

Viewpoint

Dimensions of ecosystem complexity: Heterogeneity, connectivity, and history

M.L. Cadenasso^{*a*,*}, S.T.A. Pickett^{*b*}, J.M. Grove^{*c*}

^a Hixon Center for Urban Ecology, School of Forestry and Environmental Studies, Yale University, 205 Prospect Street, New Haven, CT 06511, United States

^b Institute of Ecosystem Studies, Box AB, Millbrook, NY 12545, United States

^c USDA Forest Service, Northeastern Research Station, 705 Spear Street, P.O. Box 968, Burlington, VT 05401, United States

ARTICLE INFO

Article history: Received 2 June 2005 Received in revised form 30 June 2005 Accepted 2 July 2005 Published on line 23 January 2006

Keywords: Biocomplexity Framework Coupled systems Spatial heterogeneity Legacies Land cover classifications Urban ecosystems

ABSTRACT

Biocomplexity was introduced to most ecologists through the National Science Foundation's grant program, and the literature intended to introduce that program. The generalities of that literature contrast with the abstract and mathematical sophistication of literature from physics, systems theory, and indeed even of pioneering ecologists who have translated the concept into ecology. This situation leaves a middle ground, that is both accessible to ecologists in general, and cognizant of the fundamentals of complexity, to be more completely explored. To help scope this middle ground, and to promote empirical explorations that may be located there, we propose a non-exclusive framework for the conceptual territory. While recognizing the deep foundations in the studies of complex behavior, we take ecological structure as the entry point for framework development. This framework is based on a definition of biocomplexity as the degree to which ecological systems comprising biological, social and physical components incorporate spatially explicit heterogeneity, organizational connectivity, and historical contingency through time. These three dimensions of biocomplexity - heterogeneity, connectivity, and history - will be explored as axes of increasing complexity. Basing the description of spatial heterogeneity on either patch or continuous quantification, complexity of spatial structure increases as quantification moves from simple discrimination of patch types and the number of each type to assessment of configuration and the change in the mosaic through time. Organizational complexity reflects the increasing connectivity of the basic units that control system dynamics. At the simple end of the axis, the functional connectivity between units is low, and the processes within a unit are determined by structures or other processes within that unit. At the highest level of complexity along this axis, units in a mosaic interact through fluxes of energy, matter, organisms, or information, and the structure and dynamics of the mosaic can be altered by those fluxes. Temporal relationships in the system range from direct contemporary ones to indirect and historically contingent ones. The influence of indirect effects, legacies, the existence of lagged effects, and the presence of slowly appearing indirect effects constitute increasing temporal complexity. This framework embodies some features of both the structural approach to complexity and the approach of complexity of explanations that we extracted from the literature. It leaves the issue of what levels of each axis result in complex behavior as an important question for further research. © 2006 Published by Elsevier B.V.

* Corresponding author.

E-mail address: Mary.Cadenasso@yale.edu (M.L. Cadenasso).

¹⁴⁷⁶⁻⁹⁴⁵X/\$ – see front matter © 2006 Published by Elsevier B.V. doi:10.1016/j.ecocom.2005.07.002

1. Introduction

Ecologists have long been aware of the importance of complexity, but few have explicitly adopted it into their research programs. The opportunity to incorporate complexity came to the attention of most ecologists primarily through the National Science Foundation's granting program focusing on biocomplexity. This program spurred a burst of literature targeted at ecologists in general (Colwell, 1998; Michener et al., 2001; Cottingham, 2002). In an attempt to be accessible, this recent literature leaves much of the concept of biocomplexity, and its application and adoption, to be explored. In spite of the relatively recent general increase of interest in complexity, the theory and associated concepts such as non-linear dynamics, self-organization, emergence, criticality, etc., have been a rich topic for study in physics, thermodynamics and systems theory (Kay and Schneider, 1994; Bak, 1996; Auyang, 1998; Milne, 1998). Some ecologists familiar with these fields have applied these concepts successfully to ecological systems (Ulanowicz, 1997; Milne, 1998; Medvinsky et al., 2001; Li, 2002a). These applications are sophisticated and mathematically advanced, but their abstraction may make it difficult for empirical ecologists in general to appreciate or apply the formal concepts of complexity in their own research (Kay and Schneider, 1994; Anselin and Tam Cho, 2002). Therefore, a middle ground is needed between the very accessible and consequently general introductions (Colwell, 1998; Michener et al., 2001), and the sophisticated mathematical abstractions (Li, 2000; Bruggeman et al., 2002; Li, 2002b; Ulanowicz, 2004). This middle ground would relate biocomplexity to concepts and issues that ecologists are concerned about and familiar with but would show clear links to the general ideas of complexity. The purpose of this paper is to explore this middle ground and is under taken in the spirit of recognizing a need for a diversity of ways to conceive and apply complexity in ecology (Milne, 1998; Li, 2004; Loehle, 2004).

Ecology has long been concerned with structure-function relationships (Watt, 1947). Therefore, many ecological studies begin from a structural perspective. Even functional ecological studies which may not explicitly measure structure may implicitly use structure to frame the contrasts they investigate. The richness of ways in which ecological systems can be structured suggests a backdrop against which complex behavior can be measured. Scientists who study complexity theory often focus on understanding the behavior of systems (Li, 2002b). One of the guiding questions in complexity theory is how simple structures lead to complex behaviors (Bak and Chen, 1991; Bruggeman et al., 2002). From the formal complexity perspective, behavior refers to an entire system, which incorporates both ecological structure and function. Thus in this paper, we use "structure" in two ways. One is the complexity perspective that addresses the behavior of combined structure-function systems, and the other is the traditional ecological perspective of structure constituting system architecture and composition (Noss and Cooperrider, 1994). Understanding structural contrasts may contribute to the conceptual middle ground between complexity theory and empirical ecology.

To explore the potential middle ground, this paper articulates an empirically oriented conceptual framework. Because the concept of biocomplexity is relatively new to many ecologists, we review definitions from the literature and assess their contribution to a general ecological approach. While recognizing the deep foundations in the studies of complex behavior, we take ecological structure as the entry point for the development of this middle ground and suggest a structural definition for biocomplexity that forms the foundation of an organizing framework. This framework links to the growing interest in heterogeneity as a key driver in ecological systems (Huston, 1994) while also incorporating the increasing appreciation of historical and indirect effects (Brown, 1994) and organizational hierarchies (Allen and Hoekstra, 1992). The framework is intended to help guide the empirical quantification of structures that can yield complex behaviors. The framework can also be used to integrate social and ecological sciences and an example from the Baltimore Ecosystem Study will explore this linkage. We will demonstrate how the framework can be used to organize research and generate hypotheses across disciplinary boundaries in an effort to understand the complexity of an urban ecosystem.

2. Definitions: biocomplexity for ecology

Complexity theory (Auyang, 1998; Milne, 1998) is a precursor to the concept of biocomplexity. This theory is driven primarily by approaches from physics and mathematics and has assigned several properties to complex systems (Costanza et al., 1993; Milne, 1998; Li, 2002a). It may be better to say that these properties characterize complex behavior rather than systems, because simple systems can in some cases exhibit complex outcomes. Thus, the real issue is how simple systems produce complex behaviors. Of course complicated structures may, as well, produce complex behaviors (Frost et al., 1988; Poff and Ward, 1990; Furley, 1992; Bruggeman et al., 2002). The behaviors of interest include non-linear behavior, self organization, and emergent properties (Rosen, 1991; Colwell, 1999; Ascher, 2001). Recognizing that many ecologists have sought complex behaviors in their systems (Brown, 1994; Thompson et al., 2001; Li, 2002a; Petrovskii and Li, 2004), the field of ecology, in general, however, is beginning to develop and define the concept of biocomplexity in ways that are relevant to its broad disciplinary domain (Michener et al., 2001).

Many ecologists were introduced to complexity by the National Science Foundation program. Although this program generated much activity there remains uncertainty among mainstream ecologists about this concept. This uncertainty gave rise to a symposium at ESA in an attempt to discuss among the general ecological community the meaning of this concept and its application to a broader base of ecological research. This paper is a product from an invited talk in that symposium.

The term "biocomplexity" was introduced by Rita Colwell, then Director of the National Science Foundation (NSF), as she communicated to the scientific community that the concept would play a central role in her vision for NSF (Colwell, 1998). Coining this term and introducing it as a research focus were motivated by several perceived needs for improving the process or culture of biological science. Colwell encouraged practitioners to look beyond the boundaries of their individual disciplines to solve the increasingly large and multifactoral problems facing society and the health of the planet. She and others (Li, 2000) recognized the long history and utility of a reductionist approach in science but suggested that the concerns and problems currently facing society required a more holistic effort. Colwell (1998) characterized biocomplexity as having the goal "to discover the complex chemical, biological, and social interactions in our planet's systems. From these subtle but very sophisticated interactions and interrelationships, we can tease out the principles of sustainability" (Colwell, 1998, p. 786). In this definition she specifically addressed the need for interdisciplinary work and acknowledged that often the relationships will be subtle and difficult to extract and understand. She also focused on multiple scales, including coarse ones. This definition is aimed towards understanding sustainability of the Earth's systems.

Program officers at NSF defined biocomplexity to provide guidance for submission of proposals to the new program (Michener et al., 2001). They defined biocomplexity as "properties emerging from the interplay of behavioral, biological, physical, and social interactions that affect, sustain, or are modified by living organisms, including humans" (Michener et al., 2001, p. 1018). This definition resonates with Colwell (1998) by emphasizing the interdisciplinary nature of the concept but it specifies the list of potential disciplinary participants. The definition by Michener et al. (2001) also incorporates organisms very specifically, including humans, and how they are affected by, maintain, or change interactions. Cottingham (2002) accepted the Michener et al. (2001) definition and identified additional characteristics of biocomplexity. She stated that "biocomplexity includes nonlinear or chaotic dynamics, unpredictable behavior and interactions that span multiple levels of biological organization or spatiotemporal scales" (Cottingham, 2002, p. 793). In this paper, following Frost et al. (1988), she proposed three dimensions of biocomplexity-spatial, temporal, and organizational. Although she identified these dimensions, she did not develop their application to biocomplexity in the sense of a framework. Earlier, Frost et al. (1988) had used these dimensions, along with a dimension of experimental scale, to suggest how studies of lake system complexity might select appropriate scales and aggregation to frame research. Scalar complexity was specifically addressed by Wu (1999). He emphasized that complexity involved description or explanation that simultaneously invokes multiple levels of organization or scales (Wu, 1999). Hierarchy theory provides a clear tool for dealing with spatial scale. It suggests that all scales are equally deserving of study, not only fine scales as reductionism emphasizes. Analyses must specify the scales of focus, and to understand complex systems, examine relationships that cross scales (Ascher, 2001).

Fundamental definitions of biocomplexity have emerged from a body of research aimed at exploring the links between components in complex systems. One very useful definition is that proposed by Ascher (2001, p. 749): "complexity' is the multiplicity of interconnected relationships and levels." He suggested that the characteristics so often attributed to complexity, such as emergence and nonlinearity, are consequences of the fundamental properties identified in his definition. An important goal of this fundamental definition is to provide concepts that can be readily translated into practical analysis, such as the assessment of management structures for sustainability (Holling and Gunderson, 2002). An analogous definition, proposed to support research into complex interactions in lake communities and ecosystems states that "complex interactions result from multiple pathways linking organisms with abiotic resources" (Carpenter and Kitchell, 1988b). The surprising practicality of these fundamental definitions is in contrast to much of the literature written to characterize biocomplexity for programmatic needs (Colwell, 1999; Michener et al., 2001; Cottingham, 2002).

One conclusion to be drawn from these definitions is that biocomplexity can be taken in three distinct but related ways: first, as the structure of a system of interest (e.g. Carpenter and Kitchell, 1988a; Ascher, 2001); second, as emergent, non-linear or self organized outcomes (Kay and Schneider, 1994; Milne, 1998; Li, 2002b); finally as a highly connected explanation or model (Costanza et al., 1993; Bellmann, 2000; Schmitz, 2001). We cannot suggest that one of these approaches is better than the others. But we hope that recognizing the diverse ways in which biocomplexity has been characterized in the literature helps map out the middle ground we seek.

There are two approaches to defining a concept. The first is to articulate a definition that attempts to be as inclusive as possible. From that definition, frameworks can be constructed to organize ideas and data and to provide a structure for operationalizing the definition in particular situations. The second approach is to ask how the concept can be quantified. What metric indicates its presence or importance? The latter approach may provide short term productivity but may not be best in the long term because critical features or characteristics of the concept may be missed and researchers led astray as they search for a system best characterized by the selected metric. This approach also requires the Herculean task of agreeing on one metric or suite of metrics. Therefore, we employ the first approach of framework development as a more open-ended tool. Because frameworks are built on rigorous definitions and no single definition of biocomplexity has been agreed upon, we draw from the range of definitions suggested in the ecological literature mentioned above. For purposes of this paper, we propose a definition to address both the fundamental and the practical conceptions of complexity: Biocomplexity of structure is the degree to which ecological systems comprising biological, social, and physical components incorporate spatially explicit structure, historical contingency, and organizational connectivity. In this definition, we use three axes of biocomplexity recognized by earlier authors (Frost et al., 1988; Cottingham, 2002)-spatial, temporal, and organizational. We further emphasize crossdisciplinary integration, which will be particularly important in systems that are complex because of coupling natural and human components (Gunderson et al., 1995; Pickett et al., 1997, 2005; Corner, 1997; Alberti et al., 2003). In the next section, we define these axes and provide examples of increasing structural complexity along each one. These three axes form one operational framework for biocomplexity accessible to mainstream ecology. Additional frameworks may be established by ecologists for the study of biocomplexity (Poff, 1992; Li, 2002a; Alberti et al., 2003; Loehle, 2004). Therefore, the broad framework presented here may ultimately be complemented by other frameworks.

3. Goals of an empirically motivated framework

Our use of a framework, and the characteristics of frameworks, make clear that our attempt to establish some of the middle ground between complexity theory and empirical ecology is a preliminary one. A framework is a conceptual construct that articulates what is included in the conceptual arena under discussion, and what is not (Cadenasso et al., 2003b). It is inclusive of various systems, processes, and scales. The job of the framework is to provide a roster of components, and to suggest how the components may relate to one another (Cadenasso et al., 2003b). From the framework, a model template can be constructed so that causal relationships among the components can be empirically tested. The model template helps develop working models, specific to particular places, scales, and series of questions to test relationships among framework components. Not all components included in the framework are expected to appear in a single model. In fact, a subset of the components will become the building blocks of specific models. The components included in the model are selected based on characteristics of the precise situation the model applies to, or on the research question guiding model development. Through testing of the working model, additional components can be added or removed from the framework, and components can be organized into, for example, functional groups. The framework is not an end in itself, but rather a tool to help create models and generate hypotheses (Pickett et al., 1987; Machlis et al., 1997; Cadenasso et al., 2003a).

There is a tradeoff between specificity and inclusiveness within a given framework and the models that emerge from it (Costanza et al., 1993). However, both can be accommodated in a framework by a hierarchical structure. In other words, frameworks can accommodate appropriate reductionist *and* synthetic research approaches (e.g. Bruggeman et al., 2002). Resolving to the greatest detail describes processes at fine scales and in specific environments; whereas, the clustering of detailed specific processes exposes more general, synthetic processes. Therefore, using a general and inclusive framework requires the researcher to decide where in the hierarchy to operate by articulating the spatial and temporal scales addressed (Pickett et al., 1994; Fotheringham and Brunsdon, 2002).

4. Framework for biocomplexity in ecology

The structural framework for biocomplexity that we propose consists of three axes: heterogeneity, connectedness, and historical contingency (Fig. 1). These three axes represent a convergence of differing perspectives of system structure. For example, Frost et al. (1988) and Cottingham (2002) recognize space, organization, and time as necessary components for modeling and understanding ecological systems. Hierarchy theory (Allen and Starr, 1982) also embodies how entities are

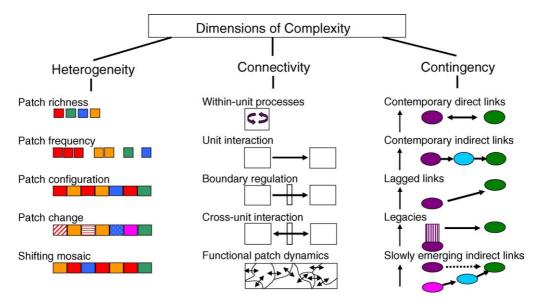


Fig. 1 – Framework for biocomplexity. The three dimensions of biocomplexity are spatial heterogeneity, organizational connectivity, and temporal contingencies. Components of the framework are arrayed along each axis increasing in complexity. For example, a more complex understanding of spatial heterogeneity is achieved as quantification moves from patch richness, frequency and configuration to patch change and the shift in the patch mosaic. Complexity in organizational connectivity increases from with-in unit process to the interaction of units and the regulation of that interaction to functional patch dynamics. Finally, historical contingencies increase in complexity from contemporary direct effect through lags and legacies to slowly emerging indirect effects. The arrows on the left of each illustration of contingency represent time.

organized and how slow and fast rates of interactions sort entities among levels of organization. Landscape ecology is based on the reciprocal interaction of structure and function and how they change through time (Forman, 1995; Pickett and Cadenasso, 1995; Wiens, 2000). Patch dynamics takes a similar approach to spatial and structural relationships (Pickett and White, 1985). Therefore, we capture the richness of all of these perspectives by using these three axes. This structural approach to systems addresses what pieces are there and how they are arranged (heterogeneity), how the pieces interact (organization or connectivity) and how they change through time (history or contingency). This framework embodies some features of both the structural approach to complexity and the approach of complexity of explanations that we extracted from the literature. It leaves the issue of what levels of each axis result in complex behavior as an important question for further research.

Complexity in structural heterogeneity refers to increasingly subtle and comprehensive quantification of spatial mosaics or fields. Ecologists often describe spatial heterogeneity as patches—discrete areas that differ in structure, composition, or function. The theory of patch dynamics has been an important tool in community organization, population dynamics, succession, disturbance, ecosystem function, and conservation (Pickett and Rogers, 1997; Wu, 1999). Patch theory can be used to evaluate complexity in ecological systems (Pickett et al., 2000), and suggests that understanding complexity in spatial structure is a powerful approach to exploring structure–function relationships.

Complexity of heterogeneity increases as the perspective moves from patch type and the number of each type, to spatial configuration, and to the change in the mosaic through time (Wiens, 1995; Li and Reynolds, 1995) (Fig. 1). At the simplest structural end of the spatial axis, systems can be described as consisting of a roster of patch types. Richness of patch types summarizes the number of patch types making up the roster. Structural complexity is increased as the number of each patch type is quantified. This measurement is expressed as patch frequency. How those patches are arranged in space relative to each other increases the complexity of understanding the heterogeneity or structure of the system (Li and Reynolds, 1993). Finally, each patch can change through time. Which patches change, how they change, and shift identity constitutes a higher level of spatial complexity. The most complex understanding of system heterogeneity is acquired when the system can be quantified as a shifting mosaic of patches, or, when the patch dynamics of the system is spatially explicit and quantified (Fig. 1). Although the passage of time is an element at the highest level of spatial complexity, this is distinct from historical complexity, where the function of such phenomena as lags and legacies is the concern.

The organizational axis reflects the increasing connectivity of the basic units that control system dynamics. Within organizational hierarchies, causality can move upward or downward (Ahl and Allen, 1996). Organizational complexity drives system resilience, or the capacity to adjust to shifting external conditions or internal feedbacks (Holling and Gunderson, 2002). Following our structural approach, we can return to the patch as an example of the basic functional unit of a system to explain this axis more fully. In this case, the simplest end of the connectivity axis is within-patch processes. As the interaction between patches is incorporated, complexity increases. Understanding how that interaction may be regulated by the boundary between patches constitutes a higher level of complexity. The organizational complexity axis continues to increase with recognition that patch interaction may be controlled by features of the patches themselves in addition to the boundary. Finally, the highest level of structural complexity on the organizational axis is the functional significance of patch connectivity for patch dynamics, both of a single patch and of the entire patch mosaic (Fig. 1). Note that from the perspective of complex behavior, each range of this axis would be considered a structure whose complex behavior could be evaluated and compared to other ranges of the gradient.

Our conception of the organizational axis differs from that proposed by Frost et al. (1988). Their conception examines the degree of resolution of components of the system. Choosing the resolution of system components is a fundamental step in building models of ecological systems (Jax et al., 1998). When such resolution is of system elements that can be expressed spatially, it will be dealt with using the first axis of the framework here, that of heterogeneity. When the resolution is of a functional sort, a different kind of gradient will be used. The functional resolution will be specific to each discipline or model. For example, resolving ecosystem components into genotypes, species, or niche functional groups will each produce very different models of ecosystem function. Alternatively, ecosystem components could be resolved into household, neighborhood, or various levels of government. Because such decisions depend on the goals of model construction, we suggest that component resolution be considered a filter that is applied in the construction of models. It thus stands as a methodological step in complexity between the more general framework and the specific models that are constructed within the context of the framework. This step is analogous to the experimental scaling dimension Frost et al. (1988) proposed as practically important.

Historical contingency, the third axis, refers to relationships that extend beyond direct, contemporary ones. Therefore, the influence of indirect effects, legacies or apparent memory of past states of the system, the existence of lagged effects, and the presence of slowly appearing indirect effects constitute increasing historical complexity (Fig. 1). To explain the steps of this axis we start with the simple or contemporary ones. Contemporary interactions includes those interactions where element A influences element B directly. Indirect contemporary interactions involve a third component, C, to transmit the effect of A on B. An interaction is lagged if the influence of element A on element B is not immediate but manifested over some time period. A higher level of temporal complexity is invoked by legacies. Legacies are created when element A modifies the environment and that modification, whether it be structural or functional, eventually influences element B. At the high end of the temporal complexity axis are slowing emerging indirect effects. These types of interaction occur when the apparent interaction of elements A and B is illusory and element B is actually influenced by some earlier state of element A and that influence is mediated through an additional element, C (Fig. 1).

Each axis in the framework is intentionally abstract so that it can be applied to different disciplinary realms. For example, the spatial heterogeneity of an urban system may be described by patches based on such varied attributes as land cover, zoning, census block groups, or soil permeability. In other words, a complex system may consist of ecological, social, and physical elements and processes that interact to influence system structure and patch dynamics. A framework that can accommodate a multiplicity of factors representing different disciplines, which act on different spatial, temporal, and organizational scales, is a powerful tool for understanding complex systems.

Many different models can be generated from the framework and they can encompass any combination of variables that are hypothesized to answer the particular research question. For example, models can be constructed (1) within one of the axes incorporating different disciplinary variables; (2) that span more than one axis while focusing on a single disciplinary realm; (3) include all axes and multiple disciplines. If all variables were included in a single model, however, it would be untestable. Importantly, frameworks do not suggest that everything is connected to everything else, at least not with equal intensity of connection. All models generated from the framework can be linked to one another or unified in the conceptual space defined by the three dimensions of the framework. This feature enhances the ability to synthesize across studies of contrasting systems and scales. We will use an example to demonstrate number 1 above and focus on the spatial structure of a metropolitan region from an ecological and social perspective. In the interest of space, we will pose testable questions for 2 and 3.

5. Application of the framework

Metropolitan areas are structured by multiple factors (Gottdiener and Hutchison, 2000; Berry, 2001; Vasishth and Sloane, 2002). For example, patch maps can be created based on population density, zoning, time of development, the distribution of income, race, or education levels of people, and land use. Each map shows a snapshot of the system structured by one variable or a suite of variables. A suite of variables is frequently converted into an index or categorization. Comparing the patch structures that emerge from two different perspectives may lend insight into the structure and function of an integrated system. We demonstrate this interdisciplinary level of complexity by comparing the structure of metropolitan Baltimore from an ecological and a social perspective. From the ecological perspective we employ land cover to describe the elements of the system. The patch array developed from the social perspective portrays differences in consumer behaviors represented by a categorization of lifestyle groups. This categorization is used as a measure for the social structure of the system. The example focuses on the spatial heterogeneity axis of the framework. It can be used to quantify patch richness, frequency, and configuration of the system from two distinct disciplinary realms. With time series data, changes in patch size, type, and configuration as well as changes in the associations of ecological and social patches types can be quantified. Through this integrative approach, we

assess whether there is a characteristic association of ecological and social patches in the system.

5.1. Ecological patch structure

Land cover is a common feature used to describe the spatial heterogeneity of a system. However, available classifications schemes (e.g. Anderson et al., 1976) do not have appropriate categorical or spatial resolution to capture the heterogeneity characteristic of cities. The major categories of urban land covers within such schemes are residential, commercial, industrial, transportation, and mixed. These schemes are also constrained by the separation of humans and nature in class definitions. Cadenasso and Pickett (Cadenasso et al., in press) have developed a new classification system that overcomes these limitations by integrating human and natural components of the system into class attributes and by increasing categorical and spatial resolution to capture the structural heterogeneity of the urban system.

This new classification scheme is therefore a reconceputalization of urban land cover. It does not simply add *complicatedness* (sensu Allen and Hoekstra, 1992) to currently available schemes by including more classes. Rather, it was designed to account more effectively for the biocomplexity of urban systems by incorporating built and human components into integrated classes.

Each class type is defined by the combination of attributes along three axes of structural variation and each axis is allowed to vary independently of the other two. The first axis is texture and proportion of vegetation. The second axis addresses the built environment by describing the type and density of buildings. The presence of massed impervious surfaces is the third axis. Each of these axes was selected because these structural characteristics are hypothesized to influence ecosystem functions, such as heat transfer, biodiversity, carbon sequestration and pollution storage and transport. Similarly, they may also influence certain social processes, while being generated by other socio-economic phenomena.

The classification scheme is hierarchical and at the topmost level, there are four categories: (1) closed canopy, coarse textured vegetation, (2) open canopy vegetation without built structures, (3) built structures and associated vegetation, and (4) miscellaneous. The closed canopy coarse textured vegetation is further classified by distinguishing crown size. The open canopy classes are discriminated by the relative proportion of coarse and fine textured vegetation occupying the patch. Classes containing built structures are defined by the type of building, the density at which the buildings exist, the texture of the accompanying vegetation and the proportion of the patch it occupies, and the presence of impervious surfaces. The fourth category contains elements of the landscape that have distinct structural signals such as interstate highways, cemeteries, and golf courses.

5.2. Social patch structure

A lifestyle marketing categorization was selected to represent the social structure of the system. Household lifestyle behavior is hypothesized to be a significant predictor of environmentally relevant decisions or capacities (Grove et al., 2006). The lifestyle categorization used is the Potential Rating Index for Zip code Markets (PRIZM), which classifies U.S. Census Bureau Block Groups into specific lifestyle clusters (Claritas, 1999). PRIZM is a hierarchical classification scheme. The categorization system has three levels of aggregation: 5, 15, or 62 categories. The five group categorization is arrayed along an axis of urbanization. Disaggregating from 5 to 15 categories adds a second axis: socioeconomic status. The 62 class disaggregation further expands the socioeconomic status axis into a lifestyle categorization with components including household composition, mobility, ethnicity, and housing characteristics (Claritas, 1999). Because this categorization is based on Census Block Groups, there is continuous cover of PRIZM clusters across the metropolitan region that can be displayed as a patch mosaic. The richness, frequency, and configuration of the patch array can be quantified, as suggested by our first axis of complexity (Fig. 1).

5.3. Integrated patch analysis: cross disciplinary complexity

The patch arrays resulting from the ecological variable of land cover and the social variable of lifestyle clusters can be compared to determine whether there are characteristic associations between the two. With this approach we are working from the same spatial axis of the complexity framework but applying it in two disciplines. We are asking whether our understanding of system structure is enhanced when we add structural complexity through the addition of multiple disciplines. What do we learn from (1) the ecological structure, (2) the social structure, and (3) the integration of the two disciplines along the structural heterogeneity axis?

The two patch arrays to be compared were generated for an 18 km² test region in the Gwynns Falls watershed (GFW). The 17,150 ha GFW (171.5 km²) is one of the research watersheds of the Baltimore Ecosystem Study, Long-Term Ecological Research program. The test region, referred to as Glyndon, is located at the headwaters of GFW and is a region that is rapidly urbanizing as remnant agricultural fields and woodlots are being converted to housing (Fig. 2).

The ecological and social patch arrays were created using the finest categorical resolution in both classifications (Fig. 3a and b). These two arrays were superimposed and a third, integrated, array created by their intersection (Fig. 3c). Each array can be evaluated to determine what each disciplinary lens reveals about the system structure and the structurally complex integrated array can be analyzed to determine whether increased understanding of system structure is achieved.

From the ecological classification the structure of the system can be described as consisting of 322 patches of 64 different types (Fig. 3a). Most of the area is occupied by built patches (60%) but 33% of the are is unbuilt and consists of forests (16%) and open space (17%). The forest and open space patches are small remnant patches. Of the land that is built, 72% of it is occupied by single structures in rows or clusters most of which are arrayed on the landscape at medium (66%) and high (30%) densities. These single structures are accompanied most frequently by a medium proportion of coarse textured vegetation (71%). Sixteen percent of the single structures maintain a high proportion of coarse vegetation cover and a low proportion is associated with 11% of the single structures. Little of the area has no coarse vegetation (1%). Connected structures occupy 14% of the built land and 55% of this building type is accompanied by parking lots. Open space patches occupy 197 ha and 61% of this area is characterized by a mix of coarse and fine textured vegetation. Sixty-seven hectares of open space patches contain bare soil, pavement, or both. Thirty-six percent of the open space is characterized by fine textured vegetation only. Forest patches with large crowns and those with small crowns occupy similar amounts of area at 17 and 18% of the total forest, respectively. Canopies more typically have mixed crown sizes (64%) and, of this

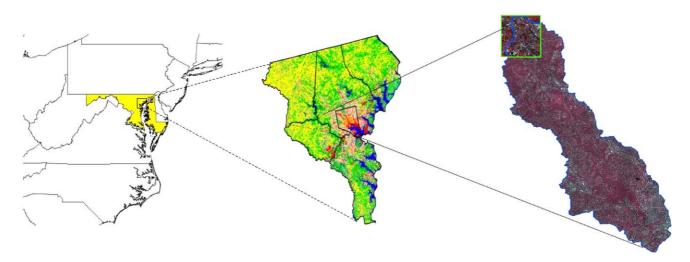
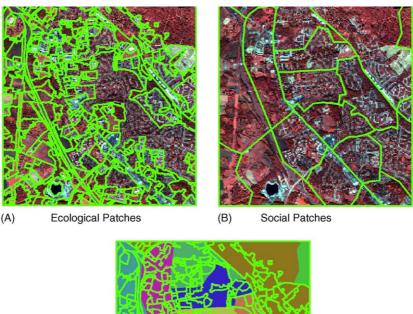


Fig. 2 – Location of the Gwynns Falls watershed in Baltimore, Maryland. The state of Maryland is in yellow. The middle panel shows the five county metropolitan areas of Baltimore and the boundary of the City of Baltimore is outlined in black within Baltimore County. The last panel is the Gwynns Falls watershed which extends from Baltimore County through the City of Baltimore and drains into the Chesapeake Bay. The area outlined in green at the top of the watershed is Glyndon and is approximately 18 km².



(C) Integrated Patches

Fig. 3 – Glyndon was classified using two approaches. The ecological land cover classification is in Panel A and the classification using the PRIZM life style clusters is in Panel B. The patches are outlined in green. The two patch arrays were merged to create a new patch array. This new patch array, Panel C, consists of patches that have unique combinations of ecological and social attributes. The original PRIZM patch array is in solid colors and the green outlines the new patches.

mixed type, approximately half of the area consists of canopies that contain between 65 and 85% large crowns.

From this analysis we can learn far more about the structural heterogeneity of the landscape using the new classification than using the standard land use/land cover classifications. Not only are class definitions integrated in the new classification to include both built and natural components of the system but the relative amounts of the different components can vary independently and, consequently, be quantified independently. For example, the density of vegetation, regardless of building type or density can be quantified and viewed spatially. Rather than quantifying vegetation only in forest patches where it exists alone such as the standard classifications allow, the new classification more accurately quantifies total vegetation in the landscape because it incorporates vegetation associated with built structures. The reconceptualization of land cover embodied in the new classification and the organization of the classification which allows flexible querying of the dataset facilitates the testing of ecological hypotheses about the structural complexity of the landscape.

The social structure of the same area can be described using a patch array derived from PRIZM. It is characterized by

19 patches of 12 types (Fig. 3b) and is divided in both patch number and patch area into four categories: (1) S1 (six patches, 26% of the total area), (2) T1 (five patches, 36%), (3) S2 (five patches, 21%) and (4) S3 (three patches, 16%). The five groups in the highest income bracket (Prizm 1, 4, 5, 14, and 15) account for more than 50% of the total land area (Table 1). These lifestyle clusters represent households with a median annual income ranging from 65 to 136 K. Each PRIZM market cluster can be further characterized with information from market research surveys, public opinion polls, and point-of-purchase receipts. These data can be used to understand the attitudes and preferences of different PRIZM groups for land management styles, products, and services as well as the most effective communication strategies to reach them in terms of media type – print, radio, TV – and messages used.

We can begin to test more sophisticated questions integrating ecological structure and social knowledge when we consider the results from an integrated patch array (Fig. 3c). This array has 468 patches of 263 types. The forest patches are associated with every type of PRIZM patch but Prizm patch 5 is most frequently associated with forests followed by Prizm patches 14 and 15. These same Prizm patch types are also most frequently associated with open space.

Table 1 – Characteristics of Prizm patches found in the Glyndon study area and their contribution to total patch number and area								
Prizm group	Median HH income (\$)	Median age of population	% Single units	% HH moved into unit in past year	% HH last moved 11+ years ago	No. patches	Total area (ha)	Percentage of study region
1	135900	41.9	97.7	11.0	43.7	2	38.7	2.1
4	67100	41.3	86.2	12.4	50.0	1	94.5	5.0
5	68900	34.4	91.7	18.1	30.0	3	364.9	19.4
14	89000	38.9	91.7	16.1	32.7	1	229.7	12.2
15	65300	36.7	87.7	16.6	34.6	3	343.8	18.3
17	52900	36.2	80.5	17.5	35.7	1	97.1	5.2
18	51700	35.8	41.8	36.3	16.5	1	113.3	6.0
19	51400	39.6	79.5	15.7	45.1	2	113.9	6.0
21	46400	33.8	50.6	30.2	23.4	1	77.0	4.1
22	47500	36.4	84.0	13.9	48.5	1	100.5	5.3
24	35600	32.4	23.1	47.1	10.7	2	150.7	8.0
26	34600	36.1	76.9	14.1	51.0	1	155.8	8.3

Open space and forest combined contribute more than 25% of the total land area of Prizm classes 4, 5, 15, 17, and 26. There is no forest or open space, however, in classes 18, 19, 21, and 22. Built class types from the ecological classification are the most dominant patch type in all Prizm groups except in Prizm 5, 14, and 26. In Prizm classes 1, 19, and 21, built patches occupy \geq 90% of the land and in patch types 1 and 19 the building type is dominated by single structures and in patches of type 21 the building types are dominated by both single and connected structures. In all Prizm patch types, the greatest proportion of built area is of the single building type, identified through the ecological classification, except for patches 18, 21, and 24, which are occupied by both single and connected structures. This multi unit housing types and mixed housing types are also identified in the PRIZM descriptions for these classes (Table 1). Of the Prizm classes, only patch type 18 was dominated by patches with low proportion of coarse vegetation, the others had equal amounts of medium and high proportion cover of coarse vegetation. Built patches containing a high proportion of coarse vegetation were a significant portion of Prizm patches 1 (73%), 14 (26%), and 15 (39%).

Integration of the ecological and social structural heterogeneity in the study region, may potentially enhance understanding of landscape heterogeneity. For example, do some lifestyle groups locate in areas with particular combinations and amounts of existing vegetation cover, while other lifestyle groups manage for and cultivate specific combinations and amounts of vegetation for the future (Grove et al., in press)? The answer is complex; for instance, some lifestyle groups may be more likely to prefer a residential landscape of mature trees, established lawns, and perennial gardens: "buy as is." Other lifestyle groups may be more likely to cultivate for a preferred residential landscape by planting new trees, replacing paved areas with grass, and putting up flower boxes: "fixer-uppers." In other words, the causal relationship between household characteristics and vegetation structure may not be in the same direction nor occur at the same rate for all lifestyle groups. A second example is the relationship among parcel size and ownership type of forested areas. A forest patch owned by a single land owner may be managed very differently than the same size forest patch owned by multiple land owners. These two social structures of management may have distinct impacts on the future ecological structure of the landscape. These types of questions can be addressed using additional data such as time series imagery and social surveys. Using only one disciplinary lens on the landscape – social or ecological – would not elucidate the patterns and mechanisms creating those patterns.

There are numerous other models that can be generated from the biocomplexity framework. A more structurally complex example would consider whether and how the structure of the system defined by one disciplinary perspective influences processes important in a different discipline. For example, are there trends or changes in the social dynamics of a neighborhood based on the ecological features of that neighborhood or its surroundings? Conversely, is the social structure and dynamics of the neighborhood reflected in the ecological structure or dynamics of the system? In addition, the framework can guide hypothesis generation employing two axes within the same disciplinary realm and multiaxial and multidisciplinary hypotheses. Within the ecological realm considering how past land use influences current vegetation structure and dynamics exploits the structural and temporal axes of the framework. The types of questions that can be posed using multiple axes and disciplines include, for example, (1) are there different rates of ecological change, lags and legacies between social patterns and processes or (2) are some ecological patches influenced by municipal level management decisions and others by decisions made at the household level?

6. Conclusion

We have proposed a conceptual framework to promote the assessment of structural biocomplexity in ecological systems. This framework draws on two of the approaches to complexity we have discovered through a review of definitions of the concept. These two are: (1) structure of complex systems, and (2) complexity of explanatory model. The third concern of complexity definitions, that of emergent, non-linear, or self organized behavior is beyond our scope here. This framework is intended to help explore a middle ground between the sophisticated mathematical abstractions of complexity theory and the practical needs of empirical ecologists. The framework is based on three dimensions identified by other ecologists interested in complexity, but which were developed for purposes of designing experiments (Frost et al., 1988) or were only enumerated and not expanded (Cottingham, 2002). Each of the three axes suggests quantifiable degrees of difference in the heterogeneity, connectivity, and historical contingency of the multiple interrelationships (cf. Ascher, 2001) that characterize complexity. The framework is also a tool to help guide the construction of models within and between disciplines that address systems at differing degrees of complexity. The dimensions of complexity represent axes along which emergence, non-linearity or self organized criticality may be detected in ecological systems.

A methodological and conceptual scheme can help explain how the framework is used to move from the metaphorical conception of biocomplexity which still dominates empirical ecology, to a rigorous definition that can support quantification and model construction (Fig. 4). The first step is to make choices about the scale and components ultimately to be included in the model (Frost et al., 1988; Jax et al., 1998). Scale in this schema refers to the grain and extent of space and time used to study the system. Frost et al. (1988) detail, using lake

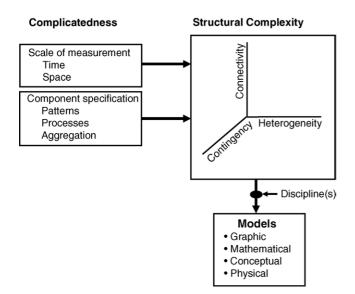


Fig. 4 – A methodological and conceptual scheme. This scheme explains how the framework is used to move from the metaphorical conception of biocomplexity to a rigorous definition that can support quantification and model construction. To use the framework, the temporal and spatial scale of measurement and the components or attributes of the system must be specified. This specification identifies features of the system that provide the context for framework application. The complexity of the system can then be quantified along spatial, temporal and organizational axes depicted as heterogeneity, history and connectivity. The framework organizes components of biocomplexity which come from many ecological, social and physical disciplines. Models of

many types and specific to a particular situation, can be generated from the framework.

examples, the importance of matching choices of scale in experiments and observations to the extent and differentials in the processes and patterns of interest.

The second kind of choice needed in model construction is the specification of the components to be include. Frost et al. (1988) refer to this as component resolution. Jax et al. (1998) suggest a more comprehensive view of the choices to be made in model construction. They include (1) the focal phenomena, (2) the degree of tightness of internal relationships in the system, and (3) the component resolution. This last feature is equivalent to that used by Frost et al. (1988) and refers to how aggregated the components or processes of the system are to be considered. A low resolution, high aggregation model might focus on the biota as a whole rather than species, decomposers rather than shredders and surface feeders, or gross N flux versus the dynamics of nitrate and ammonium, for example. These examples show that aggregation in this sense refers to what components are identified as functional in the model, rather than scale of observation. For purposes of exploring the biocomplexity framework, we can summarize the choices as specifying what patterns, processes, and degrees of aggregation the model components will represent.

Together the specification of temporal scale and spatial scale, along with the specification of components, address the *complicatedness* of the model. These decisions determine how many and what components will appear in the model. In other words, how complicated will the model be? This is qualitatively different than the next step in model construction. In that step (Fig. 4), the axes of biocomplexity as we have defined them come into play. Recall that these axes address the multiplicity of interrelationships, and how the interactions exist on different levels of spatial heterogeneity, different degrees of system connectedness, and different historical contingencies.

The third step places the specified components of the system, at the temporal and spatial scales of observation chosen, in the conceptual volume defined by the axes of biocomplexity (Fig. 4). Note that the continuum of complexity in spatial heterogeneity is different than the spatial scale of observation chosen as appropriate for the system components. Similarly, the existence of historical contingency, as expressed by the different degrees of historical complexity, is different from the choice of temporal windows and the size of the time steps used to observe the system. Likewise, organizational complexity does not refer to the traditional levels of organization recognized by ecology, but rather to the differing degrees of connectivity that system components can experience. Selecting a place for a model in this conceptual space allows structural biocomplexity to be assessed and ultimately related to the degree of complexity of system behavior.

The fourth step in addressing biocomplexity is to choose which and how many disciplinary perspectives to apply in building the model. In a sense, this represents a fourth axis of biocomplexity. We have illustrated a simple example using the generation of urban patch arrays by, on the one hand, market cluster research, and on the other, a reconceptualized land cover classification integrating ecological and built components. The integrated classification represents a multidisciplinary perspective combing ecology and urban design. A further interdisciplinary benefit is suggested by a preliminary analysis on the congruence of the patch arrays exposed by the two different classifications.

Finally, the models are the source of hypotheses and scenarios to advance the understanding and sustainability of integrated systems. The overall goal of the framework and the concepts that have been used to generate it, and its relationship to other assessments of biocomplexity, is to explore a middle ground between the abstractions of complexity theory and the methodological practicalities of empirical ecology that was left unspecified by several widely known introductions of biocomplexity for ecologists in general (Michener et al., 2001; Cottingham, 2002).

REFERENCES

- Ahl, V., Allen, T.F.H., 1996. Hierarchy Theory: A Vision, Vocabulary, and Epistemology. Columbia University Press, New York, p. 206.
- Alberti, M., Marzluff, J.M., Shulenberger, E., Bradley, G., Ryan, C., Zumbrunnen, C., 2003. Integrating humans into ecology: opportunities and challenges for studying urban ecosystems. BioScience 53, 1169–1179.
- Allen, T.F.H., Hoekstra, T.W., 1992. Toward a Unified Ecology. Columbia University Press, New York, p. 384.
- Allen, T.F.H., Starr, T.B., 1982. Hierarchy: Perspectives for Ecological Complexity. University of Chicago Press, Chicago, p. 310.
- Anderson, J.R., Hardy, E.E., Roach, J.T., Witmer, R.E., 1976. Land use and land cover classification systems for use with remote sensor data. USGS Professional Paper 964, US Geological Survey, 28 pp.
- Anselin, L., Tam Cho, W.K., 2002. Spatial effects and ecological inference. Political Anal. 10, 276–297.
- Ascher, W., 2001. Coping with complexity and organizational interests in natural resource management. Ecosystems 4, 742–757.
- Auyang, S.Y., 1998. Foundations of Complex-Systems Theories in Economics, Evolutionary Biology, and Statistical Physics. Cambridge University Press, Cambridge, p. 404.
- Bak, P., 1996. How Nature Works: The Science of Self-organized Criticality. Springer-Verlag, New York, p. 212.
- Bak, P., Chen, K., 1991. Self-organized criticality. Sci. Am. 264, 46–53.

Bellmann, K., 2000. Towards to a system analytical and modelling approach for integration of ecological, hydrological, economical and social components of disturbed regions. Landsc. Urban Plan. 51, 75–87.

- Berry, B.J.L., 2001. A new urban ecology? Urban Geogr. 22, 699– 701.
- Brown, J.H., 1994. Complex ecological systems. In: Cowan, G. (Ed.), Complexity: Metaphors, Models, and Reality. Addison-Wesley, San Francisco, pp. 419–449.
- Bruggeman, F.J., Westerhoff, H.V., Boogerd, F.C., 2002. BioComplexity: a pluralist research strategy is necessary for a mechanistic explanation of the "live" state. Philosophical Psychol. 15, 411–440.
- Cadenasso, M.L., Pickett, S.T.A., Grove, J.M., in press. Integrative approaches to investigating human-natural systems: the Baltimore Ecosystem Study. Nat. Sci. Soc.
- Cadenasso, M.L., Pickett, S.T.A., Weathers, K.C., Bell, S.S., Benning, T.L., Carreiro, M.M., Dawson, T.E., 2003a. An interdisciplinary and synthetic approach to ecological boundaries. BioScience 53, 717–722.

- Cadenasso, M.L., Pickett, S.T.A., Weathers, K.C., Jones, C.G., 2003b. A framework for a theory of ecological boundaries. BioScience 53, 750–758.
- Carpenter, S.R., Kitchell, J.F. (Eds.), 1988a. Complex Interactions in Lake Communities. Springer-Verlag, New York, p. 283.
- Carpenter, S.R., Kitchell, J.F., 1988b. Introduction. In: Carpenter, S.R., Kitchell, J.F. (Eds.), Complexity in Lake Communities. Springer-Verlag, New York, pp. 1–8.
- Claritas, 1999. PRIZM cluster snapshots: getting to know the 62 clusters. Claritas Corporation, Ithaca, NY.
- Colwell, R., 1998. Balancing the biocomplexity of the planet's living systems: a 21st century task for science. BioScience 48, 786–787.
- Colwell, R.R., 1999. Complexity and connectivity: a new cartography for science and engineering. Address to AGU Fall Meeting, San Francisco, CA, World Wide Web, 3 December 2003.
- Corner, J., 1997. Ecology and landscape as agents of creativity. In: Thompson, G.F., Steiner, F.R. (Eds.), Ecological Design and Planning. John Wiley & Sons, New York, pp. 81–108.
- Costanza, R., Wainger, L., Folke, C., Mäler, K.G., 1993. Modeling complex economic systems: toward an evolutionary, dynamic understanding of people and nature. BioScience 43, 545–555.
- Cottingham, K., 2002. Tackling biocomplexity: the role of people, tools, and scale. BioScience 52, 793–799.
- Forman, R.T.T., 1995. Land Mosaics: The Ecology of Landscapes and Regions. Cambridge University Press, New York, p. 632.
- Fotheringham, A.S., Brunsdon, C., 2002. Geographically Weighted Regression: The Analysis of Spatially Varying Relationships. Wiley, Chichester, England, p. 269.
- Frost, T.M., DeAngelis, D.L., Bartell, S.M., Hall, D.J., Hurblert, S.H., 1988. Scale in the design and interpretation of aquatic community research. In: Carpenter, S.R., Kitchell, J.F. (Eds.), Complex Interactions in Lake Communities. Springer-Verlag, New York, pp. 229–258.
- Furley, P.A., 1992. Edaphic changes at the forest-savanna boundary with particular reference to the neotropics. In: Furley, P.A., Proctor, J., Ratter, J.A. (Eds.), Nature and Dynamics of Forest-Savanna Boundaries. Chapman & Hall, New York, pp. 91–117.
- Gottdiener, M., Hutchison, R., 2000. The New Urban Sociology, 2nd ed. McGraw-Hill, New York, p. 388.
- Grove, J.M., Cadenasso, M.L., Burch Jr., W.R., Pickett, S.T.A., O'Neil-Dunne, J.P.M., Schwarz, K., Wilson, M.A., Troy, A.R., Boone, C., 2006. Comparison of social structure and vegetation structure of urban neighborhoods in Baltimore, Maryland. Soc. Nat. Resour. 19 (2), 117–136.
- Grove, J.M., Troy, A.R., O'Neil-Dunne, J.P.M., Burch, Jr., W.R., Cadenasso, M.L., Pickett, S.T.A., in press. Characterization of households and its implications for the vegetation of urban ecosystems. Ecosystems.
- Gunderson, L.H., Holling, C.S., Light, S.S., 1995. Barriers broken and bridges built: a synthesis. In: Gunderson, L.H., Holling, C.S., Light, S.S. (Eds.), Barriers and Bridges to the Renewal of Ecosystems and Institutions. Columbia University Press, New York, pp. 489–532.
- Holling, C.S., Gunderson, L.H., 2002. Resilience and adaptive cycles. In: Gunderson, L.H., Holling, C.S. (Eds.), Panarchy: Understanding Transformations in Human and Natural Systems. Island Press, Washington, DC, pp. 25–62.
- Huston, M.A., 1994. Biological Diversity: The Coexistence of Species on Changing Landscapes. Cambridge University Press, New York, p. 681.
- Jax, K., Jones, C., Pickett, S.T.A., 1998. The self-identity of ecological units. Oikos 82, 253–264.
- Kay, J.J., Schneider, E., 1994. Embracing complexity: the challenge of the ecosystem approach. Alternatives 20, 32–39.

- Li, B.-L., 2000. Why is the holistic approach becoming so important in landscape ecology? Landsc. Urban Plan. 50, 27-41.
- Li, B.-L., 2002a. A theoretical framework of ecological phase transitions for characterizing tree-grass dynamics. Acta Biotheoretica 50, 141–154.
- Li, B.-L., 2002b. Criticality, self-organized. In: El-Shaarawi, A.H., Piegorsch, W.W. (Eds.), Encyclopedia of Environmentrics. John Wiley & Sons, Chichester, pp. 447–450.
- Li, B.-L., 2004. Editorial. Ecol. Complex. 1, 1-2.
- Li, H., Reynolds, J.F., 1993. A new contagion index to quantify spatial patterns of landscapes. Landsc. Ecol. 8, 155–162.
- Li, H., Reynolds, J.F., 1995. On definition and quantification of heterogeneity. Oikos 73, 280–284.
- Loehle, C., 2004. Challenges of ecological complexity. Ecol. Complex. 1, 3–6.
- Machlis, G.E., Force, J.E., Burch, W.R., 1997. The human ecosystem. 1. The human ecosystem as an organizing concept in ecosystem management. Soc. Nat. Resour. 10, 347–367.
- Medvinsky, A.B., Tikhonova, I.A., Aliev, R.R., Li, B.-L., Lin, Z.-S., Malchow, H., 2001. Patchy environment as a factor of complex plankton dynamics. Phys. Rev. E 64 pp. 021915-1– 021915-7.
- Michener, W.K., Baerwald, T.J., Firth, P., Palmer, M.A., Rosenberger, J.L., Sandlin, E.A., Zimmerman, H., 2001. Defining and unraveling biocomplexity. BioScience 51, 1018–1023.
- Milne, B.T., 1998. Motivation and benefits of complex system approaches in ecology. Ecosystems 1, 449–456.
- Noss, R.F., Cooperrider, A.Y., 1994. Saving Nature's Legacy: Protecting and Restoring Biodiversity. Island Press, Washington, DC, p. 416.
- Petrovskii, S., Li, B.-L., 2004. Transition to spatiotemporal chaos can resolve the paradox of enrichment. Ecol. Complex. 1, 37–47.
- Pickett, S.T.A., Cadenasso, M.L., 1995. Landscape ecology: spatial heterogeneity in ecological systems. Science 269, 331–334.
- Pickett, S.T.A., Rogers, K.H., 1997. Patch dynamics: the transformation of landscape structure and function. In: Bissonette, J.A. (Ed.), Wildlife and Landscape Ecology: Effects of Pattern and Scale. Springer-Verlag, New York, pp. 101–127.
- Pickett, S.T.A., White, P.S. (Eds.), 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando, FL, p. 472.
- Pickett, S.T.A., Burch Jr., W.R., Dalton, S.D., Foresman, T.W., 1997. Integrated urban ecosystem research. Urban Ecosyst. 1, 183–184.

- Pickett, S.T.A., Cadenasso, M.L., Grove, J.M., 2005. Biocomplexity in coupled human-natural systems: a multidimensional framework. Ecosystems 8, 1–8.
- Pickett, S.T.A., Cadenasso, M.L., Jones, C.G., 2000. Generation of heterogeneity by organisms: creation, maintenance, and transformation. In: Hutchings, M. (Ed.), Ecological Consequences of Habitat Heterogeneity. Blackwell, New York, pp. 33–52.
- Pickett, S.T.A., Collins, S.L., Armesto, J.J., 1987. A hierarchical consideration of causes and mechanisms of succession. Vegetatio 69, 109–114.
- Pickett, S.T.A., Kolasa, J., Jones, C.G., 1994. Ecological Understanding: The Nature of Theory and the Theory of Nature. Academic Press, San Diego, p. 206.
- Poff, N.L., 1992. Regional hydrologic response to climate change: an ecological perspective. In: Firth, P. (Ed.), Global Climate Change and Freshwater Ecosystems. Springer-Verlag, New York, pp. 88–115.
- Poff, N.L., Ward, J.V., 1990. Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. Environ. Manage. 14, 629–645.
- Rosen, R., 1991. Life Itself. Columbia University Press, New York, p. 285.
- Schmitz, O.J., 2001. From interesting details to dynamical relevance: toward more effective use of empirical insights in theory construction. Oikos 94, 39–50.
- Thompson, J.N., Reichman, O.J., Morin, P.J., Polis, G.A., Power, M.E., Sterner, R.W., Couch, C.A., Gough, L., Holt, R., Hopper, D.U., Keesing, F., Lovell, C.R., Milne, B.T., Molles, M.C., Roberts, D.W., Strauss, S.Y., 2001. Frontiers of ecology. BioScience 51, 15–24.
- Ulanowicz, R.E., 1997. Ecology, the Ascendent Perspective. Columbia University Press, New York, p. 201.
- Ulanowicz, R.E., 2004. On the nature of ecodynamics. Ecol. Complex. 1, 341–354.
- Vasishth, A.S.H.W., Sloane, D.C., 2002. Returning to ecology: an ecosystem approach to understanding the city. In: Dear, M.J. (Ed.), From Chicago to L.A.: Making Sense of Urban Theory. Sage Publishers, Thousand Oaks, pp. 347–366.
- Watt, A.S., 1947. Pattern and process in the plant community. J. Ecol. 35, 1–22.
- Wiens, J.A., 1995. Landscape mosaics and ecological theory. In: Hansson, L., Fahrig, L., Merriam, G. (Eds.), Mosaic Landscapes and Ecological Processes. Chapman & Hall, New York, pp. 1–26.
- Wiens, J.A., 2000. Ecological heterogeneity: an ontogeny of concepts and approaches. In: Hutchings, M.J., John, E.A., Stewart, A.J.A. (Eds.), The Ecological Consequences of Environmental Heterogeneity. Blackwell, Malden, MA, pp. 9–31.
- Wu, J., 1999. Hierarchy and scaling: extrapolating information along a scaling ladder. Can. J. Rem. Sens. 25, 367–380.