of resources.

The services framework provides an opportunity for ecologists to engage with economists to promote environmental decision-making that is better informed. Economists see the services framework as an important means to evaluate, often in monetary terms, the ramifications of various possible decisions (Palmer & Filoso, 2009). Services valuation provides a means to estimate the utility of various projects, resource extraction scenarios, or land conservation scenarios. If ecosystem services address human well-being (Reid *et al.*, 2005) then they can be used, virtually by definition,

to estimate utility. In coming decades, if ecologists do not engage in providing an improved scientific underpinning for ecosystem services, then economists, managers, and policy makers will estimate these using their own approaches. The resulting decisions may fail to appreciate long time horizons, spatial interconnections in the landscape, the roles of biodiversity, cumulative effects of multiple impacts, or lag times between causes and effects. These are all important topics that are not yet addressed well in the ecosystem services framework, but need to be incorporated. If ecologists do develop this framework more fully, then decisions with long-term ramifications for ecosystems and landscapes can be better informed by our ecological understanding, facilitating a more stable coexistence for humans and nature (Kareiva *et al.*, 2007).

2. Social–ecological systems

A new interdisciplinary integration that has long been developing (Odum, 1969; Costanza *et al.*, 1993) has begun to come of age within the last few years (Carpenter *et al.*, 2009). Ten years ago, ‘biocomplexity’ was defined as the study of ‘properties emerging from the interplay of behavioral, biological, chemical, physical and social interactions that affect, sustain, or are modified by living organisms, including humans’ (Michener *et al.*, 2001). This new view for studying human societies and ecosystems embodied a landscape-scale perspective and included linkages from terrestrial to aquatic systems. This has developed conceptually to include two-way interactions between human societies and ecosystems (Pickett *et al.*, 2005); while humans depend on the flows of goods and services from ecosystems, they also alter and impact those systems, thus affecting the future flows of goods and services. The terminology has shifted from biocomplexity to the study of coupled human and natural systems (Liu *et al.*, 2007; Walsh & McGinnis, 2008) or social–ecological systems (Norberg & Cumming, 2008; Carpenter *et al.*, 2009). For the ecosystem ecologist, considering these coupled systems involves a fundamental shift in focus (Costanza *et al.*, 1993), while at the same time emphasizing some phenomena that ecologists have always emphasized. Primary and secondary production, key ecosystem processes, are closely coupled to biomass extraction in agriculture, forestry, and fisheries. Nutrient cycling and retention are closely coupled to fertilizer use, runoff, and the eutrophication of receiving bodies of freshwater, estuaries, and the coastal ocean (Galloway *et al.*, 2008). The very concept of eutrophication is an ecosystem-level concept.

Social–ecological systems should be viewed as the hierarchical level that integrates above ecosystems, particularly in human-dominated landscapes. This is a change from the traditional biotic hierarchy, which considers landscapes and biomes as levels that integrate above ecosystems. But human presence, impacts, and alteration are pervasive worldwide

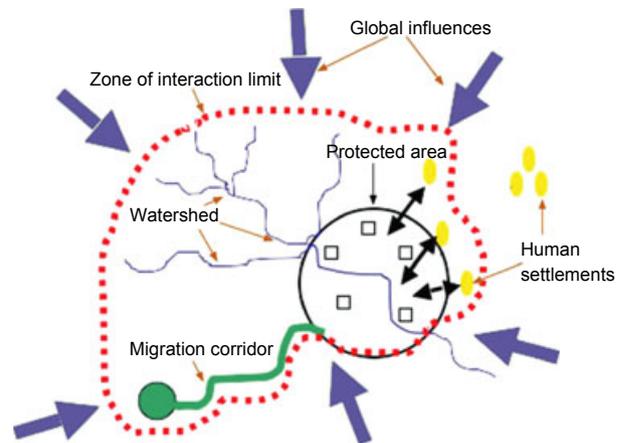


Fig. 5 The ‘zone of interaction’ concept of DeFries *et al.* (2010) for a protected area. This framework can be used to envision how ecosystem processes connect to other processes in a conceptual hierarchy. If an ecosystem under observational study is delimited by the black circle, ecophysiological and ecosystem processes can be studied in plots represented by the small black squares and whole-system budgets represented by the black circle. Yet these are connected to landscape processes (including watersheds), larger scale population–community processes (including migration), and resource use, alteration, and impacts from human settlements nearby. Global influences include climate, global biogeochemical cycles, and distant human settlements that may create markets for resources or benefit from ecosystem services. Reproduced, with permission, from DeFries *et al.* (2010).

and growing (Reid *et al.*, 2005). Ecosystem structure and function are increasingly linked to human behavior and decision-making frameworks. Researchers are developing more sophisticated approaches to study such connections, including approaches from game theory (Becu *et al.*, 2003; Janssen *et al.*, 2010). While social behavior, regulatory mechanisms, and markets should not be thought of as ecosystem processes, they are explicitly part of the framework of social–ecological systems (Carpenter *et al.*, 2009).

An interesting illustration of such a hierarchy of processes is provided by the ‘zone of interaction’ concept (DeFries *et al.*, 2010), which was meant to place a protected area in the context of its surrounding landscape (Fig. 5). This can be applied to any study area, including an ecosystem as typically delimited for study in the field. The two-way arrows between the human settlements and the locale under study (Fig. 5) indicate bi-directional interactions between ecological processes in the locale and the human population, whether it is inside or outside the boundary.

V. Conclusions and future research

In its 75 yr of development, the ecosystem concept has served as a central paradigm in ecology. This review, in its brevity, omits numerous important sub-fields. These include molecular approaches and microorganisms (Zak *et al.*, 2006) and ecosystem management and restoration

(Mayer & Rietkerk, 2004), among others. Other topics that have been the subjects of entire books are here distilled down to a few sentences, including hierarchy theory, energetics, biogeochemistry, complexity theory, disturbance and succession theory, and ecosystem modeling.

As a convenience of language, ecosystem ecologists write about ecosystems as integrated biotic systems as though they could be carefully defined. They recognize that the causal connections among processes may in fact give rise to quasi-organized, persistent characteristics and a degree of stability in biotic and abiotic state variables at an aggregate scale. But in the vast majority of terrestrial locales in nature, this level of organization cannot be viewed as a property of a complete biotic community. This is one point on which current scientific approaches break with much of the conceptual work from previous decades.

Theory needs to be translated into operational terms so that it can be tested in empirical studies. In ecosystem science, the use of a boundary has been an important operational technique, from the small watershed concept in the 1960s to the fetch of an eddy-flux tower that is widely used today. Future work to understand any organization that links population–community processes to fluxes of carbon, energy, water, and nutrients must recognize the fundamental problem that I have referred to here as the problem of partial communities. Plant and animal populations studied within a boundary may experience quite different ecological interactions outside of the boundary. Landscape ecology embraces this view: heterogeneous patches in a landscape can function as population sources or sinks at a coarser scale. The key point to understand here is the ramification for the ecosystem as an organizational concept. Ecosystem scientists today do not focus on an ecosystem as an entity or organizational level that includes a precisely defined biotic community. Instead, investigators treat ecosystem processes as an integrated set of processes that occur in a locale, strongly linked to ecophysiological, community, and landscape processes. Each of these sets of processes can be studied over a range of scales and may exhibit scale dependence. The choice of a scale and a boundary is often an operational choice needed for empirical work.

Theory may run ahead of its tests, which is acceptable when it helps lead investigators to develop research questions that test the theory. This has been a difficult challenge for complexity theory and has limited its ability to contribute to progress in ecosystem science. Complexity concepts need to be made operational for testing in the field, which will require greater attention to boundaries, to flows of matter and energy, and to the multiple scales of ecological processes. The question ‘Is an ecosystem a complex adaptive system?’ probably needs to be rephrased. As we have seen, ‘an ecosystem’ is not a rigorous organizational level that can be studied empirically. More useful research questions need to be formulated. Spatial, individual-based modeling

approaches continue to offer promise. Models need to be applied across ecologically relevant scales from neighbor interactions to landscape patches, linked to ecosystem processes at appropriate scales, and translated into state variables and fluxes that are empirically testable simultaneously using fine-scale and large-scale observational infrastructure.

Future improvements in the application of models to translate theory are likely to yield progress in two important directions in ecosystem research. The first concerns ecological stoichiometry. Recent research has yielded new insights into how nutrient ratios relate to growth rates, thus controlling energy flows and the trophic structure of food webs (Peñuelas & Sardans, 2009). Individual-based models can represent stoichiometry in different trophic levels and its relation to growth, reproduction, and energy flows and nutrient cycling. The second area concerns the longstanding debate on the relationship between biodiversity and ecosystem function (e.g. Hooper *et al.*, 2005), including properties of stability and resilience (Johnson *et al.*, 1996; Holling & Gunderson, 2002). Again, individual-based models can help to link theory with observations and experiments. But to be useful in comparing model results against observations made in the field, modeling approaches must explicitly treat issues of population ranges relative to field-study boundaries and landscape heterogeneity. For example, stability or resilience of production or other ecosystem functions within a locale may not arise from interactions in the resident biotic community in the locale, but from the variability in interactions distributed across a heterogeneous landscape.

The approaches and concepts from ecosystem science have become firm elements in the important applied field of global change research. Significant recent developments are a growing emphasis on studying human-dominated landscapes and on characterizing ecosystem services, both of which should draw to a greater extent in future decades on the knowledge base and tools of ecosystem science. Our hard-earned understanding should be applied to aid in decision-making that will include assessment of the long-term persistence or vulnerability of ecosystem processes in a locale. Future models of ecosystem processes will need to include not only spatial heterogeneity in population–community processes. They will need to include continuing human alteration of the biota and abiotic environment and should include translation of ecosystem process to services for human populations. In the Anthropocene, natural or wildland ecosystems are a shrinking minority. Spatially complex landscapes that are strongly coupled to human alteration, resource use, and decisions are fast becoming the dominant ‘units of nature on the face of the earth’.

Acknowledgements

I thank generous colleagues and mentors, discussions with whom helped to clarify my thinking about topics treated here.

They include Knute Nadelhoffer, Ed Rastetter, Bob Ulanowicz, Deborah Goldberg, John Aber, Michelle Mack, Mark Harmon, George Kling, Don Zak, Garry Peterson, David Allan, and many others. I thank my graduate students Anna Brunner, Sarah Kiger, and Meghan Hutchins for sharing the results of their literature reviews on related topics. Three anonymous reviewers provided thoughtful comments that helped a great deal. Finally, thank you to Editor Amy Austin for working with me to develop this topic for a *Tansley review*.

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